CONSERVACIÓN Y RESTAURACIÓN ECOLÓGICA DE ROBLEDALES ANDINOS AFECTADOS POR INCENDIOS

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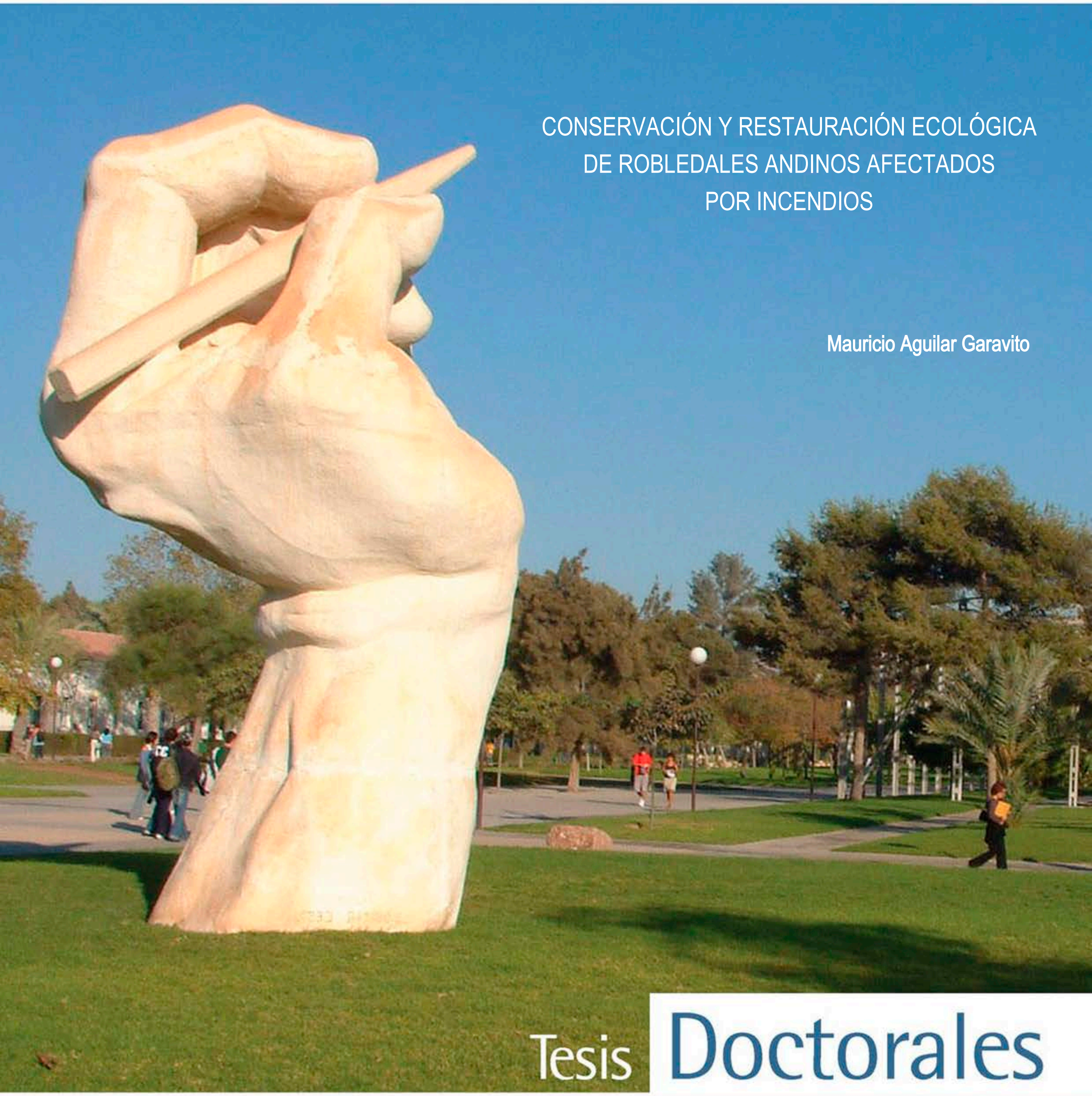

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Tesis doctoral
Alicante, marzo 2023

Universitat d'Alacant
Universidad de Alicante

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DEPARTAMENTO DE ECOLOGÍA
FACULTAD DE CIENCIAS

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MAURICIO AGUILAR GARAVITO

Tesis presentada para aspirar al grado de
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Y RESTAURACIÓN DE ECOSISTEMAS

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El Dr. Jordi Cortina Segarra, del Departamento de Ecología e Instituto Multidisciplinar para el Estudio del Medio de la Universidad de Alicante, certifica que el ecólogo Mauricio Aguilar Garavito ha realizado bajo su dirección la presente memoria, por la cual opta al título de Doctor en Conservación y Restauración de Ecosistemas, titulada: “Conservación y restauración ecológica de robledales andinos afectados por incendios”.

Firmado

Jordi Cortina Segarra

Director de la Tesis

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En memoria de:

Bellota

Hilda Garavito

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INTRODUCCIÓN

El norte de los Andes es una de las regiones biodiversas del planeta Tierra (Meyers et al., 2000; Olson & Dinerstein, 2002). Su riqueza ecosistémica, de especies raras y endémicas proporcionan invaluables beneficios para la humanidad. El agua, la provisión de alimentos y combustibles, las materias primas, los escenarios espirituales, educativos y recreativos, son algunos de ellos. Sin embargo, desde la época precolombina más del 60% de los ecosistemas del norte de los Andes se han alterado (Rodríguez et al., 2006; Etter et al., 2008). La deforestación, el uso agropecuario y los incendios de la vegetación han sido los principales motores de transformación y pérdida de estos ecosistemas (MADS, 2015; Correa-Ayram et al., 2020).

Los robledales son un tipo de bosque Andino, dominado por *Quercus humboldtii* Bonpl. (roble andino), la única especie de *Quercus* Sudamericana (Kapelle, 2006; Avella, 2016). En Colombia el roble andino tuvo una amplia distribución prehispánica (Nixon 2006, González *et al.* 2011), pero en la actualidad puede rondar entre el 40 y 10% (Rangel-Ch, 2000; Etter et al., 2008). En las regiones donde aún quedan robledales, el paisaje se compone de fragmentos boscosos inmersos en una matriz de matorrales, pasturas y cultivos (González *et al.*, 2011, Avella 2016).

Bajo estas nuevas condiciones biofísicas del norte de los Andes, exacerbadas por el cambio climático, los incendios juegan un papel clave como generadores de cambio ambiental, beneficiando a las especies adaptadas al fuego (Vargas 2000, 2002). La superficie quemada en el norte de los Andes ha incrementado en las últimas décadas (Armenteras *et al.*, 2020), al igual que en otras regiones tropicales (Earl y Simmonds, 2018; Finer & Mamani, 2019).

En Colombia, los gestores de la biodiversidad han adoptado diferentes medidas de conservación de la biodiversidad, como la creación de áreas naturales protegidas, para regular los usos y facilitar la regeneración natural (MADS, 2012; Echeverry-Galvis *et al.*, 2019). Sin embargo, estas acciones no han sido suficientes y, en algunos casos, han favorecido nuevos disturbios como los incendios y la invasión de plantas exóticas (Armenteras *et al.*, 2019; León-Parra & Vilardy, 2022). Por su parte, la gestión de incendios se ha centrado en reportar su ocurrencia y en la extinción de los mismos (Rodríguez-Buriticá, *et al.*, 2017; Armenteras *et al.*, 2020). Sin embargo, en las áreas productivas las quemas se siguen utilizando. La normatividad no ha conseguido regularizar el uso de fuegos prescritos y se ha invisibilizado el uso y significado cultural del fuego (Aguilar-Garavito *et al.*, 2019).

En algunos casos, tras el abandono de los usos productivos y su reasignación como espacios para la conservación de la biodiversidad, los arbustos y las especies arbóreas colonizan las zonas alteradas y vuelven a formar bosques (Ramírez-Marcial *et al.*, 2006;

Fernández-Méndez *et al.,* 2016). Sin embargo, los incendios forestales frecuentes suelen detener estas trayectorias sucesionales (Zahawi & Augspurger, 1999; Hobbs *et al.,* 2009; Palma *et al.,* 2021). Cuando se producen incendios recurrentes, los paisajes pasan de ser bosques diversos y resistentes, a una matriz de matorrales y gramíneas, empobrecida en especies, que puede ser propensa a nuevos incendios, siguiendo trayectorias autosucesionales (Schaffhauser *et al.,* 2012; Zouhar *et al.,* 2008).

Para la gestión de la biodiversidad en los paisajes del norte de los Andes fuertemente antropizados y actualmente afectados por fuego, es fundamental comprender el régimen de incendios, la respuesta de la vegetación, los impulsores de la sucesión post-incendio y la limitación al reclutamiento que puede presentar la comunidad vegetal.

En el norte de los Andes colombianos, el macizo de Iguaque ofrece una oportunidad única para estudiar el impacto del fuego sobre las comunidades vegetales y establecer bases ecológicas que permitan diseñar medidas efectivas de conservación y restauración. Desde épocas prehispánicas, la deforestación, los incendios y los usos agrícolas han sido intensos en este macizo. Sin embargo, por su riqueza natural y alto valor socioeconómico, en 1977 el 34% de la superficie del macizo se designó como área natural protegida, bajo la denominación de Santuario de Flora y Fauna Iguaque (SFFI). Además, las montañas de Iguaque son hábitat de *Q. humboldtii* y se conservan algunos relictos de robledal andino (Villarreal *et al.,* 2017).

En paralelo con la creación y gestión del SFFI, el macizo ha sufrido intensos cambios de uso, con el abandono de actividades agrícolas, el aumento de la actividad turística, y el incremento de los incendios. En las zonas incendiadas la regeneración de especies arbóreas, incluyendo *Q. humboldtii*, es muy escasa y el fuego parece promover la sucesión de arbustales, hierbas y gramíneas muy persistentes. También existen evidencias que los incendios están afectando al suelo, la calidad del agua y del paisaje (Villarreal *et al.*, 2017).

1. Incendios de la vegetación en el norte de los Andes

Los incendios de la vegetación son un importante motor del cambio ambiental (Hosonuma *et al.*, 2012). Las tendencias mundiales del siglo XXI sugieren que en la mayoría de zonas boscosas de todo el planeta han aumentado los incendios (Earl & Simmonds, 2018). La extensión y la frecuencia de los incendios se ha correlacionado positivamente con la densidad humana, la acumulación de combustible vegetal y las condiciones meteorológicas extremas (Godoy *et al.*, 2019; Guillaume *et al.*, 2019). También con los ciclos climáticos, como El Niño-Oscilación del Sur (ENSO; Bianchi *et al.*, 2014).

Durante el periodo comprendido entre 1998 y 2002, los incendios afectaron al 84% de la superficie de los ecosistemas más biodiversos del mundo (TNC *et al.*, 2004). En América Latina se quemaron 51 millones de hectáreas en las últimas tres décadas (FAO, 2005; 2013). Sin embargo, observaciones recientes muestran una reducción de los incendios antrópicos en algunas zonas tropicales (Andela *et al*., 2017).

La mayoría de los países de América Latina adolecen de un sistema de registro de incendios de la vegetación, o este es muy reciente (Armenteras *et al.*, 2020). Estos registros son a menudo incompletos, dispersos y en algunos casos, contradictorios en cuanto a la zona afectada, severidad o frecuencia del incendio (Anaya-Acevedo & Chuvieco-Salinero, 2010). Por ejemplo, en Colombia, los reportes oficiales de incendios están disponibles desde 1998 (UNGRD, 2018). Entre el año 2002 y 2013 se reportaron 12.978 incendios que afectaron 619.300 ha en todo el país (IDEAM, 2014). En 2015 se reportaron 3.985 incendios que afectaron 150.000 ha (García *et al.*, 2016) y se estableció que el 18% de la cubierta vegetal tiene alta susceptibilidad a los incendios (IDEAM, 2022).

En Colombia, algunos estudios han investigado la distribución espaciotemporal de los incendios, especialmente en los ecosistemas de sabana neotropical y en los ecosistemas amazónicos (Armenteras *et al*., 2005; 2009 a; b; Muñoz, 2005; Amaya & Armenteras, 2012; Barreto *et al*., 2017; Armenteras *et al*., 2019; 2020). También, se encontró que durante el periodo comprendido entre el 2001 y 2018 los bosques tropicales y andinos han presentado alrededor del 39% de los focos de incendios activos en Colombia (Armenteras *et al*., 2020). Sin embargo, estas investigaciones se han centrado en la ocurrencia de los incendios y no han abordado aspectos centrales, como el régimen de incendio, su efecto en el reclutamiento de la vegetación post-incendio o su gestión integral.

En la región Andina de Colombia, pruebas paleoecológicas, como el análisis de fragmentos de carbón vegetal, sugieren que la frecuencia de incendios fue baja durante el Pleistoceno (de siglos a milenios) y se mantuvo así durante el Holoceno (González *et al.,* 1966; van der Hammen, 1966). En la época precolombina, el fuego se utilizaba en sistemas de tala y quema (Patiño, 1965; Jantz & Behling, 2012). Estas prácticas se intensificaron tras la colonización europea a principios del siglo XVI (Castilla-Beltrán *et al.,* 2018; Koch *et al.,* 2019), al transformarse grandes extensiones de bosque en cultivos y pastos (Molano, 1995; 1996; Mora, 2012). Más recientemente, los incendios han jugado un papel importante en los ecosistemas andinos (Dull *et al.,* 2010; Valencia *et al.*, 2010). La frecuencia de incendios forestales ha aumentado de un evento cada 1.000 años, hace 2.500

años, a un evento cada 2 a 10 años, desde mediados del siglo XX (Horn, 1986; 1989; Verweij, 1995). Este cambio en el régimen de incendios puede afectar profundamente a la composición de los ecosistemas del norte de los Andes y los servicios ecosistémicos que proporcionan (TNC *et al.*, 2004; Armenteras *et al.*, 2020).

Los bosques andinos de Colombia, incluidos los robledales, han sido históricamente poco propensos al fuego y podrían no estar adaptados a él. Según la clasificación de sensibilidad al fuego, estos ecosistemas se han catalogado como independientes del fuego (Páramo-Rocha, 2011; Armenteras *et al*., 2020). Algunas especies vegetales de los bosques andinos podrían no ser incapaces de resistir el actual régimen de incendios (Vargas, 2000; 2002; Salazar *et al.*, 2020), pues la biota de estos ecosistemas ha evolucionado bajo otro régimen natural de disturbios.

Una consecuencia de la baja frecuencia natural de incendios es que el tiempo de retorno de dicho disturbio era más largo que el ciclo de vida de las especies más longevas (Vargas, 2000; 2011). Mientras que otros disturbios más frecuentes, como las heladas, podían ocurrir varias veces durante la vida de las especies de ciclo corto. La gestión de la biodiversidad en los ecosistemas del norte de los Andes requiere una caracterización del régimen de incendios, integrando sus dimensiones espacio-temporales, y describiendo su origen[1], historia y patrón de frecuencia[2], intensidad[3], severidad[4], extensión[5] y estacionalidad[6] (Falk *et al.*, 2007).

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[1] Origen: fenómeno o hecho de tipo natural o antrópico que es el principio, causa o motivo de los incendios (Bond & van Wilgen 1996)

[2] Frecuencia de incendio: tiempo entre fuegos consecutivos (Bond & van Wilgen 1996)

[3] Intensidad de incendio: cantidad de energía liberada por el frente de fuego (Key, 2006; Keeley, 2009).

[4] Severidad de incendio: pérdida o cambio de la biomasa tanto superficial como subsuperficial (Lentile *et al.*, 2006; Keeley, 2009).

[5] Extensión: tamaño del área afectada por incendios (Key, 2006; Keeley, 2009).

[6] Estacionalidad: temporada climática en el que ocurren los incendios (Bond & van Wilgen 1996)

2. Respuestas de la vegetación a los incendios

La ocurrencia de incendios modela el entorno biofísico y actúa como un motor evolutivo (Pausas *et al*., 2017; He *et al.*, 2019). Las comunidades vegetales pueden mostrar una alta resiliencia al fuego cuando su ocurrencia provocó respuestas evolutivas, mientras que la resiliencia al fuego puede ser baja cuando las especies no están adaptadas a él o a otras perturbaciones que tengan un impacto análogo (Bellingham & Sparrow, 2000; Schumacher & Bugmann, 2006). La resiliencia puede darse por la capacidad de las especies para regenerarse a partir de rebrotes o semillas, y prosperar en las condiciones posteriores al incendio (Pausas, 1999; 2006).

El aumento de los incendios en regiones donde históricamente fueron poco frecuentes puede provocar la exclusión de las especies autóctonas y favorecer la colonización de especies tolerantes al fuego, como gramíneas y algunas especies exóticas invasoras (Pausas, 2006; Russell-Smith *et al.*, 2010). Este conjunto de especies puede, a su vez, modificar los regímenes de incendios e iniciar ciclos de autosucesión (Zouhar *et al.*, 2008; Shaffhauser *et al.*, 2012a). Finalmente, se desencadena el cambio hacia comunidades vegetales adaptadas al fuego (Fig. I; Neary *et al.*, 1999; Leishman *et al.*, 2007). La dinámica no lineal y los múltiples impulsores que interactúan dificultan la capacidad de generalización y aumentan la incertidumbre de las predicciones y de las estrategias de gestión (McWethy *et al.*, 2019).

Los rasgos de las plantas, en particular su capacidad de rebrotar o establecerse a partir de semilla tras un incendio, determinan la capacidad de soportar estos disturbios (Keeley, 2009). La capacidad para rebrotar puede verse afectada por muchos factores, como el nivel de daño experimentado por la planta (Moreira *et al.*, 2007; 2009), el tamaño del individuo, el grado de protección de las yemas, el grosor de la corteza y la ocurrencia de nuevos disturbios (Silva & Catry, 2006). Las plantas con un mayor nivel de daño tienen mayor probabilidad de morir o de brotar exclusivamente del tocón (Bond & Midgley, 2003), mientras que, en niveles intermedios de severidad, las plantas pueden brotar de la base del tocón, tallo, de la copa o presentar rebrotes simultáneos de copa y tallo (Miller, 2000). Algunas especies del robledal andinos son rebrotadoras, tanto rebrotadoras obligadas, cuyo principal mecanismo de respuesta al daño de la parte aérea es el rebrote, como rebrotadoras facultativas, que combinan la reproducción sexual y asexual (Bond & Midgley, 2001; Paula *et al*., 2009). Por ello, cabría esperar que, al menos esta parte de la comunidad mostrara cierta resiliencia frente a los incendios.

Las plantas también pueden colonizar las zonas quemadas mediante semillas, bien sea semillas almacenadas en un banco persistente, como semillas procedentes de zonas colindantes. El banco de semillas, la dispersión de semillas, así como los factores que afectan su abundancia y germinación, así como el establecimiento de las plántulas en áreas afectadas por incendios, han sido estudiados en profundidad (Santos *et al*., 2010; Lipoma *et al.,* 2018; Konsam *et al.*, 2020), incluso en bosques tropicales (Cury *et al*., 2020; Jakovac *et al.,* 2021; Scheper *et al.,* 2021). En el norte de los Andes se han realizado este tipo de estudios, pero no han sido enfocados a los incendios de la vegetación (López *et al*., 2016; Velosa *et al*., 2018), por lo que se desconoce la capacidad de colonización de muchas especies post-incendio.

3. Descripción del roble andino

Quercus humboldtii es un árbol de copa globosa, entre 15 y 30 m de altura (Mahecha *et al*., 2010). Es una especie monoica, sus flores amarrillas, pequeñas y en racimo son polinizadas por el viento e insectos (Palacio & Fernández, 2006). El fruto es una bellota recalcitrante marrón, cuyo peso fresco varía entre 5 y 9 g. Su tamaño polar es de 2,7 a 5,7 cm y el diámetro ecuatorial de 2,2 a 2,5 cm (Gonzáles & Parrado, 2010). La bellota tiene un único embrión que ocupa todo su espacio (Pulido & Chiquillo, 2002). Su dispersión primaria es por gravedad y, posteriormente pueden ser redistribuidas o depredadas por ardillas (*Sciurus granatensis* Humboldt), tinajos (*Cuniculus taczanowskii* Stolzmann y *C. paca* Linnaeus), armadillos (*Dasyprocta punctata* Gray), saínos (*Tayassu tajacu* Linnaeus), zarigüeyas (*Didelphys marsupialis* Linnaeus) y aves medianas (Gómez *et al.*, 2008). Su fenología varía según la localidad y puede presentar vecería (*masting*), con máximos periódicos separados hasta tres años (Gómez & Toro 2007). La producción y caída de hojas ocurre durante todo el año, y la producción de flores y frutos muestra una distribución temporal bimodal (Burgos, 2015).

La producción de bellotas se suele dar desde mediados de la temporada seca y durante toda la temporada lluviosa (Pérez *et al*., 2013). El desarrollo de la bellota comprende entre cuatro a siete meses (Gómez & Toro, 2007). Éstas no tienen dormancia y germinan de dos a cuatro meses después de caer (Sepúlveda *et al.*, 2014). Un árbol sano puede llegar a producir entre 5 y 8 kg de bellotas (150 a 500 bellotas/kg; Nieto & Rodríguez, 2004), con tasas de germinación en campo que alcanzan el 20%, y el 80% en vivero (Fernández, 2014; Moreno & Cuartas, 2015).

El crecimiento del árbol es moderado comparado con otros árboles tropicales andinos (Mahecha *et al*., 2010). El incremento diamétrico anual en árboles de bosques poco intervenidos oscila entre 0,1 y 0,2 cm/año (Avella, 2016). En bosques abiertos, o de crecimiento secundario, alcanza 0,6 cm/año (Becerra, 1989). En los brinzales, el crecimiento es de 0,5 cm/año, aproximadamente. Las plántulas pueden presentar un crecimiento entre 0,3 y 1,9 cm/año (Avella *et al.*, 2015). También, en robledales conservados es posible encontrar alrededor de 26 plántulas/m^2 (Becerra, 1989), mientras que en robledales intervenidos, la densidad se reduce hasta 1-6 plántulas/m^2 (León *et al.*, 2009). En los fragmentos pequeños, las plántulas se encuentran de manera agregada y bajo los progenitores. En fragmentos de mayor tamaño, las plántulas se reclutan de manera irregular y lejos del progenitor (Guerrero *et al*., 2010).

Las plántulas y brinzales pueden presentar limitación en su crecimiento en suelos deficitarios en N, Ca, K y P (Sepúlveda *et al.*, 2014). No obstante, su asociación con ectomicorrizas le permite crecer bajo un amplio rango de condiciones edáficas (Cavalier, 1999). Las plántulas de roble muestran mejor desarrollo en áreas abiertas y en bordes de bosque (Avella *et al*., 2015), pero también pueden desarrollarse bajo la sombra de árboles adultos hasta ser brinzales, formando bancos de plántulas. Sin embargo, presentan alta mortalidad por escasez de luz o nutrientes (Diez *et al.*, 2017).

Quercus humboldtii muestra alta diversidad genética y baja estructura poblacional. La especie muestra un alto flujo genético local y una alta divergencia genética inter-poblacional (Paz & Palacio-Mejía, 2006, Palacio-Mejía & Fernández, 2006). También presenta una amplia variación fisiológica altitudinal e interregional en los tres ramales de los Andes colombianos (Palacio-Mejía & Fernández 2006; Rodríguez-Correa, 2007). Se ha observado que en los parches de bosque medianos o grandes se produce un nivel bajo de autofecundación y de endogamia (Fernández & Sork, 2005; 2007). Por el contrario, en los fragmentos de bosque pequeños o aislados, la polinización suele darse entre pocos árboles, los adultos pierden diversidad genética y se incrementa la endogamia (Fernández 2002).

4. Ecología y conservación del roble andino

El roble andino (*Quercus humboldtii*) es la especie más meridional del género *Quercus* en el Neotrópico y pertenece al grupo de los robles rojos, subgénero *Erythrobalanus* (Nixon, 2006). Se distribuye a lo largo de los tres ramales de la Cordillera de los Andes colombianos, en algunos macizos montañosos de la región Caribe colombiana y en las serranías del Darién colombo-panameño (Figura I; Avella, 2016, Rangel & Avella, 2011). Habita en un amplio gradiente ambiental; lugares con elevaciones entre los 750 y 3.450 m, precipitación entre 700 y 3.000 mm (Rangel *et al.*, 2009), y suelos desde moderadamente fértiles y profundos, hasta superficiales o en proceso de degradación (López, 2014). *Quercus humboldtii* es un elemento florístico del bosque subandino (750 a 2300 m de elevación) y una especie dominante o codominante en los bosques andinos (2300-3450 m de elevación; van der Hammen *et al.*, 2008). En algunas regiones de alta montaña o en laderas subhúmedas, *Q. humboldtii* genera una formación vegetal particular conocida como robledal andino (Avella, 2016).

Debido a los usos antrópicos del norte de los Andes, la distribución precolombina de los bosques andinos y del robledal se ha reducido entre el 60 y 90% (Rangel, 2000; Etter, *et al.*, 2006). Durante la época precolombina, el fuego y la deforestación se utilizó en la región Andina colombiana para despejar la vegetación y expandir los cultivos (Patiño, 1965; 1997; Márquez, 2001). Estas prácticas se intensificaron con la colonización europea, convirtiéndose la vegetación de bosque y páramo en pastizales mantenidos por incendios frecuentes (Fals Borda, 2006; Mora, 2012). Desde mediados del siglo XIX, la deforestación, los incendios, la industria extractiva y los usos agropecuarios se han venido intensificando (Bello, 2006; Avella & Cárdenas, 2010).

Como consecuencia de estos procesos, muchos robledales y bosques andinos con *Q. humboldtii* se perdieron y la especie fue clasificada como vulnerable (VU) en la Lista Roja UICN de plantas de Colombia (Calderón *et al.*, 2002; Solano *et al.*, 2005). En las últimas décadas han surgido algunas medidas de protección, como la creación de áreas naturales protegidas y la veda a la tala de esta especie (Solano *et al.*, 2005; MAVDT, 2006), pero la degradación y pérdida de estos bosques no se ha detenido (Avella, 2016; Aguilar-Garavito *et. al*., 2020).

5. Respuesta del roble andino al fuego

Muchas especies del género *Quercus* son tolerantes al fuego (Johnson *et al.*, 2002), principalmente por la concentración de yemas latentes cerca del cuello de la raíz (Espelta *et al.*, 2003). Este rasgo facilita un rápido rebrote tras un incendio. La tolerancia de estas especies al fuego depende del diámetro del tallo, el grosor de la corteza y del régimen de los incendios, por tanto, depende en gran medida de la especie y el desarrollo del individuo (Pausas, 2017; Casals et al., 2018).

En Norteamérica, las especies de roble rojo pueden tolerar intensidades de fuego entre baja y moderada, con intervalos entre incendios superiores a 14 años (Johnson *et al*., 2002; DeSantis *et al*., 2010). Los árboles con diámetro a la altura del pecho superior a 18 cm muestran mayor probabilidad de sobrevivir a la quema. La respuesta de los robles neotropicales a disturbios como el fuego no está clara. En México y Costa Rica, algunas especies de roble pueden sobrevivir a los incendios (Aus der Beek *et al*., 2006; Guariguata *et al*., 2006). Sin embargo, dependiendo de la frecuencia de incendios, la regeneración puede verse afectada (Bonfil, 2006; González-Espinosa *et al.*, 2006). En Colombia, *Q. humboldtii* rebrota hasta tres años después de la quema (Salazar *et al*., 2020), pero no está claro qué régimen de fuego soporta, ni cuáles son los efectos del fuego en su regeneración mediante bellotas. La producción de frutos es un proceso fundamental para el reclutamiento de la vegetación, así como para el restablecimiento de los ecosistemas disturbados (Dey *et al*., 2010; Ibarra-Manríquez *et al*., 2015). A través de las bellotas se da una interacción clave entre el roble y los animales, ya que éste depende, en gran medida, de la fauna para la dispersión de sus bellotas, y los animales de los frutos para sobrevivir (Delgado-Fernández *et al*., 2017).

Estudios fenológicos del roble andino reportan la dinámica de producción de frutos (Pardo & Chiquillo 2002; Burgos, 2015). Sin embargo, el efecto de los disturbios antrópicos sobre la disponibilidad de bellotas ha sido poco estudiado en esta especie. En robledales de Centro América afectados por deforestación, Guariaguata & Sáens (2002) encontraron una mayor producción de frutos en aquellos árboles que habían sido previamente talados, con respecto a los que no. Por otra parte, Jones *et al.* (2015) en robledales mediterráneos obtuvieron una mayor producción de semillas en bosques que habían sido quemados. En Colombia, González & Parrado (2010) encontraron que, en robledales afectados por uso agropecuario, la producción de bellotas disminuyó. De igual forma, en robledales fragmentados y afectados por actividades humanas, el número de bellotas con desarrollo incompleto aumentó (Diaz *et al*., 2003; Pérez *et al*., 2013).

6. Múltiple limitación al reclutamiento del roble andino

En los paisajes transformados del norte de los Andes, la regeneración natural está dominada por comunidades vegetales pobres en especies y constituidas principalmente por gramíneas, herbáceas y arbustos bajos (Vargas, 2011; Lippok, *et al.*, 2013; Arroyo-Rodríguez, *et al.*, 2017). Esta vegetación puede ser muy persistente, pudiendo soportar una alta incidencia de incendios; de hecho, algunas de las especies que las componen son potencialmente invasoras. Sin embargo, aunque la regeneración vegetativa suele ser elevada, las transiciones de herbazales a matorrales y a bosques son extremadamente difíciles (Cabrera *et al.*, 2011; Galindo *et al*., 2014; IDEAM, 2022). La liberación de sucesión detenida en estos sistemas requiere del alivio simultáneo de las múltiples limitaciones al reclutamiento que puedan estar presentando las especies arbóreas.

Comprender los factores que impulsan el establecimiento de especies arbóreas, como *Q. humboldtii*, en áreas afectadas por incendios, es crucial para la gestión integral de los incendios y para desarrollar programas de protección y restauración de la biodiversidad. Sin embargo, la limitación del reclutamiento forestal en ecosistemas andinos no ha sido estudiada en profundidad.

A nivel global se ha establecido que el pobre reclutamiento de la vegetación arbórea en áreas históricamente trasformadas y donde actualmente ocurren incendios recurrentes puede atribuirse a cinco situaciones (Nathan & Muller-Landau, 2000; Schupp *et al*. 2002): i) Baja disponibilidad de semillas viables, ii) pobre dispersión de semillas (Pulido & Díaz, 2005), iii) altos niveles de depredación de las semillas (Gómez *et al.*, 2003; Leiva & Fernández-Alés, 2003), iv) baja germinación (Rey & Alcántara, 2000, Acácio *et al.*, 2007) y v) baja supervivencia de plántulas (Pulido & Díaz, 2005; Acácio *et al.*, 2007).

Como hemos discutido con anterioridad, el roble andino puede rebrotar vigorosamente tras un incendio (Salazar *et al.*, 2020). Por el contrario, se desconoce cuál es la densidad de bellotas sanas y de plántulas post-incendio dentro del robledal o en los matorrales circundantes. Es posible que, en primera instancia, el reclutamiento del roble andino esté limitado por la disponibilidad y dispersión de bellotas. En segundo lugar, el establecimiento del roble podría estar limitado por las condiciones de las áreas quemadas (especialmente estrés hídrico y depredación de bellotas). También es probable que la germinación de bellotas esté limitada tras el incendio (Pulido & Díaz, 2005; Acácio *et al.*, 2007). Finalmente, el establecimiento de las plántulas del roble andino en las zonas quemadas podría verse dificultado por la competencia con otras especies, particularmente con especies exóticas invasoras, herbívora y limitaciones edáficas (Schupp *et al.*, 2002; Palma e*t al.*, 2021). Hasta donde sabemos, ningún estudio previo ha explorado los factores que regulan el establecimiento de *Q. humboldtii* en paisajes frecuentemente quemados en el norte de los Andes.

7. Conservación y restauración de robledales andinos afectados por incendios en el Macizo de Iguaque

En este trabajo describimos el régimen de incendios en el Macizo de Iguaque, como ejemplo de la dinámica de los incendios en robledales norte-andinos, hemos evaluado el impacto de los incendios sobre diversos aspectos de la composición, estructura y dinámica de los robledales, y finalmente hemos discutido las implicaciones de los resultados sobre su gestión. En primer lugar, a partir de modelos predictivos de idoneidad ambiental para *Q. humboldtii*, comprobamos la distribución potencial y remanente para el roble andino. Luego generamos el mapa de incendios de la región Andina colombiana usando la información de fuegos de la base de datos de detección remota de focos activos de anomalías térmicas del sensor MODIS. Con esta información establecimos la relación espacial entre la distribución de *Q. humboldtii* y la ocurrencia de incendios. Estos aspectos se presentan en el Capítulo 1 de esta tesis, titulado ***Quercus humboldtii* distribution and wildfire in Northern South America.** Nuestra hipótesis fue que el régimen actual de incendios es parte de los factores que impulsan la pérdida de hábitat de *Q. humboldtii*, y se suman a los factores históricos de pérdida y transformación de su hábitat.

Posteriormente, con la investigación titulada **Wildfire dynamics and impacts on a tropical Andean oak forest, the Iguaque mountains** (Capítulo 2), presentamos un análisis cuantitativo de la dinámica de los incendios forestales en el macizo de Iguaque, utilizando diferentes enfoques metodológicos. Con este estudio pretendimos responder las siguientes preguntas: i) ¿Cuál es la frecuencia de incendios recientes en Iguaque?, ii) ¿Existen tendencias interanuales en la frecuencia y extensión de incendios?, iii) ¿Es constante la probabilidad de incendios a lo largo del año y en todo el macizo de Iguaque?, y iv) ¿Los incendios han afectado a la extensión y distribución espacial del robledal?

En el Capítulo 3 (**The current fire regime in northern Andean shrublands hinders tree recruitment and arrest forest succession**) describimos la composición de los matorrales afectados por incendio, y evaluamos el efecto de incendios frecuentes y recientes sobre la misma. Más concretamente, intentamos responder a las siguientes preguntas: i) ¿El aumento de la frecuencia de incendios y la reducción del tiempo transcurrido desde el último incendio están asociados con la riqueza de especies, la densidad de individuos, y la cobertura y área basal de la vegetación?, y ii) ¿La riqueza de especies y la cobertura de gramíneas y especies exóticas depende del régimen de incendios?

Con la investigación titulada **Postfire resprouting and recruitment of *Quercus humboldtii* in the Iguaque mountains** (Capítulo 4), evaluamos el impacto del actual régimen de incendios sobre la capacidad del roble andino para rebrotar y establecerse a partir de bellotas, después del fuego. En Capítulo 5 (**Producción y germinación de bellotas de *Quercus humboldtii* en un robledal andino afectado por incendios recurrentes**), estudiamos el papel del fuego en la producción de bellotas viables. Para lo anterior planteamos las siguientes preguntas: i) ¿Cuál es la cantidad de bellotas viables y abortadas que se cosechan de robles andinos afectados y no afectados por incendios?; ii) ¿Existen diferencias en el tamaño, biomasa y tasa de germinación de las bellotas viables provenientes de robles quemados, respecto a las bellotas que provienen de los robles no quemados?, iii) ¿Los robles quemados producen una mayor cantidad de bellotas abortadas? y iv) ¿Cuál es la relación entre la temperatura y la precipitación respecto la cantidad de bellotas cosechadas de robles andinos afectados y no afectados por incendios?

Finalmente, en el estudio titulado ***Quercus humboldtii* germination and establishment in Andean forests affected by recurrent wildfires** (Capítulo 6), establecimos un experimento manipulativo para estudiar los limitantes de la germinación de bellotas y el establecimiento de plántulas y brinzales en condiciones de campo. Bajo bosques de robles, matorrales intactos y matorrales donde eliminamos las especies exóticas invasoras, sembramos bellotas y plantamos brinzales de *Q. humboldtii*. Luego, realizamos seguimiento a la germinación, el enraizamiento de bellotas, y el desarrollo de plántulas y brinzales. Comprobamos las siguientes preguntas: i) ¿Cuál es la cantidad de bellotas viables y abortadas que se cosechan de robles andinos afectados y no afectados por incendios?; ii) ¿Existen diferencias en el tamaño, biomasa y tasa de germinación de las bellotas viables provenientes de robles quemados, respecto a las bellotas que provienen de los robles no quemados?; iii) ¿los robles quemados producen una mayor cantidad de bellotas abortadas? y iv) ¿Cuál es la relación entre la temperatura y la precipitación respecto la cantidad de bellotas producidas por robles andinos afectados y no afectados por incendios?

Esta investigación describe la respuesta de la vegetación andina a los incendios, y concretamente, analiza los mecanismos que limitan el reclutamiento del roble andino en áreas afectadas por incendios. Por ello, aporta nuevos conocimientos sobre la ecología de incendios, y la composición y dinámica de los robledales andinos. Esta información puede contribuir a mejorar la gestión de los robledales andinos y de la biodiversidad, en paisajes transformados del norte de los Andes.

A manera de síntesis realizamos un ideograma (Figura I) donde presentamos la cartografía con la incidencia de incendios en los Andes colombianos, así como en la distribución potencial del roble andino y en el macizo de Iguaque. Posteriormente, en distintos paneles sucesivos hemos representado algunas posibles respuestas de la vegetación post-incendio, de acuerdo con los referentes bibliográficos. Primero presentamos que después de un incendio, *Quercus humboldtii* puede rebrotar y los robledales andinos pueden persistir, pero con una estructura y composición de la vegetación mucho más pobre. Luego, representamos que cuando desaparecen robles por otros disturbios y se incrementa la frecuencia de incendios, la comunidad vegetal que se puede establecer post-incendio son matorrales con presencia de especies exóticas invasoras. Además, en dichos matorrales, es probable que el reclutamiento de *Q. humboldtii* o de otras especies arbóreas sea nulo. De igual forma, en los bosques y matorrales afectados por incendios, es posible que *Q. humboldtii* presente múltiples limitaciones al reclutamiento, y que dichas limitaciones estén relacionadas con los incendios y las especies exóticas invasoras. Finalmente, es posible que con el control de las especies invasoras y la revegetación se puedan reducir los incendios e incidir en un mejor reclutamiento del roble andino, tanto en los matorrales como en los robledales post-incendio.

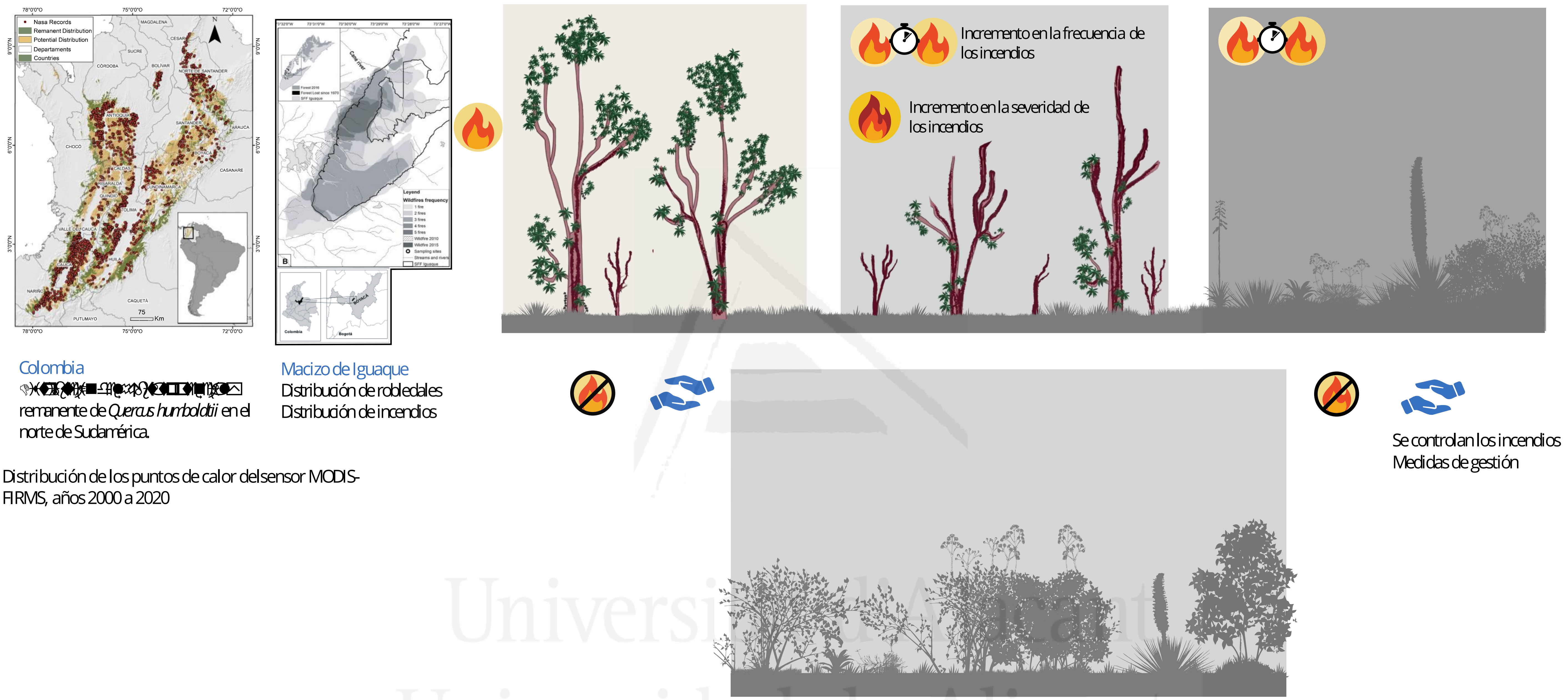

Figura I. Síntesis del contexto general de los incendios y la regeneración natural de matorrales y robledales andinos post-incendio.

CHAPTER 1. *Quercus humboldtii* (Fagaceae) distribution and wildfire in northern South America

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Quercus humboldtii (Fagaceae) distribution and wildfire in northern South America

ABSTRACT

In Northern Andes, we compared remaining and potential *Quercus humboldtii* Bonpl. (Fagaceae) distribution and its relation to wildfire occurrence. First, we made the current distribution using the Biomes of Colombia Map and our possible distribution model. Then, using map algebra, we eliminated the transformed biomes, water bodies, and páramo coinciding with the potential distribution. Then, we established the space-time distribution of burned areas in Colombia using wildfire data recorded by the Fire Information for Resource Management System, FIRMS (2000–2015). Finally, we compared the two independent datasets: the presence of *Q. humboldtii* in potential and remnant habitats and FIRMS hotspots. *Quercus humboldtii* potential habitat distribution in Colombia occurs in the three mountain ranges of the Colombian Andes, the Caribbean massifs, and some inter-Andean lowland regions. Its potential habitat extends from 900 to 3,200 m a.s.l. *Quercus humboldtii* has a wide climatic adaptation, with a preference for environments with an average temperature of 17°C and average annual precipitation of 2,024 mm. The current remaining distribution of this species was 28% of its potential distribution. The most affected departments were Caldas, Quindío, Boyacá, Antioquia, Cundinamarca, Tolima, and Valle del Cauca, where 80 and 92% of the habitat was lost. The remaining habitat distribution was little related to wildfire occurrence. Conversely, we found a positive and weak correlation between FIRMS wildfire records and the *Q. humboldtii* potential habitats distribution. The low correlation between the occurrence of fires and the species' potential habitat allows us to conclude that wildfires have added to the transformation factors that have influenced the loss of habitat for *Q. humboldtii*. Combined with global climate change and current socio-political conditions in Colombia, wildfires could soon significantly reduce the species' habitat.

KEYWORDS: Andean oak forest, Colombia, MaxEnt, Northern Andes, Predictive modeling, Species distribution.

Andean oak (*Quercus humboldtii* Bonpl.) is the southernmost species of the *Quercus* genus in the Neotropics and belongs to the red oak group, subgenus *Erythrobalanus* (Nixon, 2006). It is endemic to the northern Andes (Avella, 2016). It is distributed exclusively in the Panamanian Darien and Colombia across the three branches of the Cordillera de Los Andes, as well as in some foothills of the massifs of the Colombian Caribbean region (Rangel & Avella, 2011). Andean oak grows in a broad environmental gradient. Altitudinally it can occupy elevations ranging from 750 to 3,450 m. Regarding precipitation, its range varies from 700 to 3,000 mm (Rangel et al., 2009). Finally, it develops from moderately fertile and profound soils to those in the degradation process (López, 2014).

Quercus humboldtii usually appears as a floristic element of sub-Andean Forests and as a dominant or co-dominant species in the Andean and High-Andean forests (2300-3450 m of elevation), especially in the sub-humid and sub-xerophytic slopes (van der Hammen et al., 2008). In this region, *Q. humboldtii* generates a vegetal formation known as the Andean oak forest (Avella, 2016). The ecosystems of the Andean region are essential for beneficial sociocultural activities and biodiversity conservation (Bello, 2006; Avella & Cárdenas, 2010; Avella et al., 2015). Approximately 550 species of vascular plants (Pulido et al., 2006), 200 species of birds, 55 species of mammals, and 30 species of amphibians (Sáenz, 2010) are found in these forests.

Conceptual models (Rangel, 2000, González et al., 2006, Etter et al., 2008, González et al., 2011) were used to analyze spatial and temporal patterns of land cover change in Colombia, determining that the distribution of Andean forests in northern South America has historically decreased, showing a reduction of 60–90% compared to its pre-Columbian distribution. Since the early twentieth century, oak forests have been affected by land occupation (Bello, 2006), wood harvesting for tools, collection of raw materials for several types of construction, domestic and industrial fuel supply, and other uses (Solano & Vargas, 2006; Avella & Cardenas, 2010). As a result, many *Q. humboldtii* populations were lost, and the species was classified as vulnerable in the UICN Red List tread (Calderón et al., 2002; Solano et al., 2005).

Despite protection and closure measures, such as the natural protected areas and the logging ban (Solano et al., 2005, MAVDT, 2006), the Andean oak forest is still affected by degradation and deforestation caused by agricultural and livestock activities and the occurrence of wildfires (Avella & Cárdenas, 2010; Avella et al., 2015; Fernández-Méndez et al., 2016). The potential distributions are unknown, but there are historical records of botanical collections and vegetation studies in the Colombian Andean region (Avella, 2015). Furthermore, only a few studies have investigated the effect of wildfires on Andean oak forests (Salazar et al., 2020; Aguilar-Garavito et al., 2020), but the impact on its current distribution and its relationship with other drivers of habitat loss or with bioclimatic variables is unknown. Due to global climate change, these forests may be strongly threatened by wildfires and other disturbances (Young et al., 2011).

During the period 1998 to 2002, wildfires already affected 84% of the surface of the world's biodiversity hotspots (TNC et al., 2004). In Latin America alone, 51 million ha lost in the last three decades (FAO, 2005; 2013). Records show that 295,300 ha of the Colombian Andean region was affected by wildfires between 2001 and 2007 (Anaya-Acevedo & Chuvieco-Salinero, 2010). Official reports from the Colombian government have been available since 1998 (UNGRD 2018). Between 2002 and 2013, 12,978 wildfires were reported, affecting 619,300 ha of land (IDEAM, 2004). In 2015 alone, 3,985 wildfires were reported, affecting 150,000 ha of the Colombian region (García et al., 2016). Some studies have investigated wildfire dynamics in Colombia (Armenteras et al., 2005; 2009 a; b; Muñoz, 2005; Amaya & Armenteras, 2012; Barreto et al., 2017; Armenteras et al., 2019; 2020). However, information regarding the detailed dynamics of wildfires and their impact on tropical mountain zones is still lacking. In addition, the current wildfire regime has probably affected the distribution of species due to habitat reduction and fragmentation (Bosso et al., 2018)

In the tropical Andean region, significant changes in fire regimes have occurred during the last two million years, especially since human settlements began in the late Pleistocene (TNC et al., 2004; Armenteras et al., 2019; 2020). For example, in Colombia, paleo-ecological records confirmed the incidence of large wildfires during warm periods of the Pleistocene and Holocene (approximately 11,000 years ago; Van der Hammen, 1966; Kuhry, 1988). During pre-Columbian times, fire was used in the Cundiboyacense highlands to clear vegetation and expand crops (Patiño, 1965; 1997; Márquez, 2001).

These practices were intensified with European colonization, with forest and páramo vegetation converted to pastures maintained by frequent fires (Fals Borda, 2006; Mora, 2012). Due to human intervention, the frequency of wildfires has increased since prehispanic times, going from one event every 1,000 years to one event every year (Verweij, 1995; Vargas, 2002).

Many *Quercus* species are fire tolerant (Johnson et al., 2002), primarily owing to the concentration of dormant buds near the root collar (Espelta et al., 2003). This trait facilitates rapid post-disturbance resprouting. Oak tolerance to fire depends on stem diameter, bark thickness, fire intensity, and frequency. Thus, this trait highly depends on the species (Johnson et al., 2002; Pausas, 2017; Casals et al., 2018). In North America, red oak species can tolerate low to moderate fire intensities with relatively long intervals between fire events (more than 14 years; Johnson et al., 2002; DeSantis et al., 2010). Trees with a breast height (DBH) diameter greater than 18 cm show a higher probability of surviving wildfires (Johnson et al., 2002). The response of neotropical oaks to disturbances such as fire could be more precise. In Mexico and Costa Rica, some oak species can survive logging and fires (Aus der Beek et al., 2006; Guariguata & Sáez, 2002). However, depending on the wildfire frequency, regeneration may be arrested (Bonfil, 2006; González-Espinosa et al., 2006). In Colombia, *Q. humboldtii* resprouts up to three years after a wildfire, but it is not clear which fire regime this species is adapted to or what fire's effects on its regeneration are (Salazar et al., 2020). Several studies have suggested that Andean forests in Colombia (including oak forests) are neither fire-prone nor fire-adapted (Páramo-Rocha, 2011; Armenteras et al., 2020).

Knowing the distribution habitat of *Q. humboldtii* and the occurrence of forest fires is crucial to predicting the species' potential presence in suitable areas for survival. In the same way, the distribution of drivers and the level of incidence of forest fires can be identified. From here, we will have elements that assist in developing integrated biodiversity management strategies for crucial conservation areas of the species (Reside et al., 2012; Magadzire et al., 2018). Therefore, this study aims to generate models of potential and remaining habitat distributions of Andean oaks in Colombia to infer their relationship with the incidence of forest fires in the Colombian Andes. We hypothesize current fire regime is part of the drivers of *Q. humboldtii* habitat loss. Wildfires add to the historical loss and transformation drivers of this exclusive habitat.

METHOD

Quercus humboldtii **presence records**

The occurrences of *Q. humboldtii* were obtained from herbaria and institutional web repositories: the Herbario COL (Instituto de Ciencias Naturales, 2019), the Herbario FDM (Instituto Humboldt, 2019a), Herbario HUA (Universidad de Antioquia, 2019), TROPICOS (2019), I2D (Instituto Humboldt, 2019b) and GBIF (2019). Additionally, we included occurrences from natural protected areas in Colombia, transects retrieved from the literature (Vasquez & Serrano, 2009; Avella, 2016), and the personal database of *Q. humboldtii* Avella's (2015) studies. These data were collected and checked for quality (i.e., positional accuracy using survey efforts, a global positioning system, GPS on the field, maps, original labels of reviewed specimens, and Google Earth).

We compiled 3,429 occurrence records for *Q. humboldtii*, dated from 1783 to 2013. After applying spatial filtering and removing duplicates and vague coordinates, we retained a dataset of 1,835 unique occurrences (Appendix 1.1). This was the largest database of *Q. humboldtii* records ever collected. It is, though, a collection of multiple sources that were previously published. Spatial filtering of at least a 10 km distance was applied to reduce the effects of sampling bias using the R package `spThin´ (Aiello-Lammens et al., 2015; 1,000 repetitions) and over-fit towards environmental biases. Spatial filtering of species occurrence records refers to removing the fewest records necessary to substantially reduce the effects of sampling bias (Aiello-Lammens et al., 2015). We selected the distance of 10 km because it is a greater distance to the home range of the Andean oak´s dispensers (e.g., tinajos -Cuniculus taczanowskii, C. paca- y picuros -Dasyprocta punctata-; Aliaga-Rossel et al., 2008; Benavides et al., 2017; Guerrero-Rodríguez et al., 2010), avoiding natural aggregation in the occurrence records. Moreover, that distance was used in a previous analysis describing the species' geographic distribution (Zorrilla-Azcué et al., 2021). Spatial filtering also allows the creation of more reliable models (Boria et al., 2014; Kramer-Schadt et al., 2013; Townsend Peterson et al., 2007). We tested many other lag distances using semivariogram analysis to explore the spatial autocorrelation, but the adequate distance was around 100 km. We avoid using that distance in the spatial filtering because it could reduce the sample size and make inviable the ecological niche model for the specie. Quality testing was performed using ArcGIS 10.3. (ESRI, Redland, CA, USA).

Quercus humboldtii **potential distribution models**

We updated the geographic distribution of the Andean oak using MaxEnt 3.4.0 (Phillips et al., 2017), a presence-background ecological niche modeling technique that uses the occurrences of species and background (the whole study area that included pixels with presences) along with the selected environmental variables to build the models (Phillips et al., 2006). The `*kuenm*´ package version 1.1.1 (Cobos et al., 2019) in R version 3.5.3 (R Core Team, 2019) was used for the creation and evaluation of the models. We created candidate models based on 94 ecologically relevant environmental variables for the species distribution (Zorrilla-Azcué et al., 2021,) at 30 s (~1 km^2) of spatial resolution and Global Coordinate System WGS84. The set of environmental variables included 68 from WorldClim 2.1 data (e.g., elevation, bioclimatic variables, monthly precipitation, monthly wind speed, monthly water vapor pressure, and monthly solar radiation; WorldClim, 2019) and 26 data related with Soil-Water Balance (e.g., Mean annual AET, Monthly AET, Monthly Soil Water Stress, and Priestley-Talor Alpha Coefficient; CGIARCSI, 2019)(Appendix 1.2).

We included the complete set of environmental variables without exploring collinearity, considering that Maxent can regulate complexity in the model by downplaying the importance of redundant variables (Feng et al., 2019; Phillips & Dudík, 2008). We split the occurrences randomly into 75–25% subsets for model calibration and internal testing. A suite of candidate models with differing levels of complexity was tested, 10 values of regularization multiplier (0.2–1.0 at intervals of 0.1, 2–6 at intervals of 1), and all 29 possible combinations of five feature classes (linear = l, quadratic = q, product = p, threshold = t, and hinge = h). Maxent theory suggests that several regularization values may be needed when the number of environmental variables is much larger (Phillips & Dudík, 2008). Clog-log output format was used to describe the probability of presence (Phillips et al., 2017), which is a continuous habitat suitability range between 0 (unsuitable) and 1 (the most suitable). Traditionally, the area under the curve (AUC) is commonly used as a summary measure of the receiver operating characteristic (ROC) curve used to evaluate the classificatory performance of the models (Peterson et al., 2008). However, the model selection must be based on significance, predictive ability, and complexity (Cobos et al., 2019). Therefore, the model performance statistics follow the implemented in the *kuenm* package: partial ROC (Receiver Operator Characteristic), omission rates, and AICc (Cobos et al., 2019). The best model was selected from the candidate models, applying the three statistics: high values of partial ROC as a measure of statistical significance of the performance of binary classification based on a specificity interval given by the area AUC (Peterson et al., 2008), omission rates ≤ 5% (Anderson et al., 2003), and delta AICc ≤ 2 (Warren & Seifert, 2011). Whether more than one best model was selected by *kuenm*, we used the median of all replicates across parameters to consolidate results for the Andean oak’s potential distribution. The partial ROC significance was estimated running 500 iterations, using 50 percent of data for bootstrapping, and a low omission rate (E = 5%). We used the low omission rate (E = 5%) to select the cut-off threshold in the continuous model. This thresholding approach omitted the 5% of records with the lowest suitability, assuming this percentage of occurrences biased the modeled environmental niche of the species (Peterson et al., 2008).

Quercus humboldtii remnant habitat distribution

The construction of the distribution map of the remnant habitat of the Andean oak was based on the *Q. humboldtii* potential distribution model developed by us. We refined the distribution model using Etter's (1998) map of the current biomes of Colombia. We used a geographic information system (GIS) (ArcGIS 10.3; ESRI, 2015), map algebra, and automated operations to eliminate areas where the distribution of potential *Q. humboldtii* habitat coincided with natural covers such as paramos (elevations above 3,200 m a.s.l.) and tropical dry forest. In addition, areas where the potential distribution coincided with agroecosystems and other transformed ecosystems, such as cities, urban centers, and bodies of water, were also removed. Thus, the current distribution map removes the space occupied by the previously mentioned ecosystems from the potential distribution map.

Quercus humboldtii remnant distribution and wildfires relationship

We established the space-time distribution of the fire areas in Colombia obtained by satellite imagery (MODIS) between 2000 and 2022 (FIRMS - Fire Information for Resource Management System; NASA, 2023). First, using an aggregation of points by unit-area function in the GIS (ArcGIS 10.3; ESRI, 2015) and probability of presence and wildfire density values from FIRMS, we built hotspot maps of fires to obtain the Colombian Andes wildfire map. Second, we calculated Pearson's correlation coefficients to assess the degree of a simple relationship between the FIRMS wildfire density values and the following: 1) *Q. humboldtii* national records, 2) the potential distribution of *Q. humboldtii* habitat, and 3) the current distribution of remnant *Q. humboldii* habitat. The size of the area of distribution and remanent area was calculated by multiplying the number of pixels on each raster by 1 km^2. The functions (cor.test) and (corrplot) and the R software package `gginference´ (Bratsas et al., 2018; R Core Team, 2020) were used. Previously, the variables were checked for interval or reason, as well as the normality of the samples, using the Shapiro–Wilk tests (function (shapiro.test) from the `stats´ package, R software; R Core Team, 2020).

RESULTS

We obtained 290 candidate models with all combinations of 10 regularization multiplier settings and 29 feature classes. However, the selection criterion allows the selection of the six best models according to the high values of partial ROC, omission rates ≤ 5%, and delta AICc ≤ 2 criteria (Table 1.1). The variables that contributed the most to the Maxent models were Min Temperature of Coldest Month, Max Temperature of Warmest Month, and elevation.

Table 1.1. Performance statistics for the best models selected based on the predefined criteria.

Model	**Partial ROC**	**Omission rate at 5%**	**delta AICc**	**# parameters**
M_6_F_q	0	71	0	9
M_6_F_qt	0	71	0.01	9
M_6_F_lqph	0	71	0.49	11
M_6_F_lqpt	0	71	0.60	11
M_6_F_lqpth	0	71	0.60	11

Quercus humboldtii **potential habitat distribution**

The potential distribution of *Q. humboldtii* had an area of 171,796 km^2. The map in raster format is available in BioModelos (link BioModelo Q.humboldtii), a digital tool that allows communication between biodiversity experts to develop distribution models in Colombia collaboratively and openly platform (Velásquez-Tibatá et al., 2019). *Q. humboldtii* is distributed between 8.1254° (Panama) and 8.9507° (Colombia) north latitudes and 0.3824° south latitude, and between 71.8875° east longitude and 77.4455° (Panama) and 78. 2352° (Colombia) west longitudes, in Colombia. It covers three branches of the Cordillera de Los Andes, the Serranías Perijá, San Lucas, Iglesias, Montescrito, and Tierra Alta Mountains (Figure 1.1). It is characterized by the very humid low montane forest (bmh-MB), humid low montane forest (bh - MB), and humid montane forest (bh–M) biomes (Holdridge, 1967). Additionally, a few regions of Ecuador and Venezuela are also climatically suitable. Although these sites have the climatic potential for *Q. humboldtii*, no records exist for this species.

Our data confirm that *Q. humboldtii* has a wide climatic adaptation to the Colombian Andean Mountains. On the eastern flank of the Cordillera Oriental, the minimum altitude of the potential habitat distribution drops to 1,500 m a.s.l. It falls to 1,400 m a.s.l. in Boyacá and Norte de Santander. On the western side, it can drop to 1,000 m a.s.l. Its upper limit can lie between 3,200 and 3,374 m a.s.l. On the eastern side of Cordillera Central, it falls a minimum of 1,000 m a.s.l., but in some regions, such as Antioquia and Risaralda, it can reach an altitude of up to 1,200 m a.s.l. At the same time, its upper limit may oscillate between 3,200 and 3,700 m a.s.l. The Cordillera Occidental region had more significant variability regarding the lower limit. It is between 900 and 1,400 m a.s.l., and its upper limit can reach 3,300 m a.s.l. The regions showing the highest potential habitat distribution were Antioquia (28,754 km^2), Cauca (17,345 km^2), Cundinamarca (15,459 km^2), Santander (14,884 km^2), and Tolima (13,314 km^2). Appendix 1.3 shows the distribution of potential and remnant habitats by the department. In general terms, the climatic adaptation (Table 1.2) of the species included an average rainfall of 2,024.1 mm/year, with a minimum of 69 mm/year and a maximum of 623 mm/year, and a yearly mean temperature of 17.1 °C, with a maximum temperature of 26.6 and a minimum of 4 °C (Appendix 1.4).

Table 1.2. Climate variables (temperature and rainfall) for *Quercus humboldtii* potential and remnant habitat distributions

Data	**Mean annual temperature (ºC)**		**Mean annual rainfall (mm)**	
	Mean ± SD	**Min. – Max.**	**Mean ± SD**	**Min. – Max.**
Quercus humboldtii Potential Habitat distribution	17.1 ± 4	4 - 27	2,024 ± 703	623 - 6,978
Quercus humboldtii Remnant Habitat Distribution	16 ± 4	4.8 - 26	2051 ± 719	716 – 6,978

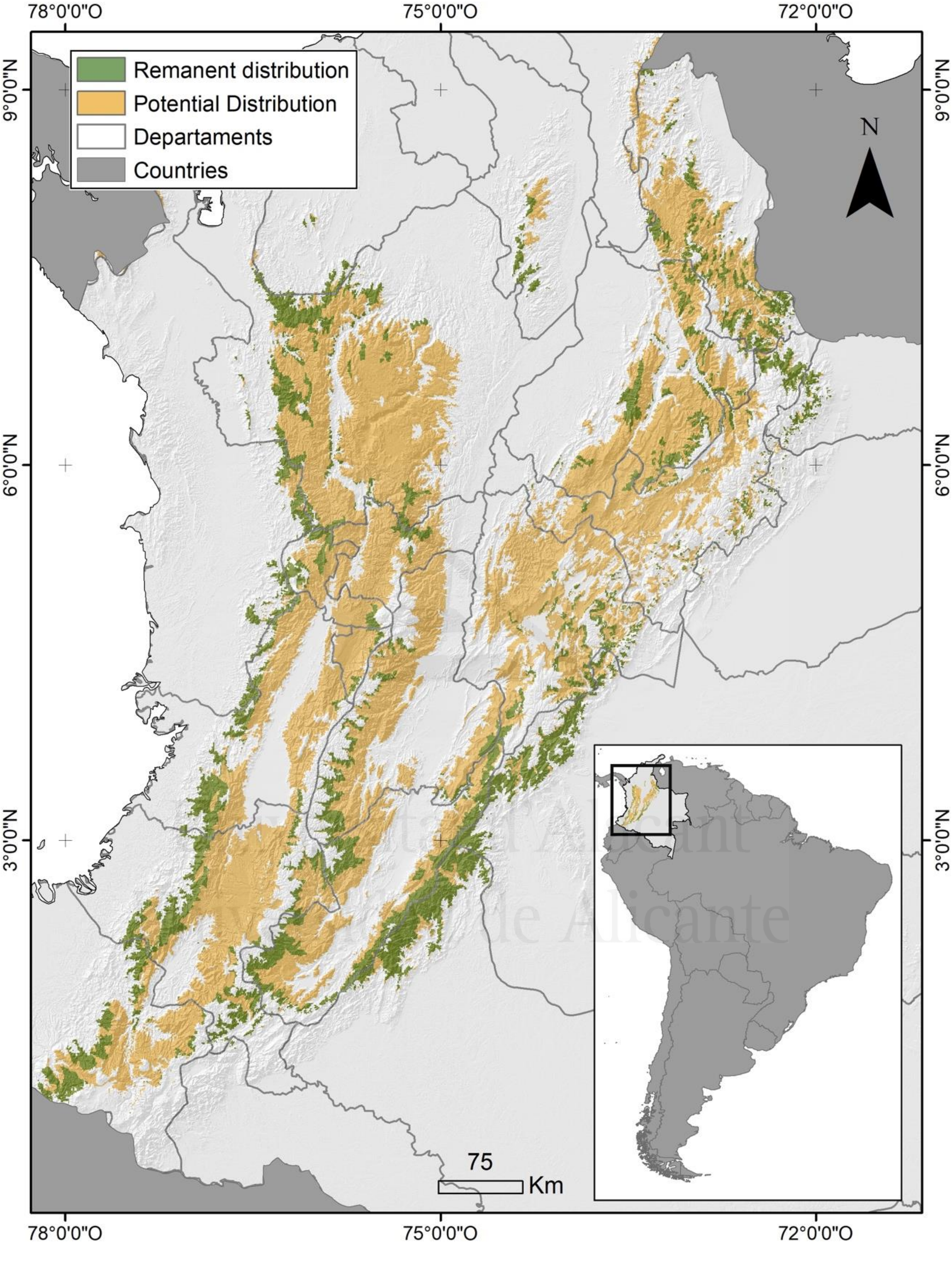

Figure 1.1. Potential and remnant habitat distributions of *Quercus humboldtii* in Colombia. They were obtained using the MaxEnt algorithm.

Quercus humboldtii remnant distribution model

The remnant distribution of the *Q. humboldtii* habitat had an area of 48,583 km^2, showing a 72% reduction of the potential Andean oak habitat distribution. Regions with the highest allocations of remnant habitat were Antioquia (5,265 km^2; 18% of the remnant area), Cauca (5,190 km; 30% of the remnant area), Huila (4,374 km^2; 38% of the remnant area), Caquetá (3,994 km^2; 86% of the remnant area), and Norte de Santander (3,817 km^2; 33% of the remnant area). The departments of Caldas, Quindío, Cundinamarca, Boyacá, Valle del Cauca, Tolima, Santander, Risaralda, and Cesar were the regions with the lowest distribution of remnant habitat for *Q. humboldtii* (with a range of loss between 92 and 70%). Finally, the regions showing less than 30% of habitat loss for *Q. humboldtii* were Putumayo, Arauca, Meta, Caquetá, Córdoba, and Chocó (Appendix 1.5).

The minimum altitudinal range on the eastern flank of the Cordillera Oriental is between 1,700 and 2,000 m a.s.l. However, in some areas, it can be as low as 1,500. On the western flank, the lower limit was 2,200 m a.s.l. In the Central Cordillera, the minimum altitudinal range lies between 2,500 and 3,000 m a.s.l. It is only lower in the department of Caldas, where it drops to 1,500 m a.s.l. In Western Cordillera, the lower limit varies between 1,100 and 1,600 m a.s.l. with some exceptions, it can go down to 1,000 m a.s.l. According to the models, the climatic conditions in the remaining habitat for the species are characterized by moderate temperatures of around 16 ºC, with minimum temperatures of 4.8 ºC in Boyacá and maximum temperatures of 26.4 ºC in the department of Tolima (according to the mean annual temperature). Moreover, under annual precipitation conditions of around 2,051 mm., with a minimum of 716 mm. in Cundinamarca and a maximum of 6,978 mm in the department of Chocó (see Table 1.2 and Appendix 1.5).

Quercus humboldtii distribution and wildfires

Between 2000 and 2015, 4,772 wildfire hotspots reported by FIRMS were found in the Colombian Cordillera de Los Andes, distributed in 22 departments and 770 municipalities. According to this report, the most significant accumulation of wildfires in the three mountain ranges coincides with intervened and anthropized areas. There is a low incidence of wildfires in natural areas. Seventy-nine percent (3,379) of the hotspots occurred in the potential distribution area of the *Q. humboldtii*. 31% of the hotspots in the potential distribution area of *Q. humboldtii* were located in the departments of Cauca (17%) and Antioquia (14%). Another 32% of the FIRMS hotspots were in five departments: Tolima (8%), Nariño, and Norte de Santander, each with 7%, Boyacá (5%), and Huila (4 %). Five departments accounted for 14% of the FIRMS hotspots: Cundinamarca (4%), Valle del Cauca (3%), Santander (3%), Bolivar (2%), and Cesar (2%). The remaining 3% of the FIRMS hotspots in the potential distribution area were in seven departments (Caldas, Risaralda, Caquetá, Quindío, Meta, Chocó, and Casanare) with less than 1% of the FIRMS hotspots. Finally, three departments had no FIRMS hotspots in their potential or remnant area (Arauca, Córdoba, and Putumayo). Figure 1.2 shows the distribution of potential and remnant *Q. humboldtii* habitats and the locations of FIRMS hotspots.

For the potential distribution area, 16% of the municipalities (124) had more than seven FIRMS hotspots during the period 2000 to 2015, 8% of the municipalities (61) had between five and seven FIRMS hotspots, while 17% of the municipalities (131) had between four to two FIRMS hotspots. Finally, 13% of the municipalities (100) presented only one FIRMS hot spot, and 46% (354) had no FIRMS hot spot.

In the remaining *Q. humboldtii* distribution area, 4% (170) of the FIRMS hotspots were detected from 2000 to 2015. The departments with the highest percentage of FIRMS hotspots in the remaining area (4%) were Antioquia (1%), Norte de Santander (1%), Nariño (1%), Santander (0.3%), Cesar and Tolima (0.2% each) and Cauca, Bolivar, and Boyacá (0.1% each). On the other hand, the six departments (Bolívar, Huila, Caldas, Caquetá, Cundinamarca, and Valle del Cauca) have 0.4% of the FIRMS hotspots in the remaining area, each with less than 0.1%. In comparison, eight departments had no reported FIRMS hotspots in the remaining area of distribution of *Q. humboldtii*. In the remaining area, only two municipalities (0.2%) had more than seven FIRMS hotspots, five municipalities (0.5%) between five and seven FIRMS hotspots, 74 municipalities (9%) between two and four FIRMS hotspots, 38 municipalities (4%) one FIRMS hot spot. In contrast, 697 (86%) had no hotspots.

We found a positive but weak correlation between FIRMS wildfire hotspot records and the distribution of potential *Q. humboldtii* habitats (Pearson's $r = 0.35$, $p = 2.2^{-16}$, n =7296). We also found a weaker correlation between FIRMS wildfire hotspot records and the actual remnant *Q. humboldtii* habitat (Pearson's $r = 0.16$, $p = 2.2^{-16}$ =, $n = 7296$), confirming that wildfires that occurred during the last few years partially affected the area of remnant habitat. As shown in Figure 1.2, these wildfires occurred mainly around the remnant *Q. humboldii* habitat in regions of the species' historical potential distribution habitat. In contrast, we found a strong negative correlation between FIRMS wildfire hotspot records and remnant *Q. humboldtii* distribution (Pearson's $r = - 0.71$, $p = 2.2^{-16}$, n =7296).

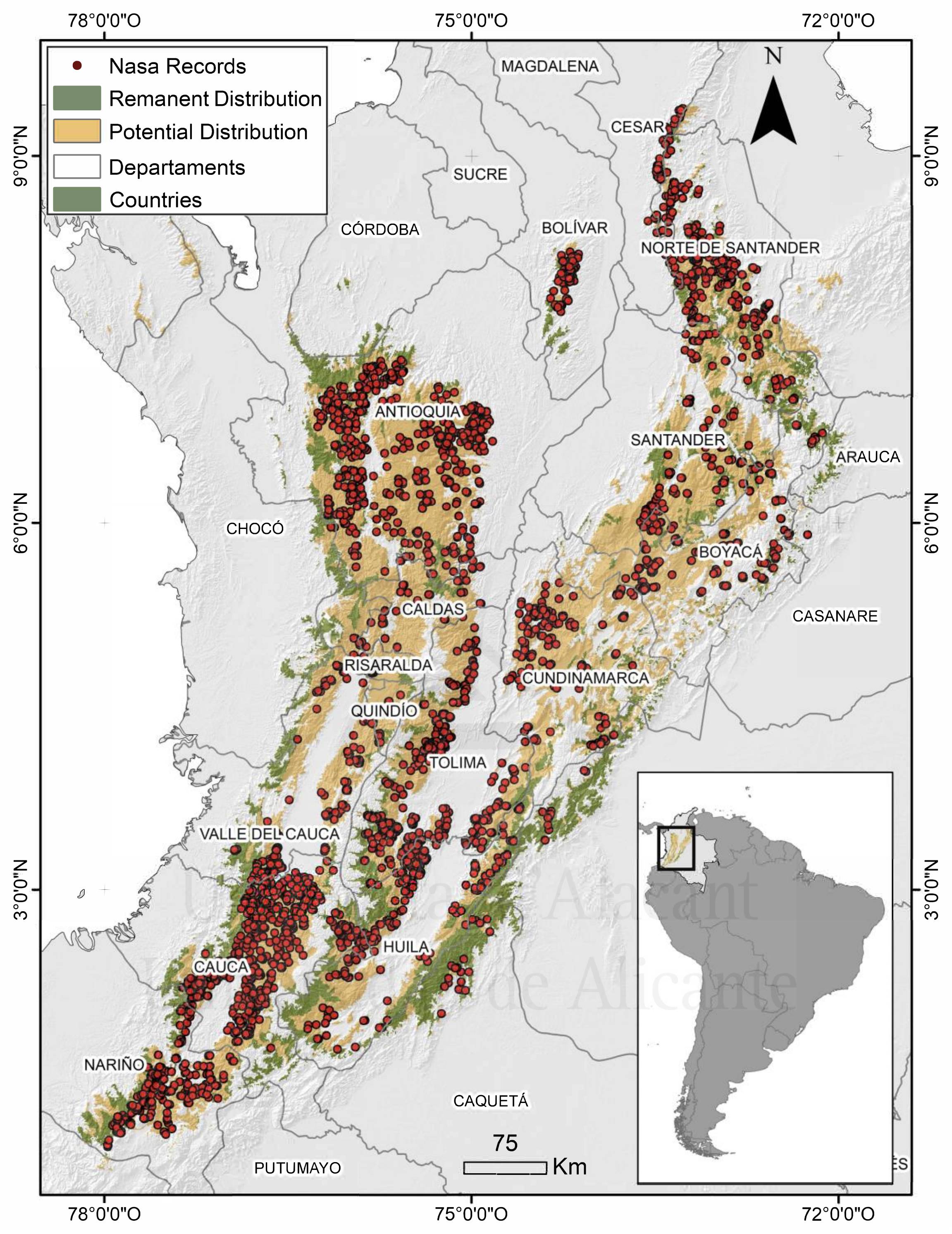

Figure 1.2. Potential and remnant habitat distributions of *Quercus humboldtii* and wildfire locations (based on FIRMS hotspot records) in Colombia from 2000 to 2015.

DISCUSSION

Our study aimed to predict the potential and remaining distribution of *Q. humboldtii* in Colombia and its relationship with wildfires that occurred during the last 15 years. The results showed that *Q. humboldtii* has wide suitability in locations around from low (900 m a.s.l.) to high elevations (3,200 m a.s.l.) and wet to dry environments (623 mm/year – 6,978 mm/year), with a mean temperature of 4 ºC to 26.6 °C. The suitability distribution of *Q. humboldtii* modeled is consistent with the records collected by other authors in the last decade (Rangel & Avella, 2011; Avella, 2016; Avella et al., 2017; Rangel, 2017; Zorrilla-Azcué et al., 2021). Furthermore, results predict the species distributions across 22 out of the 33 departments of Colombia (Antioquia, Arauca, Bolívar, Boyacá, Caldas, Caquetá, Casanare, Cauca, Cesar, Chocó, Córdoba, Cundinamarca, Huila, Meta, Nariño, Norte de Santander, Putumayo, Quindío, Risaralda, Santander, Tolima, and Valle del Cauca).

***Quercus humboldtii* potential habitat distribution model**

We found that our model of potential habitat distribution for *Q. humboldtii* coincides with the potential distribution of this species determined by other authors (Rodríguez-Correa, 2008, González et al., 2006; 2011, López, 2014; Zorrilla-Azcué et al., 2021). However, we used discrimination thresholds integrating several geographic resources, including biomes of Colombia (natural covers such as paramos and tropical dry forest) and excluding others (agroecosystems, cities, urban centers, and bodies of water), making a more rigorous adjustment to the remanent habitats that the species could inhabit and used a more robust database regarding the number of observations. Recommendations for climatic variables from previous distribution studies were also considered.

The *Q. humboldtii* potential distribution includes regions in the departments of Antioquia, Arauca, Bolívar, Boyacá, Caldas, Caquetá, Cauca, Cesar, Chocó, Córdoba, Cundinamarca, Huila, Meta, Nariño, Norte de Santander, Quindío, Risaralda, Santander, Tolima, and Valle del Cauca. Similar to other distribution models of *Q. humboldtii* (Zorrilla-Azcué et al., 2021), we found that our model also predicts that the species develop in areas where the climate is constant throughout the year, preferably in areas located at an altitude of approximately 2,100 m a.s.l., with continuous temperatures of roughly 17 °C and annual rainfall close to 1,900 mm, which could refer to the conditions that meet the *Q. humboldtii* forest belt that is distributed throughout Los Andes (Table 1.2).

In addition, this distribution allows us to recognize some zones outside the areas where there are no records of the existence of natural populations of *Q. humboldtii*, such as the eastern foothills of the Cordillera Oriental (Putumayo, Arauca in Saravena, Fortul, and Tame municipality; Caquetá in Puerto Rico and San Vicente de Caguán municipality, Huila in the eastern municipalities, as well as in the western cities in the meta departments) and the east slope of the Cordillera Central (in all Tolima and Huila municipalities in the east). It is also necessary to verify their distribution in Ecuador and Venezuela in the areas identified by the model. Although there are no botanical records for the species for these locations, distribution models identify them as areas of potential distribution. Global change and current and historical sociopolitical dynamics would make these spaces potentially suitable for the species.

Quercus humboldtii remnant habitat distribution model

The intense transformation of the Colombian Andes (Etter, 1998; Etter et al., 2008) caused by agricultural and livestock uses, logging, fires, and urban expansion (Avella, 2016) had a direct impact on the reduction of up to 72% of the potential habitat of *Q. humboldtii*. Other studies have proposed similar proportions (60–70%) of habitat reduction for this species (Fernández, 2002). They have also predicted future scenarios where habitat reduction will be much more significant (Correa-Ayram et al., 2020). However, the distribution of the remaining habitat of *Q. humboldii* in some regions may be slightly underestimated; for example, in Cundinamarca, Boyacá, and Santander, where we found some forests and areas in successional growth with a size close to 400 ha or interspersed with shrublands (Vasquez & Serrano, 2009, Aguilar-Garavito, et al. 2020) that were eliminated from the model of remnant habitat because these areas in the Etter (1998) Colombian Ecosystems map were considered anthropized areas. However, in other regions, such as the eastern slopes of the Cordillera Oriental, where no reports of *Q. humboldtii* have ever been recorded, the model may overestimate both potential and remnant habitats.

Quercus humboldtii remnant habitat distribution and wildfires relationship

Recently, wildfires in Colombia occurred mainly in areas where historically, there was potential habitat for *Q. humboldtii*. However, we also found that the incidence of wildfires on the remnant distribution of *Q. humboldtii* is low and almost on the periphery of the current remaining habitat, as observed in the oak forests of the Iguaque Mountains (Aguilar-Garavito et al., 2020) and the El Robledal Forest Reserve (UNGRD, 2018). This may be because a large proportion of the remaining habitat is part of protected natural areas, where many drivers of biodiversity loss are controlled. This result highlights the need to generate comprehensive fire management programs at the interface between protected areas and areas with more intense use. Similarly, developing ecological restoration protocols in these areas is essential to recover the recently affected zones by wildfires. Further, other species distribution models have predicted that the current remaining distribution area may be reduced by 13–60% by 2080 due to a global (López, 2014).

Ninety-eight municipalities had more than seven FIRMS hotspots in the potential area of *Q. humboldtii* distribution and zeroed in on the remaining space. Among these municipalities, the following stand out in Boyacá: Duitama, Gachantivá, Paipa, Ráquira, San Miguel de Sema, and Villa de Leyva. In the department of Cundinamarca in Fúquene, Guachetá, Simijaca, Soacha, Tibacuy, and Ubaté. In the Santander in Charalá, Coromoro, el Encino, Gambita, Mogotes and San Juaquín. The historical use of *Q. humboldtii* has cultural importance in these municipalities. Some are essential conservation areas for the species (Rodríguez et al., 2005; Solano et al., 2005; León et al., 2009; Avella, 2016). Therefore, these places are significant for studying *Q. humboldtii* regeneration dynamics under different fire regimes.

Conservation and restoration implications for *Q. humboldtii*

In the Colombian Andes, the habitat of *Q. humbol*dtii encompasses a wide gradient of altitude, and climate, representing the general environmental conditions of the northern Andes. Moreover, *Q. humboldtii* can resprout after logging or fire and presents innumerable benefits for humans. Therefore, *Q. humboldtii* could be widely used in the Andean region for preservation and restoration processes that contemplate reforestation or population reinforcement of the species and as arboreal elements for different farm uses. In this sense, generating landscapes where different densities and age groups of *Q. humboldtii* are present in forest relicts, regenerating areas, and productive regions can result in the conservation of the species and the maintenance of its current habitat.

Andean oak has the following characteristics: climatic and altitudinal niche amplitude, capacity to grow in open or transformed lands, resprouting capacity, moderate growth, nutrient cycling, high contribution of resources for fauna, and numerous anthropic uses (among other features of the species). Therefore, restoration projects in the Andean region of Colombia between 1,000 and 3,200 m of elevation should consider Andean oak as a candidate species for revegetation projects. However, due to different genetic considerations, it would be advisable to use seeds or seedlings from the same region where they will be planted and to guarantee genetic material from the same department, the slope of the mountain range, and the altitudinal range.

CONCLUSIONS

According to our distribution models, 72% of the *Q. humboldtii* potential habitat distribution is missing. This habitat loss is related to historical drivers of biodiversity loss in the Colombian Andes. The relationship between the incidence of wildfires and the distribution of the *Q. humboldtii* potential habitat analyzed in this study is attributed to the vast space occupied by *Q. humboldtii* in the Colombian Andes and the random possibility of wildfire occurrence. However, wildfires are now an increasingly frequent disturbance in the Northern Andes. Wildfires mainly affect the areas of natural regeneration and the peripheries of the remnant *Q. humboldtii* distribution. Wildfires add to the transformation factors that have affected the loss of *Q. humboldtii* habitats. When wildfires are combined with climate change and current sociopolitical conditions, this pressure could significantly reduce the species' habitat shortly.

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SUPPLEMENTARY MATERIAL 1

Appendix 1.1. Andean oak (*Quercus humboldtii*) records and models of their potential and remnant distributions.

Appendix 1.2. Bioclimatic variables used for modeling the distribution of *Quercus humboldtii*.

Appendix 1.3. Total potential and remnant habitat area of *Quercus humboldtii* classified by the department and their corresponding habitat loss percentage.

Appendix 1.4. Values of 19 bioclimatic variables (BIO from WordClim) for potential habitat distributions of *Quercus humboldtii.*

Appendix 1.5. Values of 19 bioclimatic variables (BIO from WordClim) for remnant habitat distributions of *Quercus humboldtii*

CHAPTER 2. Wildfire dynamics and impacts on a tropical Andean oak forest (the Iguaque mountains, Colombia)

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Wildfire dynamics and impacts on a tropical Andean oak forest (the Iguaque mountains, Colombia)

ABSTRACT

Wildfires have increasingly damaged Andean tropical forests. However, a poor understanding of wildfire dynamics and ecosystem response limits awareness about the magnitude of the problem and design management strategies. We estimate the impacts and significant drivers of wildfires by dating and mapping recent wildfires in an Andean tropical forest area, the Iguaque mountains. A large part of Iguaque hosts a population of the only *Quercus species* in South America, *Quercus humboldtii*. We used remote sensing, official reports, and social mapping to reconstruct the recent history of wildfires and changes in oak forest patches in Iguaque. Between 1990 and 2017, 25 wildfires were recorded, with fire intervals between 4 and 21 years. These events burned 28.4% of the Iguaque mountains and showed a significant increasing trend in extent. Wildfires mainly occurred in the south, during the driest months, and their number and extent showed substantial interannual variations related to El Niño–Southern Oscillation cycles. Wildfires contributed to a 45% reduction in oak forests and the fragmentation of existing populations. Our study presents evidence of the extent and impact of wildfires in Iguaque and provides new insights into fire dynamics in Andean tropical forests.

KEYWORDS: Andean forests, climate change, Colombia, deforestation, ENSO cycles, fragmentation, oak forest management, *Quercus humboldtii*, wildfire.

Wildfires are a significant driver of environmental change globally (Geist & Lambin, 2001; Hosonuma *et al.*, 2012) and affect the dynamics, structure, and composition of plant communities and ecosystem services (Ahlgren &Ahlgren, 1960; TNC *et al.*, 2004). Although 21st-century global trends suggest a reduction in human-caused burning in many seasonally dry tropical areas due primarily to the expansion of developed agriculture in savanna regions (Andela *et al.*, 2017), the number, frequency, and extent of wildfires have increased in many forested (or formerly forested) areas worldwide (Simon *et al.,* 2004; Tansey *et al.,* 2008; Earl & Simmonds, 2018). Wildfire extent and frequency have been positively correlated with population density, proximity to roads and suburban areas, accumulation of dead refined fuel, and extreme weather conditions (Godoy *et al.*, 2019; Guillaume *et al.*, 2019). They have also been related to El Niño–Southern Oscillation cycles (ENSO; Barlow & Peres, 2004; Bianchi *et al.*, 2014).

Wildfires have affected 84% of the surface in the world's biodiversity hot spots (TNC *et al.*, 2004), and in Latin America alone, 51 million ha have burned in the last three decades (FAO 2005, 2013). However, wildfire records have only recently been maintained in most tropical Andean countries (Armenteras *et al.*, 2020). Moreover, those records are often incomplete, scattered, and sometimes contradictory regarding the affected area (Anaya-Acevedo & Chuvieco-Salinero, 2010). For example, the Colombian Andean region records show 295,300 ha burned between 2001 and 2007 (Anaya-Acevedo & Chuvieco-Salinero, 2010). Official reports from Colombia have been available since 1998 (UNGRD 2018). Between 2002 and 2013, 12,978 wildfires were reported, affecting 619,300 ha (IDEAM 2004). In 2015 alone, 3,985 wildfires were reported, affecting 150,000 ha in Colombia (García *et al.*, 2016). Some studies have investigated wildfire dynamics in

Colombia (Armenteras *et al.,* 2005, 2009a, 2009b; Muñoz, 2005; Amaya & Armenteras, 2012; Barreto *et al.,* 2017; Armenteras *et al.,* 2019, 2020), but many lack information about the detailed dynamics of wildfires, their impact in tropical mountain zones, and their relationship with land use, climatic conditions, and vegetation.

There is a need to understand better wildfire occurrence and dynamics in the tropical Andean region, where there have been significant changes in fire regimes during the last 2 million years, especially since human settlement began in the Late Pleistocene (TNC *et al.,* 2004; *Armenteras et al.,* 2019, 2020). For example, in Colombia, Paleo-ecological records confirm large wildfires during hot phases of the Pleistocene and the Holocene (significantly 11 000 years ago; González *et al.,* 1966; Van der Hammen, 1966; Kuhry 1988). During pre-Columbian times, fire was used in the Cundiboyacense highlands to clear vegetation and expand crops (Patiño 1965, 1997; Márquez, 2001). These practices intensified with European colonization until now, with forest and páramo vegetation converted to pastures maintained by frequent fires (Fals Borda, 2006; Mora, 2012). In some areas of the Colombian Andes, wildfire frequency has increased since pre-Hispanic times from one event every 1000 years to one event yearly owing to human intervention (Verweij, 1995; Vargas-R, 2002).

The Iguaque Mountains provide an example of the increasing frequency of wildfires in the Andean region. Its lowland areas have been used for intensive agriculture for a long time. Large extents of the mountain range were designated a National Park in 1977 because of their high socio-ecological value. Since then, the area has witnessed numerous wildfires, affecting soil stability, water quality, and landscape structure

(Villarreal *et al.*, 2017). Additionally, wildfires may have reduced the extent of the Andean oak (*Quercus humboldtii* Bonpl.) forest (Fernández-Méndez *et al.*, 2016).

Quercus humboldtii is endemic to the northern Andes (Nixon, 2006; Avella, 2016). It is the southernmost species of this genus in the Americas and belongs to the red oak group (subgenus *Erythrobalanus*; Nixon, 2006). Andean oak is distributed exclusively in the Panamanian Darien and Colombian Andes Mountains, along a broad environmental gradient ranging from 750 to 3450 m in elevation and 700 to 3000 mm mean annual rainfall (Rangel *et al.*, 2009; Rangel & Avella, 2011). In the Colombian Andes, historical transformations have reduced at least 60% of the original distribution of *Q. humboldtii* (Rodríguez *et al.*, 2004; Etter *et al.*, 2006). Some remnants of these forests have been protected, but these measures have been insufficient to arrest deforestation, wildfires, and the spread of invasive species (Avella, 2010; Salazar *et al.*, 2020).

Many *Quercus* species are fire-tolerant (Johnson *et al.*, 2002), owing chiefly to the concentration of dormant buds near the root collar (Espelta *et al.*, 2003). This trait facilitates rapid post-disturbance resprouting. Oak tolerance to fire depends on stem diameter, bark thickness, and fire intensity and frequency and is thus highly dependent on species (Johnson *et al.*, 2002; Pausas, 2017; Casals *et al.*, 2018). In North America, red oak species tolerate low to moderate fire intensities and relatively long fire intervals (more than 14 years; Johnson *et al.*, 2002; DeSantis *et al.*, 2010). Trees with a diameter at breast height (DBH) greater than 17.8 cm show a higher probability of surviving wildfires. The response of Neotropical oaks to disturbances such as a fire has yet to be discovered. In Mexico and Costa Rica, some oak species survive logging and fire (Aus der Beek *et al.*, 2006; Guariguata *et al.,* 2006). However, depending on fire frequency, regeneration may be arrested (Bonfil, 2006; González-Espinosa *et al.,* 2006). In Colombia, *Q. humboldtii* resprouts up to three years after the fire, but it is not clear which fire regime this species is adapted to or what the effects of fire on its regeneration are (Salazar *et al.,* 2020). Several studies have suggested that Andean forests in Colombia (including oak forests) are neither fire-prone nor fire-adapted (Páramo-Rocha, 2011; Armenteras *et al.,* 2020).

As in many forests of the tropical Andean region, the frequency and extent of wildfires in the Iguaque mountains have yet to be studied in detail. Consequently, their causes and consequences are mostly unknown. Knowledge of fire regime and its relationship with vegetation community composition, land use, and climate is key to understanding the temporal and spatial dynamics of *Q. humboldtii* forests and could help to protect biodiversity and sustain human wellbeing in these areas (Syphard *et al.,* 2008; Aguilar-Garavito *et al.,* 2019).

Here, we present a quantitative analysis of wildfire dynamics in the Iguaque mountains using three methodological approaches. With this study, we aim to answer the following questions: i) what is the frequency of wildfires in Iguaque? ii) Can we detect interannual trends in the magnitude and frequency of wildfires; iii) Is wildfire probability constant throughout the year and the mountain range? and iv) have wildfires affected oak forests' extent and spatial distribution?

METHOD

Study area

The Iguaque mountains (22,000 ha) are located in the Eastern Colombian Andes (5°36′02″–5°44′38″ N and 73°22′57″–73°31′20″ W; Figure 2.1), in Boyacá state. The protected area Santuario de Fauna y Flora Iguaque (SFFI; 2400 to 3890 m above sea level (asl); 6,750 ha) is surrounded by a buffer zone at lower elevations (2,200 to 24,00 m asl).

The Iguaque mountains extend over 22 km along two crests separated by the Cane–Iguaque watershed and are formed by structural sandstones of the Arcabuco Formation. To the south, shale outcrops create hilly landscapes. The topography is strongly wavy and broken, with slopes steeper than 15%. Soils are shallow, acidic, and moderately evolved (Villarreal *et al.*, 2017). The average annual temperature and precipitation of the whole range are 18°C (mean maximum 22°C, mean minimum 10°C) and 810 mm. Rainfall follows a bimodal distribution, with maxima in March–May, and September–November. The rainiest months are April–May, with 201 mm on average, and the driest months are December–February, with 40 mm on average. The rains also decrease the gradient towards the southwest (Villarreal *et al.*, 2017).

Páramo and Andean forests cover the northern part of the Iguaque mountains. In contrast, partly due to historical agricultural use and later abandonment, the south and southeast areas are covered by herbaceous vegetation on slopes and open shrublands on flat areas. Open *Quercus humboldtii* forests are currently confined to narrow discontinuous forest fragments along streams and river canyons (Marín & Betancur, 1997; Fernández-Méndez *et al.*, 2016). The Park's buffer area presents a mosaic of herbaceous and shrubby vegetation mixed with pastures, farmland, and recreational houses. Tourism activity has increased near Villa de Leyva over the last decades. This has intensified the demand for natural resources, mainly water, and promoted visitation by people unfamiliar with Iguaque. The situation may worsen shortly as neighboring villages pursue similar growth plans (Villarreal *et al.*, 2017).

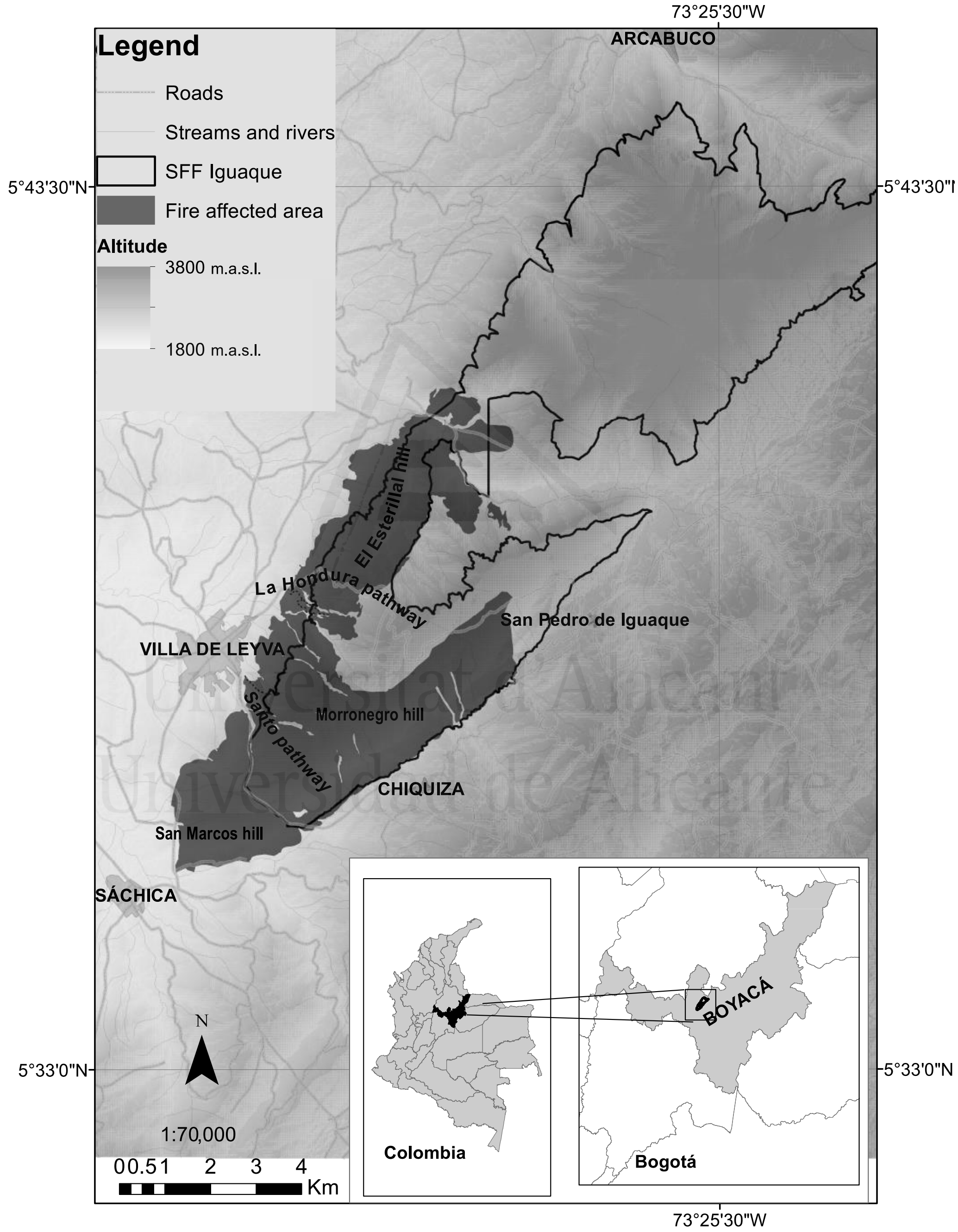

Figure 2.1. Location of the Iguaque mountains in Boyacá and Colombia.

Wildfire occurrence and location

We used free remote sensing images and GIS (geographic information systems) to draw the boundaries of wildfires between 1991 and 2015 and estimate their extent (Landsat, Rapideye, and Google Earth images from 1991, 2010, and 2015). We summarized this information in a 'remote sensing' GIS map. In addition, we reviewed official wildfire reports (SFFI 2006, 2014; 2016; Villa de Leyva 2012, 2014*a*, 2014*b*; UNGRD, 2018; Villarreal *et al.*, 2017). Again, we summarized the information from both sources in an 'official report' GIS map.

In September 2015, we conducted semi-structured interviews with 50 key informants, namely Park neighbors (31), public officers at the Villa de Leyva Mayor's Office (4), managers at SFFI (6), and local firefighters (9). We asked them to provide details on the dates and geographical extent of wildfires, including drawing a polygon for each wildfire using basic Iguaque topographic maps (1:25 000). We then summarized this information in the 'social wildfire' GIS map. Finally, we conducted our spatial analyses using ArcGIS *10* (ESRI 2015).

The trend in the burnt area

We used a non-parametric Mann–Kendall test ($\alpha \leq 0.05$ and Z statistic = 1.96, obtained from the standard normal table) to detect temporal trends in the burnt area. (Mann 1945; Kendall 1975). In addition, we employed the *mk.test* function in the *R* 'trend' package (R Core Team 2020; Thorsten, 2020).

Wildfire frequency

We estimated wildfire recurrence using the information contained in remote-sensing, official reports, and social wildfire maps utilizing map algebra and Boolean operators (union) for multicriteria analysis (Franco, 2011). First, we calculated the level of accuracy of the coincidence among maps obtained with the different data sources. Because we do not have field control points for past wildfire periods, we used the remote-sensing map as ground truth (reference map) and the recurrence of wildfires in official reports and social maps as classes (compared maps). Then, we built a confusion matrix and calculated the kappa index (Chuvieco-Salinero, 1990), using the count value per class, to estimate the correlations between the remote sensing map and the other maps.

Wildfires and climate

We explored the relationship between the number and extent of wildfires in Iguaque and ENSO cycles by using 336 monthly observations of the Ocean Niño Index (ONI) between 1989 and 2017 (NOAA, 2018). We then used a variety of statistical tests to assess these relations, as the sample size was small and wildfire probability low. First, we calculated Pearson and tau Kendall associate correlation coefficients as initial diagnostic methods to evaluate the degree of a simple relationship between both phenomena: wildfires and ONI, in a parametric and non-parametric way, respectively (Bratsas *et al.*, 2018; R Core Team 2020). Second, the number of wildfires obtained from official reports and ONI data was sufficient to conduct a time series analysis, including the computation of the autocorrelation function (ACF) and the cross-correlation function (CCF). Third, monthly wildfire counts were compared with monthly ONI. Finally, as we found that the series was not stationary, we computed the differences between consecutive observations just once. This is known as differencing (Hyndman &Athanasopoulos, 2018).

ACFs were examined for the wildfire counts and ONI data to assess serial autocorrelation, trends, and seasonality. Stationarity tests were performed before comparing CCF and ONI (Dickey–Fuller stationarity test) (Said & Dickey, 1984; Banerjee et al.,1993). To achieve these analyses, we used the Dickey–Fuller test, the ACF, and the partial autocorrelation function (PACF) to determine if the series were stationary. Further, finally, we applied the CCF. All analyses were implemented in the *R* package 'tseries' (Trapletti *et al.*, 2018; R Core Team, 2020).

Oak forest distribution and wildfires

We mapped the distribution of oak forests in the unburned and frequently burned areas of the Iguaque mountains using aerial photographs from 1970 and images from SPOT 2006 and Google Earth 2016. These maps were validated with data from a field survey. As access was difficult, we could not use a grid of random observations. However, the oak cover pattern obtained with aerial and satellite images was confirmed by statements made from spots where access was feasible.

We used the GIS and the formula of Puyravaud (2003) to calculate the following basic landscape metrics and compare 1970, 2006, and 2016 images: (1) the area covered by oak forests; (2) the average size of forest patches; (3) the largest forest patch; and (4) the number of forest patches (McGarigal *et al.*, 2012). Next, we validated forest fires and oak forest boundaries by performing a supervised classification (maximum livelihood algorithm), with training areas selected from multispectral images (Chuvieco-Salinero 1990, 2008). Finally, we compared the four landscape metrics mentioned above between the unburned area and the burned area, using the Pearson chi-square test (chisq. test in the

R ‘stats’ package) (R Core Team 2020) to assess the probability that any observed differences between the datasets were due to randomness.

RESULTS

Wildfire occurrence, location, surface burned, and trends

Using remote sensing images, we recorded 25 wildfires and 6236 ha burned in the Iguaque mountains between 1990 and 2017. The wildfire initiated on 24 February 2003 was the largest ever recorded in the mountain range, affecting 1300 ha (Figure 2.2). The southern ridges were the most heavily affected by wildfires. Fire extent showed a significantly increasing monotonic trend from 1990 to 2017 ($Z = 2.19$, $P < 0.05$, Figure 2.3).

Only six of the twenty-five dated wildfires affected more than 260 ha each (Figure 2.3) and were concentrated in the southern and central parts of the study area. Therefore, we considered these events the largest wildfires (600; 900; 1,300; 1,245; 477, and 887 ha; 24% of the total wildfires), which occurred only once a year. In contrast, most wildfires were smaller (19 events of 1–260 ha, 76%) and coincided with other small wildfires occurring during the same year.

Wildfires recorded in our work coincided with the fire records reported by environmental authorities since 1990 and the national information system since 1998. We also found records of additional wildfires from 1908, 1910, 1927, 1980, and 1986 in local reports from the Villa de Leyva Mayor’s office (SFFI 2006; Villa de Leyva 2014), but those events were excluded from our analysis because their geographical borders could not be mapped. Wildfires occurred exclusively during the driest months (Figure 2.4). 15 (60%) and 10 (40%) wildfires occurred between 20 August and 20 September, and 1 January and 28–29 February, respectively.

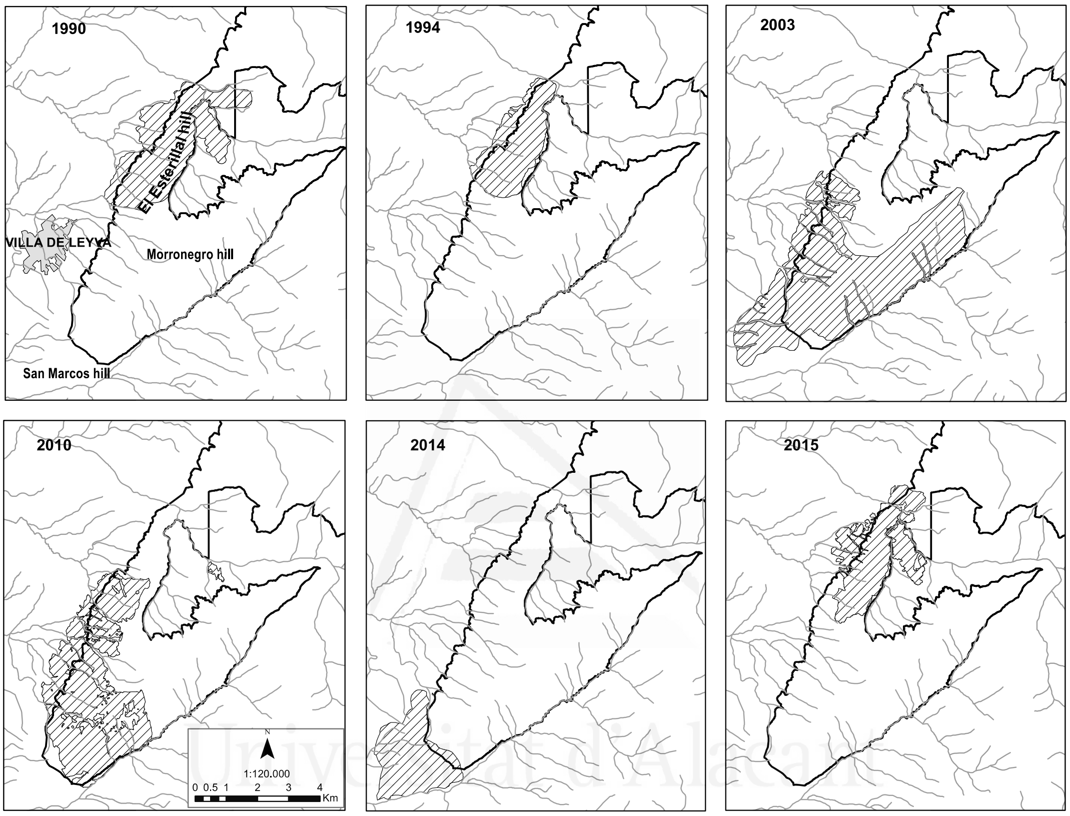

Figure 2.2. The geographical extent of significant wildfires occurring in the Iguaque mountains (Colombia) between 1990 and 2015 was estimated using remote-sensing images (Landsat, Rapideye, and Google Earth).

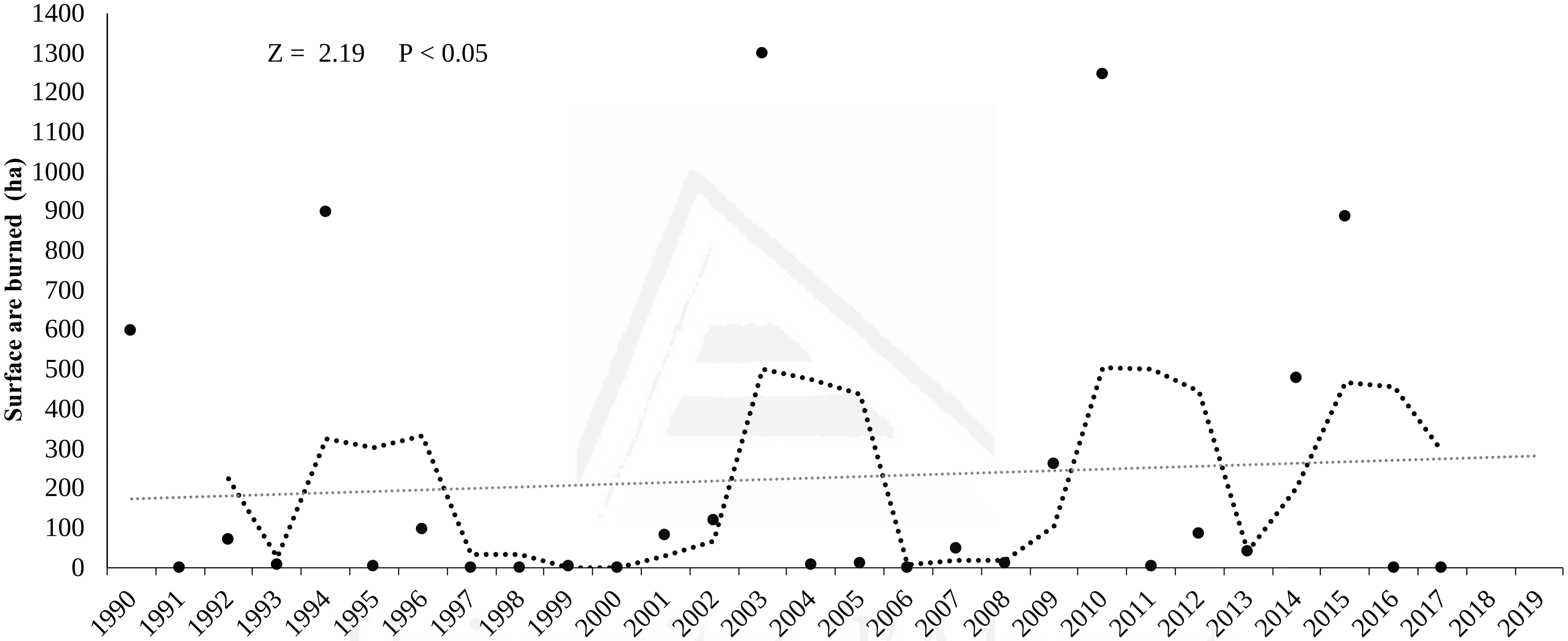

Figure 2.3. The surface area burned annually (dots), surface area burned 3-year moving average (thick dotted line), and linear surface area burned trend (thin dotted line) in the Iguaque mountains (Colombia), estimated from official reports and validated by analyzing.

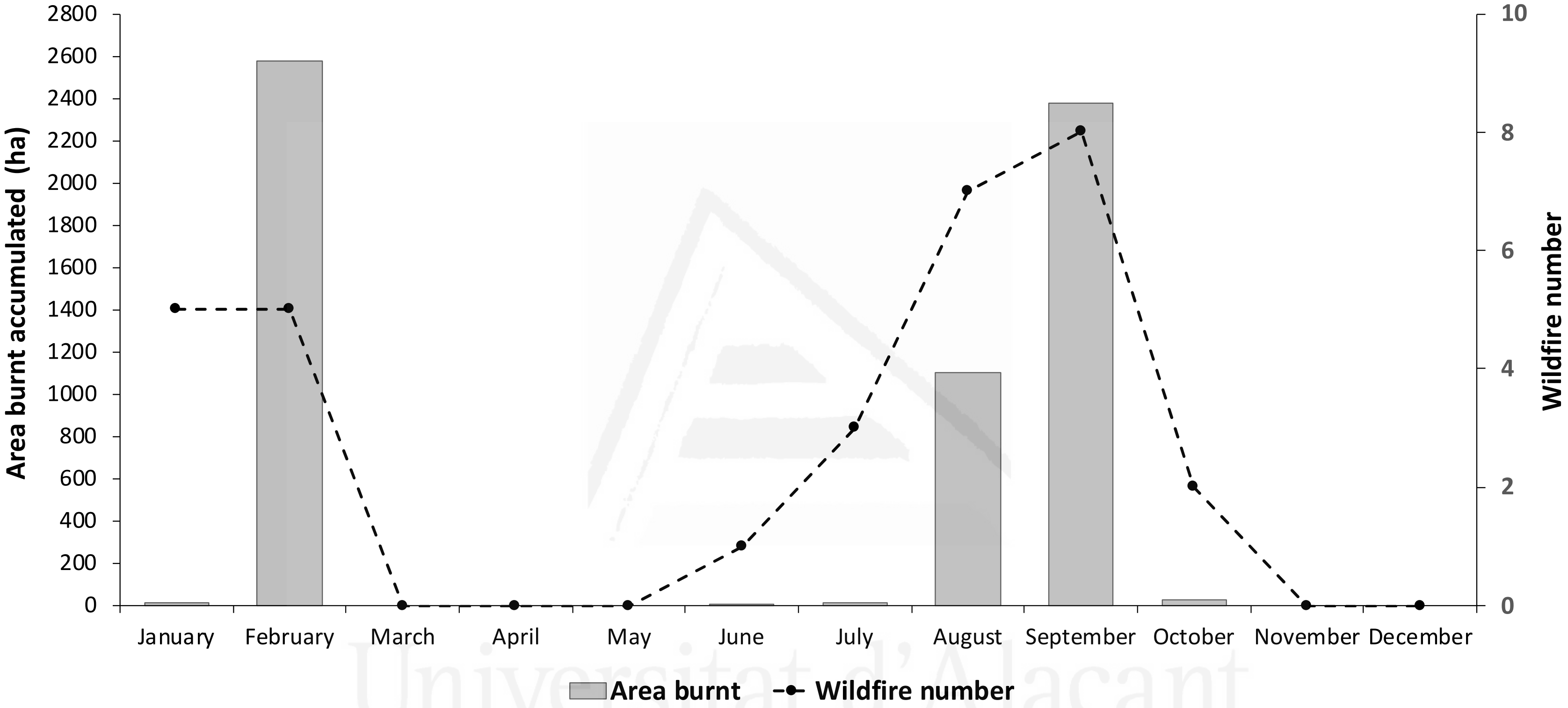

Figure 2.4. Monthly wildfire occurrence and surface area burned in the Iguaque mountains (Colombia) between 1990 and 2017.

Interview participants reported 20 wildfires between 1990 and 2015. SFFI officers and firefighters mentioned wildfires between 1940 and 1970, the oldest dates preserved in community memory. Wildfires were almost entirely anthropogenic. Interview respondents and official reports identified intentional causes such as uncontrolled agricultural and domestic waste burning (27%), hunting (13%), and retaliation aimed at environmental authorities (10%) as significant causes. More than one-third of the participants (36%) mentioned accidents caused by tourist bonfires, night torches, and fireworks. Finally, 14% of the interviewees suggested that drought (8%), certain types of vegetation (i.e., pine, grass, and common bracken, 4%), and lightning (2%) facilitated wildfires.

Wildfire frequency

Since 1990, the central part of the Iguaque mountains showed the highest wildfire recurrence and the peripheral areas the lowest (Figure 2.5). In addition, we found very high wildfire frequency around oak forest relicts – wildfires occurring in 1990, 1994, 2009, 2010, and 2015 directly impacted these forests. In the areas most affected by the fires, the social map showed a recurrence of seven fires. In contrast, the map of official reports and remote sensing images showed recurrences of five and four wildfires, respectively.

The social maps showed four areas with a frequency of six and seven fires in 27 years (589 ha), seven areas with four and five wildfires (1403 ha), and a larger number of sites with one to three wildfires (3190 ha) (Figure 2.5*c*). The analysis of maps obtained from official reports showed an intermediate frequency of wildfire compared with the other two maps but a significant coincidence in the high-frequency areas. According to the interviewees, wildfires have occurred almost annually since 1990 and were usually small. Both official reports and social maps showed a low degree of coincidence with the map derived from remote-sensing images (kappa index: 0.33 and 0.39; accuracy 33 and 39%, respectively).

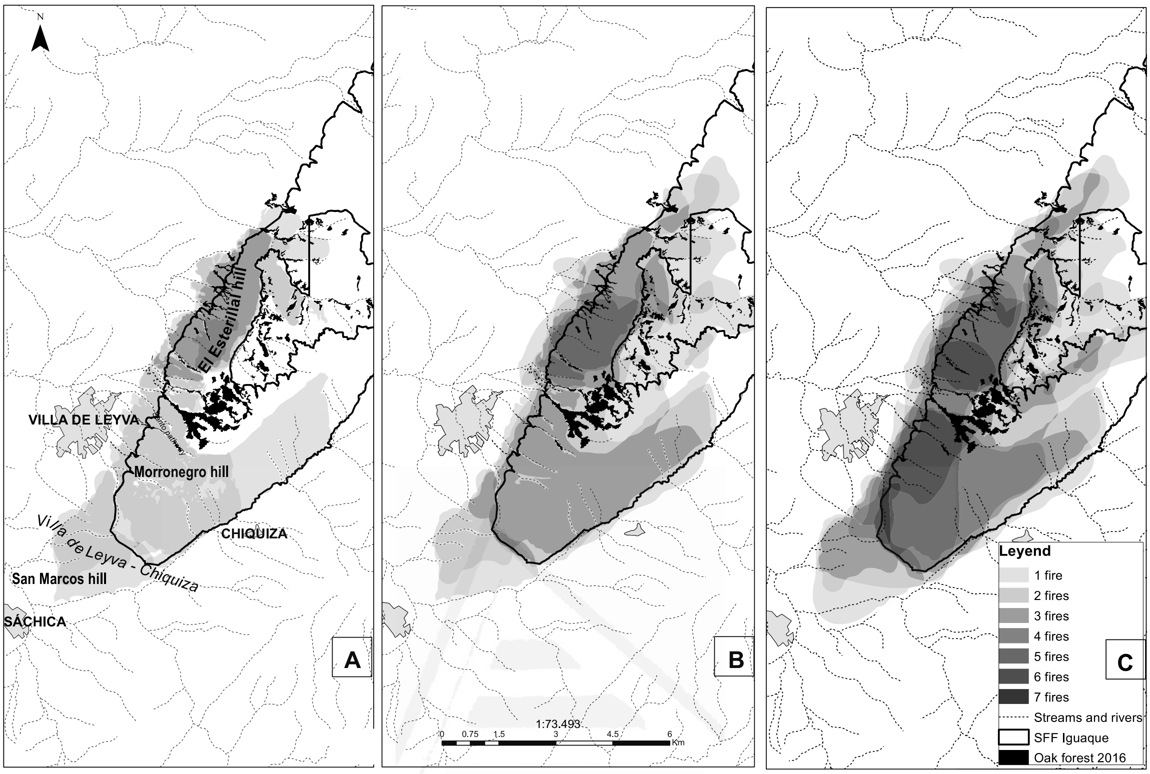

Figure 2.5. Wildfire recurrence between 1990 and 2015 in the Iguaque mountains (Colombia). Estimates are based on three different sources of information: (a) remote-sensing images; (b) official reports; and (c) social maps.

Wildfires and climate

We found a positive but weak correlation between ONI-ENSO and the annual percentage of burned area in Iguaque (Pearson's $r = 0.15$, $P = 0.006$, $n = 346$) and a weak association between the number of wildfires and ONI-ENSO (Kendall's tau = 0.076, $P = 0.08$, $n = 346$) (Appendix 2.1). In addition, the CCF (Appendix 2.2) confirmed the existence of a seasonal pattern in both climate and wildfires, with several significant positive correlations ahead of and behind the lags.

Wildfires and oak forest distribution

The extent of oak forests in the southwestern and western slopes of the Iguaque mountains was substantially reduced between 1970 (113 ha) and 2016 (51 ha; Figure 2.6, Table 2.1). This decline was paralleled by fragmentation of the original population: the number of patches increased from 27 to 34 during this period, while the average patch size decreased from 1.65 to 0.32 ha. Similarly, the largest forest patch's surface area was reduced from 36 ha in 1970 to 26 ha in 2016.

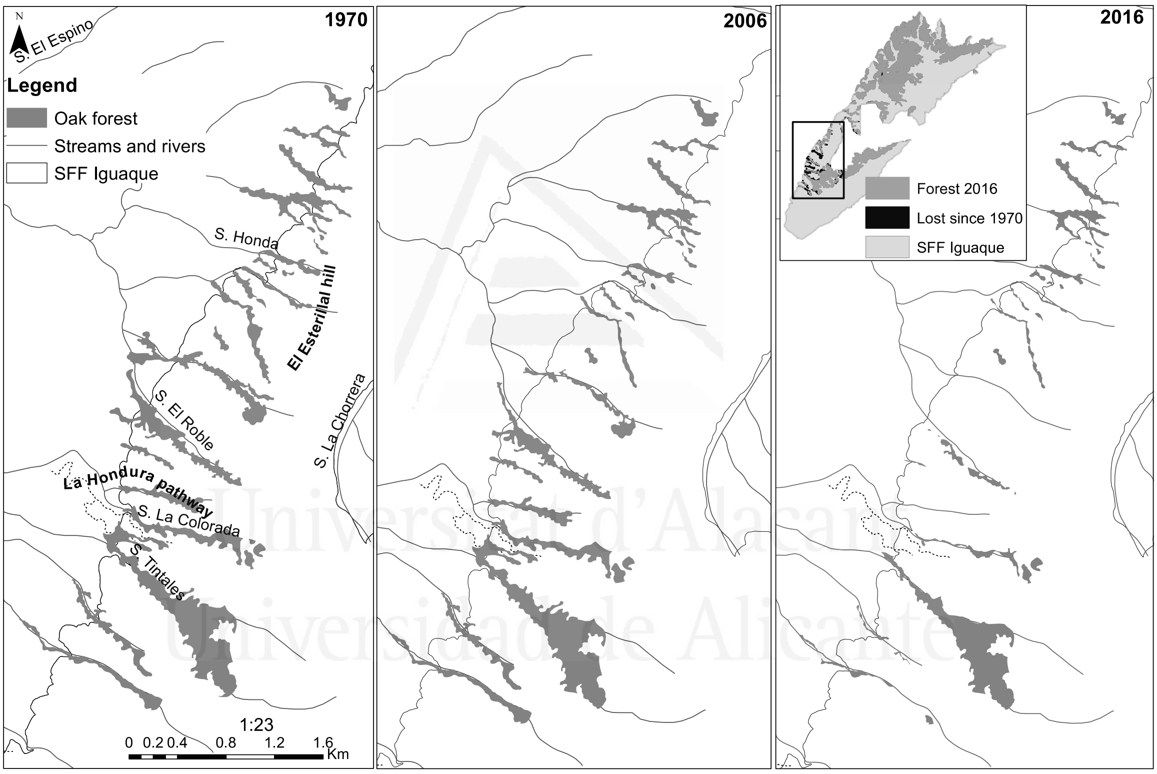

Figure 2.6. Oak forest distribution in the southwestern Iguaque mountains (Colombia) in 1970, 2006, and 2016.

Oak forest decline was restricted to the burned areas, as we found no evidence of wildfire in the northern range of the Iguaque mountains, and the forest loss rate between 1970–2006 and 2006–16 in these areas was virtually zero. We found a significant association between the previous occurrence of wildfires and (1) a reduction in the surface area covered by oak forest (Pearson chi-square test *df* = 2, *p* << 0.0001) and (2) the average size of forest patches (Pearson chi-square test *df* = 2, *p* << 0.0001) in the Iguaque mountains burned areas.

DISCUSSION

Wildfire dynamics and drivers

Wildfire frequency and extent in the southern sector of the Iguaque mountains showed substantial temporal variation. The burnt area showed a significantly increasing monotonic trend between 1990 and 2017. This aligns with observations made in other regions of Colombia (IDEAM, 2004; Armenteras *et al.*, 2005; Pabón-Caicedo, 2011; Rodríguez-Buriticá *et al.*, 2017; Aguilar-Garavito *et al.*, 2019; Armenteras *et al.*, 2019), Latin America (Manta & León, 2004; Chuvieco-Salinero *et al.*, 2008; Armenteras *et al.*, 2020) and some regions of the world (Boschetti *et al.*, 2006; Chen *et al.*, 2017; Earl & Simmonds, 2018).

Wildfires in Iguaque followed the ENSO cycles: the largest wildfires predominantly occurred during ENSO years, and wildfire occurrence was weakly but significantly related to ONI. Large wildfires have often shown consistent relationships with ENSO dynamics: during La Niña, plant biomass increases, and with it, the risk of wildfire during ensuing El Niño droughts (Kitzberger, 2002; Fuller & Murphy, 2006). Other studies describe ENSO effects on tropical wildfires (Kitzberger *et al*., 1997; Chen *et al*., 2017; Mariani *et al*., 2017), and indeed, ENSO may create the conditions for 20–30% of wildfires in tropical regions (Chen *et al*., 2017). Wildfires in Iguaque were concentrated mainly in the two periods of low rainfall (February and August–September), high temperatures, and southeasterly trade winds. They coincided with the largest tourist date visitation numbers to Villa de Leyva (Villarreal *et al*., 2017; Google Trends, 2020). These findings have important implications for the future of Iguaque ecosystems in the context of climate change and emphasize the need to develop a fire management program that integrates climate change scenarios.

In addition to climate, other interrelated factors probably influenced the wildfire regime in Iguaque, including an increasing human population density (Pausas, 2004; FAO, 2005; Bianchi *et al.,* 2014), land-use change (TNC *et al.,* 2004), biomass accumulation and fuel continuity (Fuller & Murphy, 2006; Bianchi *et al.,* 2014). For 500 years, tree felling, slash-and-burn techniques, intensive agriculture, and grazing have shaped the Iguaque landscape (Fals Borda, 2006; Mora, 2012; Villarreal *et al*., 2017). However, after the designation of the Iguaque mountains as a protected area (SFFI) in 1977, abandoning traditional land uses may have favored colonization by pioneer plant species and increased fuel accumulation and continuity (Fernández-Méndez *et al.,* 2016; Salazar *et al.,* 2020). Since 1977, farmers have not been allowed to clear vegetation for cropping and grazing, unregulated tourism has increased, and the resident population has decreased, reducing the chances of wildfire control.

Our interviews revealed the existence of socio-environmental conflicts due to the designation of the protected area, which may have increased the risk of intentional ignition. Interviewees identified social conflicts and poor management of human activities in the Park's buffer zone as significant causes of wildfires. Tourism has substantially increased in the study area over the last decades and has been suggested as an important driver of wildfire frequency (Villa de Leyva 2012, 2014*a*, 2014*b*, 2016; Villarreal *et al*., 2017;

Google Trends, 2020). Determining the importance of social factors in an increasing wildfire is crucial to designing effective management programs. These programs should involve strengthening the capacity for fire prevention, monitoring, and firefighting and expanding environmental education and awareness efforts. In addition, management programs can promote conservation agreements between SFFI, landowners, farmers, and the government and thus strengthen the regulatory framework.

The origin of wildfires in Iguaque was largely anthropogenic. Thus, the increase in urban and peri-urban populations (51% between 2005 and 2018; DANE 2005, 2020), in addition to insufficient knowledge about forest dynamics and wildfire risk, has likely led to an increase in the frequency of ignition (Pechony & Shindell, 2010; Knorr *et al.*, 2016). This anthropogenic origin agrees with national and international reports for Colombia and elsewhere (MAVDT 2002; IDEAM 2004; Pausas, 2004; FAO, 2005; Parra, 2011; Aguilar-Garavito *et al.*, 2019; Armenteras *et al.*, 2019, 2020).

Oak forest dynamics

A century ago, large extents of the southern watersheds of Iguaque were covered by dense, tall forests dominated by *Quercus humboldtii* and *Clusia multiflora* Kunth along streams, river canyons, ravines, plains, and low hills (Marín & Betancur, 1997; Rodríguez *et al.*, 2005; Mendoza-Cifuentes, 2017; Salazar *et al.*, 2020). In the southern Iguaque mountains, sub-xerophytic shrubs were dominant on the slopes, and open, low oak forests covered the low hills (Mora, 2012; Fernández-Méndez *et al.*, 2016; Mendoza-Cifuentes, 2017; Villarreal *et al.*, 2017). Since then, the Iguaque landscape has profoundly changed owing to a reduction in the surface area covered by oaks, increased fragmentation of oak populations, and the disappearance of forest patches (Fernández-Méndez *et al.*, 2016;

Mendoza-Cifuentes, 2017; Salazar *et al.*, 2020). These effects have been particularly intense in areas where wildfire recurrence was higher, especially where oak forests burned three to six times between 1990 and 2015, with fire return intervals of less than 21 years. The fire-free gaps in these areas may not be long enough to allow periodic oak recruitment (Johnson *et al.*, 2002; Salazar *et al.*, 2020). Consequently, the current fire regime in Iguaque may favor the establishment of a homogeneous shrubby grassland with isolated old trees, put oak populations at risk, and thus compromise forest resilience.

The incidence and effects of wildfires in the Iguaque oak forests have been reported elsewhere (Fernández-Méndez *et al.*, 2016; Salazar *et al.*, 2020) and support our results. However, this interaction has not been studied in other Colombian oak forests. Other studies have associated wildfires with a reduction in the surface area covered by different types of Andean Forest and páramos (Vargas-R, 2002; IDEAM, 2004; Muñoz, 2005; Parra, 2011; Amaya &Armenteras, 2012; Rodríguez-Buriticá *et al.*, 2017; UNGRD 2018; Aguilar-Garavito *et al.*, 2019).

Quercus humboldtii as a 'fire-persistent' tree that can resprout after a fire (Salazar *et al.*, 2020). Many other *Quercus* species also exhibit fire resistance (Johnson *et al.*, 2002; Espelta *et al.*, 2003), and in Mediterranean and temperate ecosystems, some oaks species have replaced other trees that cannot withstand frequent or severe wildfires (DeSantis *et al.*, 2010; Leverkus *et al.*, 2014). Nevertheless, in the Iguaque mountains, *Q. humboldtii* did not respond positively to wildfires. We speculate that the resprouting ability was quickly depleted in this species owing to the high frequency of fire such that the oaks could not withstand the recurrent fires. However, further studies on *Q. humboldtii* morphofunctional and reproductive responses to wildfires are needed before fully understanding the impact of wildfire on the oak forests described in our research.

In Iguaque burned areas, the structure of the plant community has shifted towards botanically impoverished shrubby grasslands (Marín & Betancur, 1997; Fernández-Méndez *et al.*, 2016), where highly flammable alien species thrive (*Pteridium aquilinum* (L.) Kuhn, *Melinis minutiflora* P. Beauv., *Andropogon lehmanii* Pilg. and *Heteropogon contortus* (L.) P. Beauv. Ex Roem. and Schult) (Fernández-Méndez *et al.*, 2016; Mendoza-Cifuentes, 2017). They provide fuel loads ranging from 4 to 35 Mg ha^{-1} (Aguilar-Garavito *et al.*, 2016). These formations correspond with Anderson's (1982) fuel models Type 3 and 4: dense grasslands, dense thickets or trees, high horizontal and vertical continuity, and abundant live and dead fuel accumulation (Rothermel, 1972; Albini, 1976). Fire spreads rapidly across these vegetation fuel types models, generating tall flames. These fuel models agree with the results of our interviews about fire behavior.

The approach to the wildfire problem in Iguaque and the Andean oak forests should consider a paradigm shift in fire management, which has historically been focused on fire suppression. Our results suggest that past management approaches may be insufficient and should be complemented with other measures, such as the reduction of fuel loads in the boundaries between farms and the protected area and the boundaries between forests and different land-cover types (urban, grasslands, shrublands) (Baeza *et al.*, 2002, 2006; Lloret, 2004). Prescribed fire at appropriate intervals and intensities and applied in strategic areas eventually could be a tool, in the short term, to reduce fuel loads and maintain open forest habitats with suitable conditions for oak regeneration (Johnson *et al.*, 2002). However, less aggressive alternatives should also be considered, such as the manual and mechanical removal of invasive plants. Studies to evaluate the technical and socioeconomic feasibility of such measures and their impact on ecosystems, landscape diversity, and function are necessary to design efficient management programs. Furthermore, vegetation management should focus on forest restoration by promoting oak recruitment and controlling invasive species.

Finally, the SFFI administration and the Mayor's Offices, environmental authorities, and fire departments around the Iguaque mountains should improve fire prevention programs and educate local people and tourists about fire risk, prevention, and management in the Iguaque mountains. Similarly, a landscape management strategy should include agricultural and peri-urban lands, the protected area, fuel quantity, and continuity reduction. It is also necessary to be more efficient in identifying and penalizing those who violate Colombian environmental legislation concerning wildfires (Prestemon *et al.*, 2019). These measures could help develop a wildfire management policy to prevent socio-ecological damage and losses caused by future fires in the Iguaque mountains (Moreira *et al.*, 2020).

CONCLUSIONS

Wildfires in the Iguaque mountains have been common in recent decades, particularly towards the south of the protected area. Using a combination of remote sensing, official reports, and social maps, we estimated the extent and dynamics of wildfires in sites with missing or non-standardized records. Our methodological approach can be extended to other places where wildfires have not been systematically documented.

Complementary techniques, like analyzing fire scars on *Quercus humboldtii* trunks, could further refine these maps, particularly for wildfires before 1990.

Our findings indicate that wildfires in Iguaque are associated with climate dynamics and human activities. Wildfires will likely increase shortly due to climate change, land-use change, and social habits. Wildfires have significantly contributed to reductions in oak forests' extent and their populations' fragmentation. Given the critical role that *Q. humboldtii* plays in community structure and ecosystem functioning, measures towards reducing the frequency and impact of wildfires and restoring degraded forests should be urgently pursued.

Our results suggest that a combined effect of land-use changes, wildfires, and increased tourism activities, accentuated in the last decade, are significant challenges for biodiversity management in the study region. Further, our study contributes to understanding wildfire regimes in Andean forests and Andean oak population dynamics. It provides essential insights into designing wildfire management strategies and creating biotic and social communities adapted and resilient to global change.

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SUPPLEMENTARY MATERIAL 2

Appendix 2.1. Correlation analysis to compare the relative surface area burned in the Iguaque mountains (Colombia) with El Niño Ocean Index (ONI).

Appendix 2.2. Cross-Correlation Function (CCF) plot for relative surface area burned in the Iguaque mountains (Colombia) and the El Niño Ocean Index (ONI) series.

CHAPTER 3. The current fire regime in northern Andean shrublands hinders tree recruitment and arrests forest succession.

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The current fire regime in northern Andean shrublands hinders tree recruitment and arrests forest succession.

ABSTRACT

The northern Andes is a biodiversity hotspot. However, historical land use and the current increase in wildfires have profoundly altered the landscape. There is an urgent need to understand how successional processes and wildfires operate to support biodiversity management in this region. We studied the effect of wildfire frequency and time since the last fire on vegetation regeneration patterns in a heavily transformed northern Andean landscape. In the past, Andean forests were typical in this region. *Quercus humboldtii*, the only *Quercus* species native to South America, was frequent in these forests. Using the Iguaque mountains (Colombian Andes) fire map, we selected areas with different fire frequencies (three and five fires in thirty years) and the time since the last fire (one to six years) to study post-fire vegetation structure and composition. Resprouting herbs and small shrubs dominated post-fire communities, and their design was closer to subpáramo vegetation (greater richness and density of shrubs than tree species) than to Andean forests. Indeed, forest species were virtually absent from burned sites, as were obligate seeders. The richness, density, and cover of herbaceous species returned to pre-fire levels soon after the fire.

In contrast, the richness and density of small and large shrubs increased one to six years after the last fire. Fire frequency did not affect the composition and structure of the herbaceous layer in the current study.

Conversely, there was a general trend towards a reduction in species richness, cover, and the proportion of obligate resprouters of woody species, which was only significant for the basal area of large shrubs and trees. Exotic species were largely herbaceous and were dominated by *Andropogon lehmannii* and *Melinis minutiflora*. Their cover increased from the first (3.6%) to the sixth (34.3%) year after the fire but decreased with fire frequency (3.6 to 2.2%). In contrast, *Pteridium aquilinum* cover increased on recently burned sites, reaching between 12 and 17.2% on average. Our results show that current wildfire regimes in the Iguaque Mountains favor the persistence of fire-tolerant herbs and shrubs, compromise tree recruitment, and arrest forest succession. Therefore, new integrated fire management strategies are needed to protect remnant forests and establish oak forests in burned shrublands.

KEYWORDS: auto-succession, Fire regime, Postfire vegetation, *Quercus humboldtii*, Successional trajectory, Tropical Mountain ecosystems.

The northern Andes are a biodiversity hotspot and supply many benefits to local communities (Meyers *et al.*, 2000; Olson & Dinerstein, 2002). Its high diversity of ecosystems, the richness of rare and endemic species, and the supply of fresh water and raw materials for humans are some of its main characteristics. However, approximately 60% of northern Andean ecosystems are extensively altered (Rodríguez *et al.*, 2006; Etter *et al.*, 2008). Deforestation, agriculture, grazing, and wildfires are the main drivers of this transformation (MADS, 2015). Moreover, in most cases, these drivers have operated intensely and simultaneously. It is important to note that most of the wildfires in the northern Andes are currently of anthropogenic origin (Aguilar-Garavito *et al.*, 2020; Armenteras *et al.*, 2020).

Biodiversity managers have adopted measures to conserve biodiversity in these transformed landscapes of the northern Andes, such as creating natural protected areas and allowing passive restoration (MADS, 2012; Echeverry-Galvis *et al.*, 2019). However, these actions have not been sufficient and, in some cases, have favored further disturbances and land abandonment by farmers (MADS, 2015; Villarreal *et al.*, 2017).

After land abandonment, succession in the northern Andes may follow multiple pathways (Arroyo-Rodríguez *et al.*, 2017). The plant community can recover after disturbance in scarcely transformed landscapes, such as those dominated by a forest matrix and little human intervention. (Sarmiento, 1997; Lippok *et al.,* 2013). Conversely, in highly disturbed landscapes, such as rural landscapes, with invasive species or change in the disturbance regime, ecological succession is often arrested (Zahawi & Augspurger, 1999; González-Rivas *et al.*, 2009; Hobbs *et al.,* 2009), resulting in a persistent mosaic of shrubs, ferns, lianas and grasses (Lippok *et al.*, 2013; Arroyo-Rodríguez *et al.*, 2017).

According to Royo and Carson (2006), The expansion and monopolization of the landscape by a narrow set of plant species is often the unintended result of policies and management decisions that deviate from natural vegetation disturbance regimes. These alterations involve changes in the frequency and scale of disturbances, which release a restricted species from the forest's original competitive constraints. Once released, these species dramatically increase their abundance and cover large landscape areas. However, after establishment, this resistant vegetation layer interferes with tree regeneration through several direct and indirect mechanisms, including competition, allelopathy, microhabitat-mediated seed (or seedling) predation, litter accumulation, and mechanical damage. Consequently, this recalcitrant layer inhibits tree regeneration and dramatically influences the species that establish and survive under its canopy.

Under novel ecosystem conditions exacerbated by climate change, wildfires now play a role as a generator of environmental change and a benefit to species that can regenerate after this disturbance. Over the last decades, the surface area burned has increased in tropical regions (Brando *et al.*, 2019; Godoy *et al.*, 2019; Cardil *et al.*, 2020) and northern Andes (Armenteras *et al.*, 2020), affecting biodiversity hotspots (Earl & Simmonds, 2018; Finer & Mamani, 2019). For biodiversity management in these heavily anthropized north Andean landscapes, it is critical to understand fire dynamics, vegetation response to wildfires, and the drivers of post-fire succession.

The impacts of wildfires on community composition and ecosystem functioning largely depend on fire history, i.e., the extent to which wildfire occurrence has shaped the physical environment and acted as an evolutionary driver (Pausas *et al.*, 2017; He *et al.*, 2019). Plant communities may show high resilience to fire when its occurrence elicits evolutionary responses, whereas resilience to fire may be low when species are not adapted to it (Bellingham & Sparrow, 2000; Schumacher & Bugmann, 2006). Resilience may be conferred by the species' capacity to endure fire, regenerate from resprouts and seeds, and thrive under postfire conditions (Pausas, 1999; 2006).

The increasing occurrence of wildfires in areas where these disturbances were historically rare may exclude fire-intolerant species and reduce the richness of native species (Eugenio *et al.*, 2006; Russell-Smith *et al.*, 2010) while enhancing colonization by fire-adapted species and eventually triggering a shift toward fire-adapted communities (Neary *et al.*, 1999; Leishman *et al.*, 2007). The increase in niche availability after a fire may also facilitate colonization by exotic and invasive species, either as a direct short-term effect of the disturbance or as a lasting effect of species exclusion (Vargas, 2000; Brooks & Lusk, 2008). Exotic and invasive species may, in turn, modify wildfire regimes and initiate auto-successional cycles (Zouhar *et al.*, 2008; Schaffhauser *et al.*, 2012a).

Catastrophic shifts in community composition and ecosystem functioning depend on many interacting factors, including the ecological traits of local species and potential colonizers, soil and climate conditions, and fire frequency and severity (Jucker Riva *et al.*, 2016; van den Elsen *et al.*, 2020). Consequently, nonlinear dynamics and multiple interacting drivers hamper the ability to generalize and increase uncertainty in model predictions and management strategies (McWethy *et al.*, 2019).

In the northern Andes, paleoecological evidence, such as charcoal, suggests that wildfire frequency was low during the Pleistocene (between centuries and millenniums) and remained down during the Holocene (González *et al.*, 1966; van der Hammen, 1966). In pre-Columbian times, the fire was periodically used in slash-and-burn systems (Patiño, 1965; Jantz & Behling, 2012). These practices intensified after European colonization in the early 16th century (Castilla-Beltrán *et al.*, 2018; Koch *et al.*, 2019), as large extents of forest were transformed into crops and pastures (Molano, 1995; 1996; Mora, 2012). More recently, fires have played a significant role in northern Andean ecosystems (Dull *et al.*, 2010; Valencia *et al.,* 2010). Wildfire frequency has increased from one event every 1000 years, 2500 years ago, to one event every 2 to 10 years since the mid-20th century (Horn, 1986; 1989; Verweij, 1995). This shift in the wildfire regime can profoundly impact the composition of northern Andean ecosystems and the ecosystem services they provide (TNC *et al.,* 2004; Armenteras *et al.,* 2020).

Currently, oak forests, dominated by Andean oak (*Quercus humboldtii* Bonpl.), occupy 4,858 ha of the northern Andes, 28% less than its pre-Columbian distribution (Rangel, 2000; Etter *et al.,* 2008). Since the early twentieth century, oak forests have been affected by land occupation (Bello, 2006), wood harvesting for tools, collection of raw materials for several types of construction, domestic and industrial fuel supply, and other uses (Solano & Vargas, 2006; Avella & Cardenas, 2010). As a result, many *Q. humboldtii* populations were lost, and the species was classified as vulnerable on the Red List tread (Calderón *et al.,* 2002; Solano *et al.,* 2005).

Andean oak is the only *Quercus* species in South America, and it colonized the northern Andes 250,000 to 470,000 years ago (van der Hammen *et al.,* 2008). Like other *Quercus* species (DeSantis *et al.,* 2010; Leverkus *et al.,* 2014), *Q. humboldtii* is a fire-resistant tree that can resprout from roots, stump, and crown to three years after a fire (Salazar *et al.,* 2020). However, the impact of the wildfire regime on oak regeneration has yet to be studied. Furthermore, Andean forests in Colombia, including oak forests, may not be adapted to fire (Armenteras *et al.,* 2020). Only a reduced set of native plant species may withstand increased fire frequency and severity.

In Colombia, the Iguaque Mountains offer a unique opportunity to study post-fire vegetation dynamics in heavily human-transformed Andean landscapes intended for conservation. In the Iguaque Mountains, oak forests are valuable for their uniqueness, high levels of biodiversity, and the ecosystem services they provide to local communities (Villarreal *et al.*, 2017). Previous studies revealed that the frequency of wildfires had increased south of the Iguaque Mountains in recent decades (Aguilar-Garavito *et al.,* 2020). Wildfires affect both successional vegetation and remnants of oak forests (Fernández-Méndez *et al.,* 2016; Aguilar-Garavito *et al.*, 2020). Wildfires have likely favored the recent decrease in oak forest cover and accelerated fragmentation (Aguilar-Garavito *et al.*, 2020). Furthermore, invasive species such as Pteridium aquilinum (L) Kuhn are abundant in burned areas, and its cover may increase with recurrent fires (Fernández-Méndez *et al.*, 2016; Salazar *et al.*, 2020).

In this study, we examined the effects of fire frequency and time since the last fire on the composition and structure of early successional vegetation in the Iguaque Mountains, following several decades of abandonment after a historical and intense transformation. More specifically, we tested the following hypotheses: i) increased fire frequency and reductions in the time since the last wildfire are likely to be negatively associated with the richness, density, cover, and basal area of vegetation; ii) Richness and cover of grasses and other exotic herbaceous plants increase under the current fire regime. We also give special attention to oak forest species' presence and resprouting ability.

METHODS

Study area

The Iguaque Mountains (22,000 ha) are located in the northern Andes, on the western slope of the eastern mountain (Cordillera Oriental, the name in Spanish) range of Colombia (5°36'02 "- 5°44'38" N and 73°22'57 "- 73°31'20" W, Figure 3.1), in the Boyacá Department. The area comprises the protected natural area Santuario de Fauna y Flora Iguaque (SFFI; 2,400 to 3,890 m; 6,750 ha) and is surrounded by a protected buffer zone at lower elevation (2,200 to 2,400 m), where agricultural and livestock uses and deforestation are regulated.

The landscape is hilly, and the topography is strongly wavy and broken, with slopes steeper than 9°. The soils are shallow, acidic, moderately evolved, and formed by structural sandstones of the Arcabuco Formation (Villarreal *et al.*, 2017). The average annual temperature and precipitation of the whole range are 18°C (average max. 22°C, average min. 10°C) and 810 mm, respectively. Rainfall follows a bimodal distribution, with peak precipitation between March-May and September-November. The rainiest months are April-May, with 201 mm on average, and the driest months are December-February, with 40 mm on average. Rainfall decreases toward the southwestern area (Villarreal *et al.*, 2017).

The southern ridges of the Iguaque Mountains have been intensely affected by deforestation, agriculture, and grazing (Mora, 2012). As a result, soils are degraded, and rocky outcrops are abundant. However, some fragments of *Q. humboldtii* forest along streams and river canyons persist. In contrast, wildfires are uncommon on the northern ridges, where land use intensity has historically been low. These areas, on average 5 km from the wildfire-affected zone, present preserved native vegetation. Between 2400 and 3200 m elevation, they are dominated by conserved Andean oak forest and above 3200 m elevation by subpáramo and páramo (Mendoza-Cifuentes, 2017).

With the declaration of the SFFI in the 1970s, anthropogenic pressure on most of the landscape decreased, which allowed the colonization of native and exotic grasses and shrubs (Fernández-Méndez *et al.*, 2016; Villarreal *et al.*, 2017). Subsequently, recurrent wildfires affected successional communities reaching the remaining forest patches (Aguilar-Garavito *et al.*, 2020). In a previous study, we recorded twenty-five wildfires in the Iguaque Mountains between 1990 and 2017, affecting an accumulated area of 6236 ha (Aguilar-Garavito *et al.*, 2020). This corresponds to local wildfire recurrence ranging from one to seven events in 30 years. However, the fires were relatively small (73% of wildfires covered less than 260 ha), and their occurrence was related to different factors: El Niño Southern Oscillation (ENSO) cycles, high fuel accumulation, unregulated tourism, agricultural activities at the wild-rural interface and socioenvironmental conflicts.

Site selection

We identified three areas on the southwestern ridges that were affected differently by wildfires in terms of fire frequency (3 and 5 fires since 1990; FR3-1 and FR5-1, respectively) and time since the last fire (1 and 6 years; FR3-1 and FR3-6). We compared the FR3-1 areas (low frequency and short time) to sites with higher fire frequency but a short time (FR5-1) and longer time since the last wildfire (FR3-6) but with low wildfire frequency. These fire regimes are standard in the southern Iguaque Mountains.

Accessibility, climate, soil properties, and topography were similar in all areas (Figure 3.1, Table 3.1). FR3-6 burned in 2003, 2009, and 2010. FR3-1 burned in 1990, 1994, and 2015. Finally, FR5-1 burned in 1990, 1994, 2003, 2010, and 2015. In these areas, we established transects at elevations ranging from 2,400 to 2,800 m asl and on slopes ranging from 20° to 40°. Ridges and steep valleys were excluded during site selection to avoid azonal conditions.

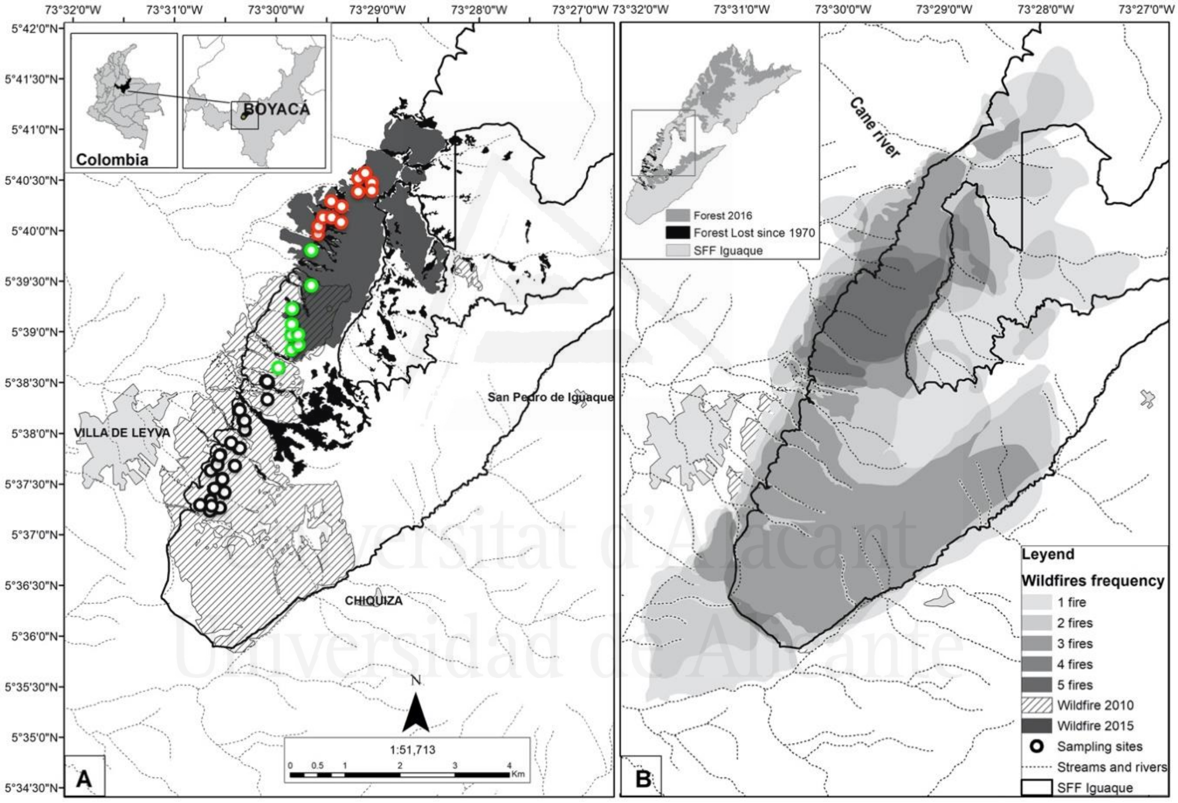

Figure 3.1. Location of the Iguaque Mountains in Boyacá Department, Colombia, northern Andes, and the area affected by wildfires in 2010 and 2015 (A). Wildfire frequency between 1990 and 2015 (B). Dots represent the sampling sites, black FR3-6 (six years and three wildfires), red FR3-1 (one year and tree wildfires), and green FR5-1 (one year and five wildfires).

Vegetation survey

We modified Rangel and Velázquez's (1997) methods to analyze community plant composition, richness, density, and cover (%) in different vegetation layers; trees and large shrubs, small shrubs, and herbaceous layers.

We established replicated transects of 50 x 4 m separated by at least 150 m (north–south oriented). We also estimated environmental factors in each transect, such as elevation (m) and slope (%). We set up nineteen transects for FR3-6 and ten for the other two fire regimes. Along each transect, we measured the diameter at breast height (DBH > 2.5 cm to 130 cm in height) and stem height of trees and large shrubs. We also established three 4 x 4 m plots randomly distributed along each transect (57 plots for FR3-6, 30 plots for FR3-1, and 30 plots for FR5-1) and measured the basal stem diameter (BSD > 1 cm, DBH < 2.5 cm to 130 cm in height) and stem height of small shrubs. Finally, we established one 1 x 1 m quadrat in the center of each plot (57 for FR3-6, 30 for FR3-1, and 30 for FR5-1) to survey the herbaceous and seedling layers. We recorded the cover (%) of all individuals with BSD < 1 cm in these quadrats. The potential differences between fire regimes are caused by the studied factor and not by the aggregation of sampling points within the same area.

We estimated the stand basal area at the base of the stem (small shrubs) and a 130 cm height (large shrubs and trees) by calculating the cross-sectional area of all individuals in the sampling units, assuming circular stems for BSD and DBH. We evaluated the cover in the herbaceous layer as species cover (Fehmi, 2010). The cover of each herbaceous species in the quadrat was assessed independently of the cover of other species. Therefore, it is the independent aerial cover of each species, expressed as a percentage of the area occupied by each species in each quadrat. Vegetation surveys were completed between August and December 2016.

Table 3.1. A sampling design was used to study the effect of the fire regime on plant community composition and structure in the Iguaque Mountains.

Fire regime	Last fire date	Fire dates since 1990	Transects (Large shrub layer)	Plots (Small shrub layer)	Quadrats (Herbaceous layer)
FR3-6	2010	2003, 2009, 2010	5	15	15
			5	15	15
			4	12	12
			5	15	15
FR3-1	2015	1990, 1994 2015	2	2	6
			2	2	6
			3	3	9
			3	3	9
FR5-1	2015	1990, 1994, 2003, 2010, 2015	3	3	9
			3	3	9
			2	2	6
			2	2	6

We checked most of the specimens and their determinations in JSTOR Global Plants (JSTOR, 2019), the Colombian plant catalog (Bernal *et al.*, 2016), and the TROPICOS database (TROPICOS, 2019). Finally, for Angiosperm families and genus grouping, we use the APG III proposal (Stevens, 2001).

Plant regenerative strategy and exotic species

We classified species according to the type of postfire regenerative strategy (Bond & Midgley, 2001; Paula *et al.*, 2009): resprouting species (plant species that persist in the burned area and grow mainly from vegetative structures, bark, or underground have protected), obligate seeders (species with a high germination capacity after the fire, whose primary strategy is to generate a fire-resistant seed bank), and facultative species (species using both strategies, without one necessarily being dominant over the other). In all cases, field observations confirmed the findings of previous studies concerning regenerative strategy. Then, we calculated the proportions of individuals showing the different methods per sampling unit.

We also classified species according to their distribution and invasive potential (Blackburn *et al.*, 2011), where species were identified as native species (species that inhabit an area within their natural past or present range) and exotic species (species outside their natural history or current scope; Baptiste *et al.*, 2010; Cárdenas-López *et al.*, 2017). We obtained the data from the Humboldt Institute's online catalog of biological information (Instituto Humboldt, 2020) and other published studies (Vargas, 2000; Cárdenas-Arévalo & Vargas, 2008; Mendoza-Cifuentes, 2017; Vasquez-Valderrama & Solorza-Bejarano, 2018).

Data analysis

We estimated sampling efficiency through species accumulation curves of species richness estimators (Moreno & Halffter, 2000). Species accumulation curves were nearly asymptotic across all fire regimes, indicating that the sampling scheme allowed a rough estimate of the number of plant species present in the current fire-transformed and fire-affected landscape (Appendix 3.1).

Based on all vegetation data, we used canonical correspondence analysis (CCA; ter Braak, 1986) to examine patterns in plant community composition and responses to fire regime and environmental factors (elevation and slope) and tested the significance of the predictor variables and the whole model.

We assessed the impact of fire frequency and time since the last fire on species richness and individual density whit PERMANOVA (Anderson, 2001) using Euclidean distance and 999 permutations (Significant $p < 0.05$). Next, we used the Wilcoxon Mann Whitney Test (Significant $p < 0.05$) to evaluate the fire frequency and time since the last fire on herbaceous species cover, small shrubs stump basal area, large shrubs basal area, exotic species cover and obligate resprouting species proportion.

Proportions were transformed using the arcsine of the square root of each variable $arcsin(\sqrt[2]{X})$ (Schmider *et al.*, 2010; Magnifico, 2016). Other variables were transformed by calculating the square root, i.e., $\sqrt[2]{x + 0.5}$, to correct for deviations from normality and homoscedasticity (Shapiro–Wilk and Fisher–Levene tests, respectively). After transformation, all variables were homoscedastic but were not normally distributed. All statistical procedures were performed using R statistical computing software, precisely, the packages 'BiodiversityR,' 'funrar,' 'ggplot2', 'reshape,' 'tidyr,' 'vegan' and 'pwr' (R Core Team, 2020).

RESULTS

Plant community composition

The vegetation types in the study areas (in the three fire regimes) ranged from open shrubby grasslands to closed shrublands. The herbaceous layer was dominated by grasses, herbs, and stemless rosettes (Appendix 3.2). Exotic species, such as *P. aquilinum, A. lehmannii*, and *M. minutiflora*, were abundant in this layer (average cover 19.2%, maximum cover 25.4%). Small shrubs were abundant and reached an average height of 99.4 ± 1.78 cm. This layer was dominated by native phanerophytes such as *Dodonea* *viscosa*, *Bejaria resinosa*, *Miconia squamulosa*, *Morella parvifolia*, and *Ageratina glyptophlebia* and species with caulescent rosettes such as *Espeletiopsis pleiochasia* and *Puya bicolor.* Large shrubs and trees were scarce and dominated by *Myrsine coriacea, Clethra fimbriata, Cestrum buxifolium, Ilex kunthiana,* and *Symplocos theiformis.* The average stem height was 165 ± 8.06 cm.

We recorded 1738 individuals of 87 species, 72 genera, and 39 families, corresponding to a density of 0.22 individuals m^{-2}. The families with the most significant number of species were Asteraceae (25 spp.), Poaceae and Rubiaceae (6 spp.), Ericaceae (5 spp.), Melastomataceae (4 spp.), and Solanaceae (3 spp.). The most widely represented genera were *Baccharis* (4 spp.), Ageratina, and *Chromolaena* (3 spp.), all from the Asteraceae family. *B. resinosa* showed the most significant number of individuals (0.03 individuals m^{-2}), followed by *D. viscosa* (0.025 individuals m^{-2}), *P. aquilinum* (0.02 individuals m^{-2}), and *E. pleiochasia* (0.016 individuals m^{-2}).

The ordination model explained a highly significant amount of the variation in plant community composition ($X^2 = 0.82$, $p < 0.05$, N = 4; Fig. 2). However, the proportion of variance explained by axes 1 and 2 (18.4%) was relatively low. All predictors in the analysis were significant. Axis 1 was related to the fire regime, as it segregated FR3-6 sites from FR3-1 and FR5-1 sites. Axis 2 was related to slope and elevation: positive values corresponded to high, flat areas. This gradient was less evident for recent wildfires.

The CCA (Figure 3.2, Appendix B) describes the plant community composition in different areas of the Iguaque mountains affected by fire and groups the sampled sites according to fire regimes (FR3-6: black, FR3-1: red, and FR5-1: green). The one-year post-fire sites (FR3-1 and FR5-1) shared a high number of species and showed apparent differences in species composition to the six-year post-fire sites (FR3-6). In this last wildfire regime, there is some internal differentiation in species composition among sites according to plot elevation.

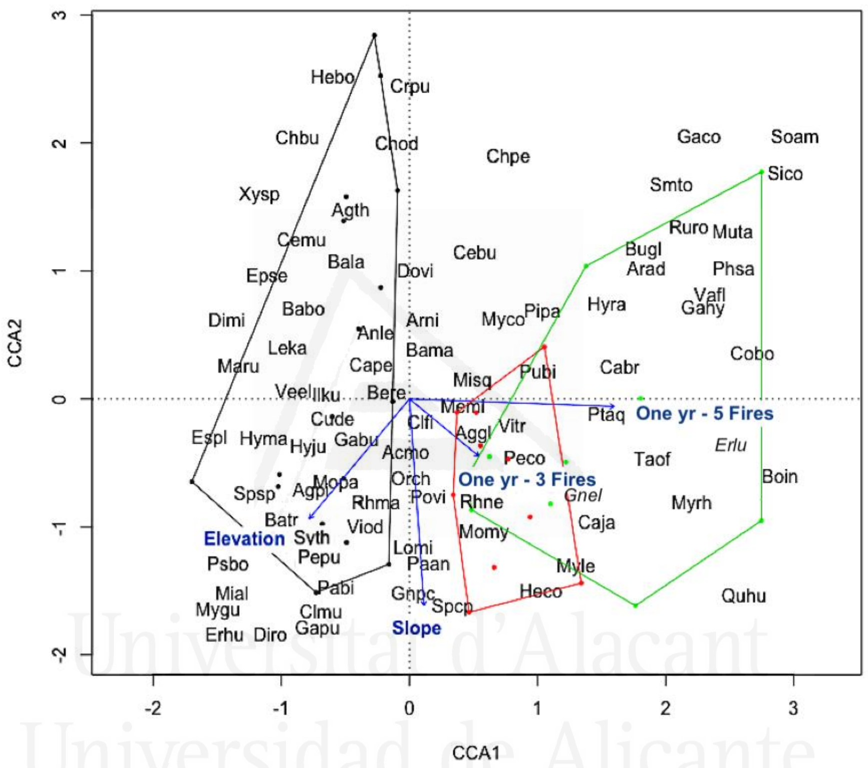

Figure 3.2. Canonical correspondence analysis (CCA) describing plant community composition in different areas of the Iguaque Mountains affected by the fire. Polygons correspond to fire regimes FR3-6 (black, six years and three wildfires), FR3-1 (red, one year and tree wildfires), and FR5-1 (green, one year and five wildfires). Vectors represent explanatory variables. Abbreviated names in black identify species (see Appendix 3.2 for the complete list of names), and sampling sites are shown as colored dots.

Vegetation patterns and time since the last fire

Herbaceous species richness, density, and cover were higher at sites six years after the last wildfire than at sites one year after the last of the three wildfires (Figure 3.3,

Appendix 3.3. to 3.8). The cover of *A. lehmannii,* other exotic species, and, marginally, *P. aquilinum* was higher six years after the fire than one year after this disturbance. Conversely, the cover of obligate resprouting herbaceous species decreased with time since the last fire (Figure 3.3, Appendix 3.6 and 3.7).

Small shrubs' species richness and stem density increased from year one to year six after the fire (Figure 3.3, Appendix 3.3 to 3.5). The trend was similar for large shrubs and trees. Basal area and the proportion of obligate seeders of woody species were similar one and six years after the fire.

Vegetation patterns and fire frequency

Fire frequency did not affect the species richness, density, cover, and proportion of obligate resprouters of the herbaceous layer or the cover of exotic herbaceous species one year after the last fire (Figure 3.4, Appendix 3.3 to 3.6). We identified seven exotic species in this layer, including three potentially invasive species (*P. aquilinum, M. minutiflora,* and *A. lehmannii*) (Appendix 3.7 and 3.8).

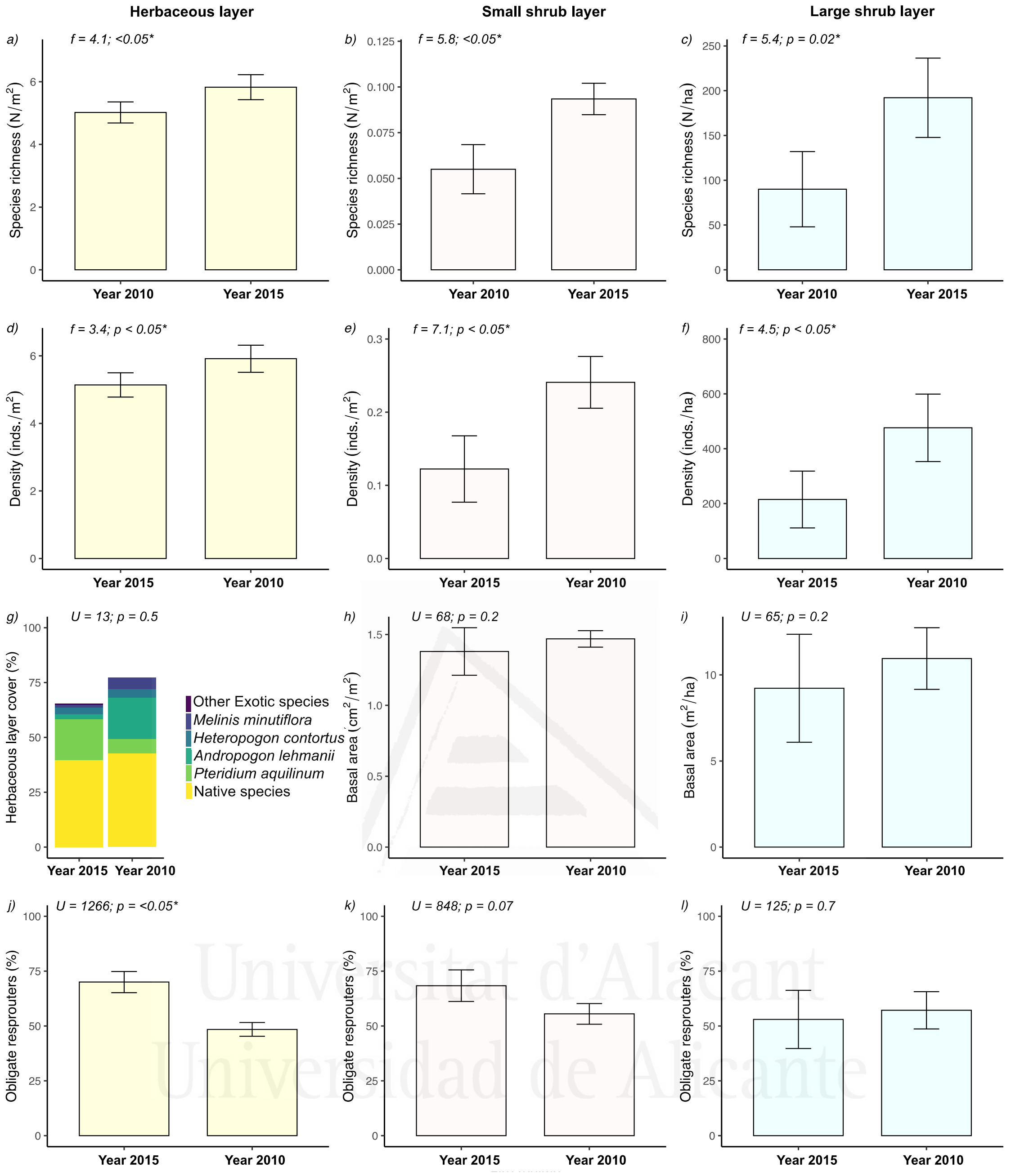

Figure 3.3. Effect of time since the last fire on species richness, individual density, basal area, the cover of native and exotic species, and proportion of obligate resprouters in the herbaceous layer (a, d, g, and j, respectively), small shrubs layer (b, e, h, and k, respectively), and large shrubs and trees layer (c, f, j, and l, respectively) one and six years after the fire (FR3-1 and FR3-6, respectively) in the Iguaque Mountains (Colombia). Error bars correspond to ± 1 SE. Statistical test values for herbaceous layer cover (g): Other exotic species: $U = 247$; $p = 5.0^{-2}$, *Melinis minutiflora:* $U = 122$; $p = 0.5$, *Heteropogon contortus:* $U = 101$; $p = 0.6$, *Andropogon lehmanii:* $U = 135$; $p = 2.2^{-2}$, *Pteridium aquilinum:* $U = 284$; $p = 8.0^{-2}$, and native species: $U = 194$; $p = 0.7$.

Fire frequency affected the small and large shrubs layer species richness and density but had a marginal effect on the proportion of obligate resprouters of woody species. The magnitude of the differences was substantial (e.g., 215 ± 103.6 large shrubs and trees/ha in areas burned three times in 30 years, compared to 10 ± 6.7 large shrubs and trees/ha in areas burned five times in 30 years). The basal area of small shrubs was not affected by fire frequency, whereas the basal area of large shrubs and trees was lower in more frequently burned areas. All woody species were resprouters.

Bejaria resinosa was the only large shrub in sites with the highest fire frequency. Other large shrubs and trees common in Andean oak forests, such as *Viburnum tinoides, Pentacalia corymbosa, Pentacalia pulchella, Verbesina elegans, C. fimbriata, Clusia multiflora, Cavendishia bracteata, Croton purdiei, Miconia squamulosa, Miconia alborosea, Myrcianthes leucoxyla, Myrcianthes rhopaloides,* and *Bocconia integrifolia* were absent under this fire frequency (Appendix 3.2 to 3.4).

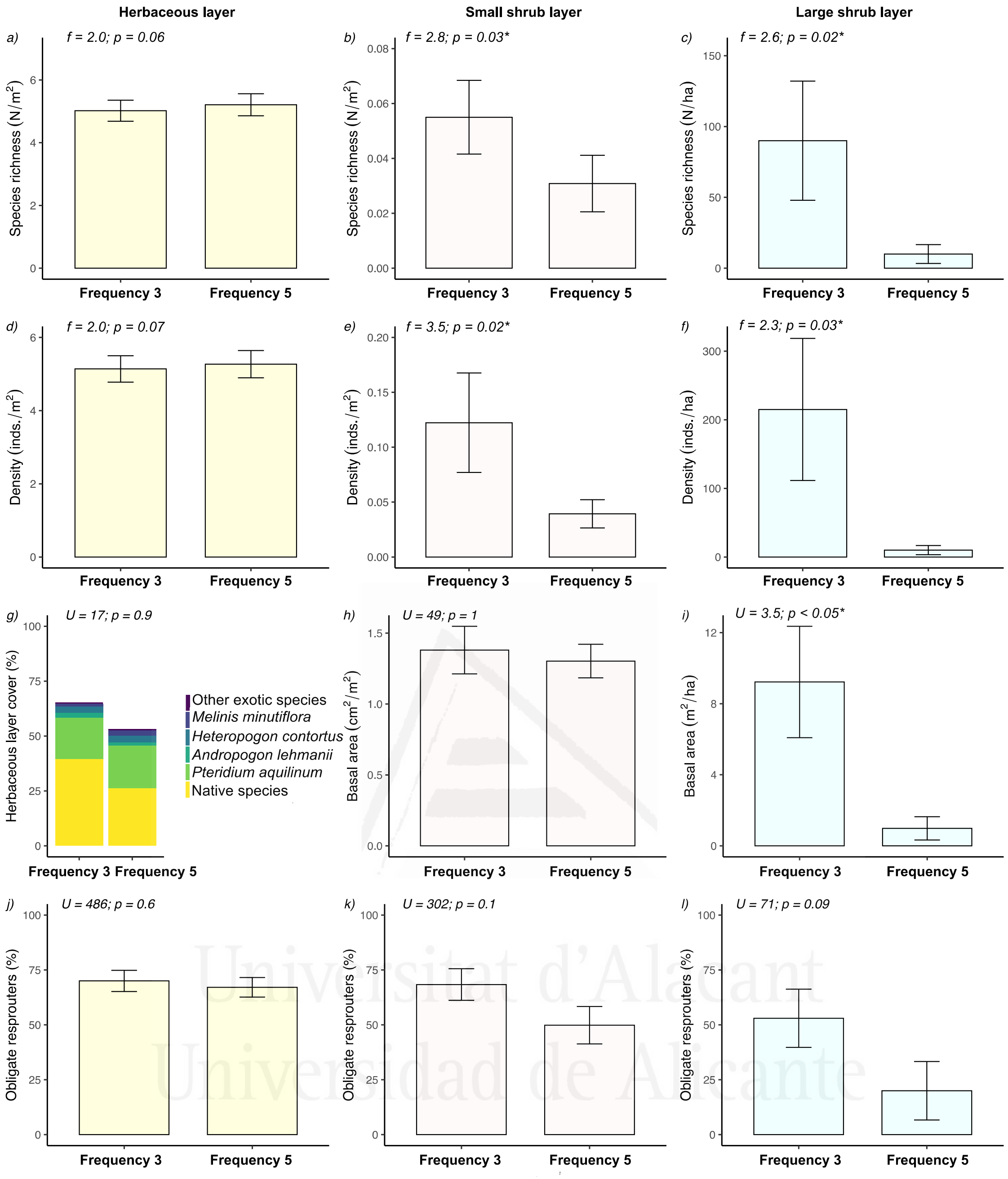

Figure 3.4. Effect of fire frequency on species richness, individual density, basal area, the cover of native and exotic species, and proportion of obligate resprouters in the herbaceous layer (a, d, g, and j, respectively), small shrubs layer (b, e, h, and k, respectively), and large shrubs and trees layer (c, f, j, and l, respectively) one year after the fire under two different fire frequencies (FR3-1 and FR5-1, corresponding to 3 and 5 fires over 30 years) in the Iguaque Mountains (Colombia). Error bars correspond to ± 1 SE. Statistical test values for herbaceous layer cover (g): Other exotic species: U = 137; p = 0.6, *Melinis minutiflora:* U = 122; p = 0.6, *Heteropogon contortus:* U = 101; p = 0.6, *Andropogon lehmanii:* U = 119; p = 0.7, *Pteridium aquilinum:* U = 89; p = 0.3, and native species: U = 137; p = 0.3.

DISCUSSION

Studies addressing the effects of fire regimes on tropical mountain ecosystems are scarce (Armenteras *et al.,* 2020). Conditions favoring repeated fires are unusual (Salvador *et al.,* 2005; Vilà-Cabrera *et al.,* 2008), mainly because fuel accumulated slowly after the fire and extended drought events are uncommon (Fuller & Murphy, 2006; Bianchi *et al.,* 2014). However, in tropical areas affected by El Niño Southern Oscillation dynamics, fire risk increases as La Niña, a phase of high productivity, is followed by drought (Fuller & Murphy, 2006; Bianchi *et al.,* 2014). On the southern ridges of the Iguaque Mountains, wildfire frequency has recently increased following El Niño cycles, setting a new ecological scenario (Aguilar-Garavito *et al.,* 2020). In our study, we have described vegetation composition and structure in areas differing in fire frequency and time since the last fire in this human-modified northern Andean landscape, thus providing new insights into vegetation responses to changes in the disturbance regime, the effects of repeated fires on native and invasive species, the post-fire regeneration patterns, and the potential evolution of shrublands and oak forests. This approach helped us analyze whether, in the short term, the plant community may persist under the current fire regime or facilitate the transition toward oak forests.

Plant community composition

The environmental conditions in the study area correspond to those of the Andean oak forest (Avella *et al.,* 2017; Villarreal *et al.*, 2017), as shown by previous studies on Andean oak forest distribution (González-Orozco *et al.,* 2011), and evidenced by the presence of remnant oak forest patches (Aguilar-Garavito *et al.,* 2020). However, species richness, plant density, and basal area were low compared with those observed in tropical Andean forests under similar environmental conditions (Fernández-Méndez *et al.*, 2016;

Avella *et al.,* 2017; Mendoza-Cifuentes, 2017). This may be related to the legacy of disturbances occurring in the Iguaque Mountains before 1970, affecting forest species' abundance (Mora, 2012). Opportunities for forest recovery after abandonment was probably missed as fire frequency increased since 1990. Current vegetation, dominated by rosettes, herbaceous species, and shrubs, is closer in composition to subpáramo vegetation than to Andean oak forests (Rangel, 2000; Avella *et al.,* 2017). This was particularly true at high elevation, where the floristic similarity with subpáramo vegetation was highest (i.e., the abundance of *Baccharis tricuneata, B. resinosa, Calea peruviana, E. pleiochasia, I. kunthiana, H. marahuacanum,* and *H. juniperinum,* among others). These plant communities may persist under the current environmental conditions and disturbance regime because of their ability to resprout and colonize burned areas.

The expansion of subpáramo plant communities to lower elevations has been observed in other disturbed high-mountain northern Andes regions (Sarmiento, 2002; Vargas, 2011). This herbaceous and shrubby vegetation moves downward in transformed landscapes due to its high capacity to adapt to novel anthropogenic, hydric and edaphic stress conditions (Hernández-Camacho, 1997; Velásco & Vargas, 2007). In this type of landscape, subpáramo vegetation has a greater recruitment capacity than trees.

Furthermore, the persistence of shrublands has been described in heavily modified Andean and tropical landscapes (Sarmiento, 1997; Lippok *et al.,* 2013; Arroyo-Rodríguez *et al.,* 2017). In the burned areas of the Iguaque Mountains, the absence of forest species that are common in nearby unburned forests, such *as Q. humboldtii, Alchornea* spp., *Clethra* spp., *Clusia* spp., *Cinchona* spp., *Drimys granadensis, Ilex jaramillana, Oreopanax* spp., *Schefflera* spp., *Ternstroemia meridionalis,* and *Weinmania tomentosa*, is remarkable and suggests that most forest species may be unable to colonize shrublands under the current environmental conditions and wildfire regime. Andean forest species developed in environments where the fire was uncommon (Vargas, 2000; Armenteras *et al.*, 2020), and they may be vulnerable to the new disturbance regime (González *et al.*, 1966; Kuhry, 1988). However, the increase in species richness and stem density of woody species one to six years after the last fire suggests that protecting the shrublands from the fire could facilitate the colonization of some tree species and eventually lead to the long-term recovery of oak forests.

Impact of time since the last fire on vegetation

The different vegetation layers varied in their responses one year after the fire. Herbaceous vegetation recovered quickly and showed scarce changes one to six years after the fire. Fire severity in the Iguaque Mountains is low (Aguilar-Garavito *et al.*, 2020), and its impact on underground tissues may be limited. Also, herbaceous and small shrub species may be able to complete their life cycle during fire-free intervals. In addition, fire may provide opportunities for fast-growing species to colonize open spaces (Vargas, 2000; Lippok *et al.*, 2013).

In contrast, the richness and density of woody species increased with time since the last fire, as has been observed elsewhere (Delitti *et al.*, 2005; Keeley *et al.*, 2011). This suggests that fire may be an obstacle for some species and an opportunity for others (Capitanio & Carcaillet, 2008; Duguy & Vallejo, 2008). Some species, including *Ageratina pichinchensis, Ageratina theaefolia, C. multiflora, Hypericum marahuacanum, Hypericum juniperinum, Psychotria boqueronensis,* and *V. elegans*, were absent immediately after the fire. In contrast, other species, such as *M. rhopaloides* and

Vaccinium floribundum, only appeared in the recently burned areas. In other words, the first group of species was exclusive to sites FR3-6, while the latter were to sites FR3-1 and FR5-1. These species are widely distributed in the landscape to colonize recently burned areas. The second species group appeared at sites FR3-1 and FR5-1 but at low density. These species being resprouting shrubs could also be present in sites FR3-6, and their presence could be confirmed with a more significant sampling effort.

The basal area of small shrubs was not affected by the time elapsed after the fire. That occurred despite reductions in the density of individuals. Thus, the few individuals that resprouted or colonized the area one year after the fire accounted for most of the potential basal area of small shrubs, and small shrubs established between the first and sixth year contributed little to the cover of this stratum.

Obligate seeders were absent from all burned sites. Obligate seeders are common in fire-prone areas and usually play an essential role in post-fire colonization (Kazanis & Arianoutsou, 2004; Pausas *et al.*, 2008). Obligate seeders such as *Alchornea* spp., *Cinchona* spp., *D. granadensis*, *I. jaramillana*, *Oreopanax* spp., *Schefflera* spp., and *T. meridionalis*, are common in Andean oak forests, and their absence in the study sites may be associated with the suppression of woody species with long life cycles typical of Andean oak forests. These species may present recruitment problems, such as the availability of seed sources, dispersal, and establishment limitations (Rey & Alcántara, 2000; Acácio *et al.*, 2007). In the Iguaque Mountains, seed sources may be too far away, seed dispersers may be unavailable, and post-fire conditions may be unsuitable for dispersal, germination, and seedling establishment (Fernández-Méndez *et al.*, 2016; Salazar *et al.*, 2020). The resprouting ability of Andean species probably evolved in response to other disturbances that were common in the area before and during the Holocene (Vargas, 2000).

Resprouters respond rapidly after the fire (Brooks & Lusk, 2008; Paula & Labbé, 2019). In the Iguaque Mountains, obligate or facultative resprouters such as *A. lehmannii, C. peruviana, Lepidaploa karstenii, M. minutiflora, Orthrosanthus monadelphous, P. viridis,* and *P. aquilinum* accounted for more than 50% of the herbaceous species cover. These species were present one year after the last fire and remained dominant after six years, although their proportions decreased. The relatively dry conditions following the previous fire (NOAA, 2020) may have favored the dominance of obligate resprouters over facultative and obligate seeders by hindering germination and establishment.

Impact of fire frequency on the vegetation community

Fire frequency did not affect the structure and composition of the herbaceous community throughout our study. Additional monitoring over time that may include pre-fire vegetation data could begin to show trends in species promoted by fire. However, our data show that the long history of use and transformation in the Iguaque Mountains, including the current fire regime, has probably acted as a filter to select resprouting, fire-resistant herbaceous species (Lippok *et al.*, 2013; Arroyo-Rodríguez *et al.*, 2015; Palma *et al.*, 2021). Herbs and graminoid species such as *A. lehmanii, C. peruviana, C. jamesonii, Eragrostis lugens, G. hypocarpium, Heteropogon contortus, M. minutiflora, O. chimboracensis, Polypogon virdis, P. aquilinum,* and *Rhynchospora nervosa* are common herbs in both FR3-1 and FR5-1.

Conversely, woody species, huge shrubs, and trees were vulnerable to increased fire frequency. The decline in woody species richness and density was parallel: species disappeared as individual density decreased. The impact of fire frequency on small shrubs was largely species-specific. Thus, some species, such as *Lepidaploa karstenii*, *Monochaetum myrtoideum*, *M. leucoxyla*, *Pinus patula,* and *Viburnum tinoides* only occurred in areas that burned five times over the last 30 years. In contrast, other species such as *Baccharis latifolia*, *Bucquetia glutinosa*, *I. kunthiana*, *Palicourea angustifolia, P. paniculate,* and *S. theiformis* disappeared when fire frequency increased to five fires in 30 years. Differences may be related to the species' ability to maintain active bud banks or use the available post-fire resources to recruit (Bond & Midgley, 2001; Moreira *et al.*, 2009). In this study, many species show resprouting capacity due to adaptations to typical high mountain disturbances such as frost, intense rainfall with hail, high solar radiation, or herbivory (Vargas, 2000). Therefore, those that exhibit these traits will have a more remarkable persistence in the plant community that regenerates after fires.

The effect of fire frequency on large shrubs and trees was more substantial. Significant species such as *B. latifolia, B. integrifolia, B. glutinosa*, *I. kunthiana, M. rhopaloides, P. angustifolia, P. paniculata, P. pulchella, Phytolacca rugosa, Rubus robustus,* and *S. theiformis* were present in areas burned three times in 30 years but could not stand the increase in fire frequency. Although these species may manage to establish in burned areas, they may be unable to complete their life cycle or generate protective structures when fire return time is too short (Schaffhauser *et al.*, 2012a; Arroyo-Rodríguez *et al.,* 2017; Palma *et al.,* 2021). In addition, the wildfire frequency may have a greater incidence of bud bank replenishment (or the seeds germinate) and stem elongation than drought periods since the rainfall regime in Iguaque is normally bimodal, with two rainy periods per year. In Iguaque, these usually occur a few weeks after the fires (Aguilar-Garavito *et al.*, 2020).

Quercus humboldtii and other native forest species were scarce throughout the study area, despite the proximity of the remnant forest patches (less than 1 km from most study plots). These results are consistent with previous observations describing a gradual reduction in the extent of oak forest in burned areas of the Iguaque Mountains (Aguilar-Garavito *et al.*, 2020). As *Q. humboldtii* is considered a fire-resistant species (DeSantis *et al.*, 2010; Salazar *et al.*, 2020), we may conclude that human transformation of the Andean landscape in the Iguaque Mountains and the current disturbance regime exceeds the oak’s capacity to expand. Overall, these results warn of the impact that recurrent fires and historical land uses may have on the current and future oak forests' status and the threat to the conservation of oak forests. Other studies have reported the failure of oak species to regenerate and establish after the fire (Johnson *et al.*, 2002; Leverkus *et al.*, 2014). Furthermore, in human-modified landscapes, succession may progress to highly persistent auto-shrubby successional vegetation (Royo & Carson, 2006; Zouhar *et al.*, 2008; Arroyo-Rodríguez *et al.*, 2017).

The proportion of resprouting woody species was close to or above 50% and was not affected by the fire regime in our study. The only woody species of the large shrub layer in areas burned five times over the last 30 years was a resprouter, *B. resinosa*. However, its density is lower than in the sites with a more extended post-fire period (FR3-6). Many large shrubs and tree species were obligate or facultative resprouters (such as *B. latifolia, B. tricuneata, D. viscosa, I. kunthiana, H. marahuacanum, V. elegans*, and *P. boqueronensis*) were absent from the frequently burned sites. Despite the inherent resilience of resprouters, excessive disturbance frequency may limit their ability to activate their shoots (Bellingham & Sparrow, 2000; Espelta *et al.*, 2003). Seedlings of these species were found in the herbaceous stratum of some FR3-1 sites and sometimes reached the upper layers, whereas they were absent from the herbaceous stratum of FR5-1 sites.

Impact of fire on exotic species

We found seven exotic species in the herbaceous layer and none in the woody vegetation layers. Their cover was relatively high soon after the fire and was affected by fire return time. *Pteridium aquilinum* was the most abundant species and was present under all fire regimes. Three of the species found in the Iguaque Mountains, *P. aquilinum, M. minutiflora,* and *A. lehmannii,* are highly invasive in Colombia and have been reported in almost all climatic zones (Cárdenas *et al.*, 2010). These species are also widespread throughout the Americas (CABI, 2019a; 2019b) and have been associated with open spaces in forest edges, secondary forests, roadsides, pastures, and crops (Mora-Goyes & Barrera-Cataño, 2015). They often form dense stands that limit the establishment of other species and reduce the diversity of vascular plants. Fire contributes to dispersal by suppressing competition, stimulating rhizome bud resprouting, increasing soil pH, and promoting germination (Cárdenas-López *et al.*, 2017).

In addition, standing *P. aquilinum, M. minutiflora,* and *A. lehmannii* necro mass facilitate the occurrence of new fires (Pinzón *et al.*, 2012; Mora-Goyes & Barrera-Cataño, 2015). This pattern has been found in areas where fires were historically rare but has increased in recent decades (van der Wal *et al.*, 2008; Keeley & Brennan, 2012). The cover of *A. lehmannii,* other exotic species, and, marginally, *P. aquilinum* increased with time since the last fire, either by vegetative growth or successive colonization. These results suggest that six years after the fire, the increase in the cover of exotic species did not wholly exclude herbaceous native plants in our study. Nevertheless, it is necessary to continue monitoring the vegetation, as mentioned above. Only one exotic tree species, *P. patula*, was present in the study area, but its density was extremely low. Therefore, exotic tree species do not currently threaten native vegetation in the Iguaque Mountains, even under high fire frequency regimes.

Remarks for future research

We made a critical sampling effort reflected in the species accumulation curves; however, it is feasible that the number of quadrats needs to be increased to represent the entire herbaceous community of the Iguaque mountains. Therefore, it is advisable to increase the number of plots and quadrats. It is possible to replicate the sampling in other altitudinal ranges.

We were aware of a possible spatial pseudo-replication between the sampled areas. It is challenging to mix sampling points in fire ecology field studies spatially. The particular conditions of each fire limit the possible sampling areas. Despite its difficulty in the field, it is advisable to carry out complete random sampling designs. Therefore, it would be advisable to include edaphic and microclimatic variables. Design generalized linear models with a random location factor would also be essential.

Finally, it is advisable to maintain a monitoring program of the plant community to increase knowledge about post-fire succession in the northern Andes and to design better biodiversity management programs. In addition, such monitoring will provide long-term data on pre-fire and post-fire vegetation under different fire regimes.

CONCLUSIONS

Wildfire frequency has increased in the Andean region. The current fire regime promotes the persistence of herbaceous and shrubland vegetation and may hamper forest regeneration in the human-modified northern Andean landscapes. Vegetation can respond quickly after a fire due to the abundance of resprouting herbaceous and small shrub species. These plants protect the soil and initiate community assembly. However, frequent fires represent an obstacle for structural forest species, such as large shrubs and trees. These species can colonize burned areas only through seed dispersal from neighboring unburned areas or assisted recruitment. In addition, fire creates colonization opportunities for exotic species, especially those in the herbaceous stratum. Our results emphasize the risk that recent and frequent fires may pose to the natural regeneration and conservation of oak forests in northern Andean landscapes. They also underscore the need to control the frequency and extent of fires, protect unburned forest patches and facilitate tree regeneration.

Implications for Andean Forest community conservation and land management

Fire frequency has recently increased in the Iguaque Mountains (Aguilar-Garavito *et al.*, 2020). We have shown that frequent fire affects woody species' richness, density, and basal area. Many large shrubs and tree species are absent from frequently burned areas, and *Q. humboldtii* is missing from burned areas. Our results prove that oak forests may not recover under the current combination of past land use and fire regime. To protect and expand oak forests, the Iguaque Mountains administration, the mayor's office, environmental authorities, and fire departments around the Iguaque Mountains should improve fire prevention programs, educate local people and tourists about the risk of fire, and implement fire prevention and management measures. An integrated biodiversity management strategy should consider fuel fire load accumulation and continuity and promote mosaics of shrubs, forests, and open areas free from *P. aquilinum, M. minutiflora,* and *A. lehmannii*. Furthermore, such management should be implemented in protected areas and neighboring agricultural, periurban, and tourist areas to be effective. In the short term, manual and mechanical removal of invasive plants, applied in strategically selected locations, could be an effective tool to reduce fuel loads (Baeza *et al.,* 2002; 2006; Lloret, 2004).

The Iguaque Mountains will likely burn again. Integrated wildfire management (Moreira *et al.,* 2020) carried out during the years following a fire should focus on maintaining fuel discontinuity and low fuel loads while protecting the remaining forest. Priority should also be given to managing fuel loads in areas around the current oak and subpáramo and páramo relicts, riverbanks, and canyons. Furthermore, vegetation management should focus on forest restoration by promoting oak recruitment and assisted regeneration. Studies assessing such measures' technical and socioeconomic feasibility and their impacts on ecosystems, landscape diversity, and function are necessary to design efficient management programs.

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SUPPLEMENTARY MATERIAL 3

Appendix 3.1. Species accumulation curves for all transects and fire regimes studied.

Appendix 3.2. Species, attributes, and number of individuals of the vascular flora of the Iguaque Mountains.

Appendix 3.3. Richness, density, and representative species in the different vegetation layers of the Iguaque Mountains under three fire regimes.

Appendix 3.4. Results of PERMANOVA to assess the effects on time after the last fire and the frequency on species richness and density.

Appendix 3.5. Results of Wilcoxon Mann-Whitney tests (*U*) to assess the effects one and six years after the last fire (FR3-1 and FR3-6) on the cover, basal area, native and exotic species proportions (%), and cover (%) of native species and invasive species.

Appendix 3.6. Cover, BSD, DBH, and height of plants under different fire regimes in the Iguaque Mountains.

Appendix 3.7. The proportion of obligate resprouting species under the fire regimes

Appendix 3.8. Cover native species, invasive species, and bare soil under the fire regimes.

Appendix 3.9. Results of Wilcoxon Mann-Whitney tests (*U*) to assess the effects of fire frequencies on the cover, basal area, native and exotic species proportions (%), and the significance of cover (%) of native species and invasive species under two different fire frequencies.

CHAPTER 4. Postfire resprouting and recruitment of *Quercus humboldtii* in the Iguaque Mountains (Colombia)

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Postfire resprouting and recruitment of *Quercus humboldtii* in the Iguaque Mountains (Colombia)

ABSTRACT

Anthropogenic disturbances, including wildfires, threaten the diversity of tropical Andean ecosystems. However, the response of tropical Andean plant communities to wildfires in human-modified landscapes has to be discovered. *Quercus humboldtii* is the southernmost species of this genus in the Neotropics and is almost exclusively distributed in Colombia. While the extent of *Q. humboldtii* forests has decreased recently, to what time these results from the species' inability to thrive under the current climate and disturbance regimes are still being determined. In this study, we describe post-fire resprouting and acorn and seedling density in and around *Q. humboldtii* forest patches in the Iguaque mountains in Colombia. We discuss the implications for the conservation and restoration of these forests. Resprouting probability was high in burned trees two years after the fire (ca. 80%). Resprouting ability depended on fire severity and tree size. The proportion of trees resprouting from the stump was related to the severity of fire damage and tree size. Acorn density was higher in burned than unburned areas and depended on the slope, distance to the forest edge, and distance to the nearest oak. Conversely, the density of healthy acorns was low across all sites, particularly in burned areas. Seedling density was relatively high in unburned areas, but seedlings could not withstand recurrent fires. The density of acorns and seedlings decreased in the periphery of forest patches. Despite the strong impact of fire on forest structures, *Quercus humboldtii* adults may withstand the current fire regime thanks to their strong capacity for vegetative and sexual regeneration. However, the ability of this species to establish in areas where oaks are no longer present is scarce. As *Q. humboldtii* forest cover and spatial continuity have decreased in response to the increasing frequency of wildfires, the current fire regime represents a threat to the recovery of this species. Our results have important implications for the management of *Q. humboldtii* and Andean forests as they emphasize the need to control the severity and frequency of wildfires and to use assisted regeneration to restore *Q. humboldtii* forests in degraded areas.

KEYWORDS: Andean tropical forest, Acorn, Resprouting, Seed, Seedling survival, Fire severity, Wildfire

The historical transformation of the northern Andean region affected at least 60% of the area since European colonization (Etter *et al*., 2008). Now, wildfires have increased in ecosystems where they were historically rare (Valencia *et al*., 2010; Armenteras *et al*., 2020). For example, in the Colombia Andean region, paleoecological evidence, such as charcoal fragments, suggests low wildfire frequency during the Pleistocene (centuries to millennia) and remained so during the Holocene (González *et al*., 1966; van der Hammen, 1966).

In pre-Columbian times, the fire was used in slash-and-burn agricultural systems (Patiño, 1965; Jantz & Behling, 2012). These practices intensified after European colonization in the early 16th century (Castilla-Beltrán *et al.*, 2018; Koch *et al*., 2019). The forests were transformed into crops and pastures (Molano, 1995; 1996; Mora, 2012). Fires have recently played an important role in northern Andean ecosystems (Dull *et al.,* 2010; Valencia *et al.,* 2010). The wildfire frequency has increased from one event every 1,000-2,500 years ago to one event every 2-10 years since the mid-20th century (Horn, 1986; 1989; Verweij, 1995). This fire regime shift may profoundly affect the natural forest regeneration, the composition of northern Andean ecosystems, and the ecosystem's human benefits (TNC *et al*., 2004; Armenteras *et al.,* 2020).

However, these fire patterns were not and are not homogeneous in the northern Andes. The wildfires depend on population density, human fire uses vegetation fuel accumulation, extreme weather conditions (Godoy *et al*., 2019; Guillaume *et al.,* 2019), and climatic cycles, such as El Niño-Southern Oscillation (ENSO; Bianchi *et al.,* 2014). This situation has been reported in various tropical Andean countries (Armenteras et al., 2005, 2009a, b, 2019, 2020; FAO, 2005, 2013; Barreto *et al.,* 2017). Therefore, the shift in wildfire regime could profoundly impact biodiversity, ecosystem functioning, and humans' benefits from nature in the northern Andes (The Nature Conservancy *et al.,* 2004).

In the Iguaque Mountains (Colombia), previous studies revealed that wildfire frequency had increased recently, burning patch forests 3 to 7 times in the last 30 years (Aguilar-Garavito *et al*., 2020). Wildfires affect both successional vegetation and oak forest remnants hindering tree recruitment and arresting forest succession (Aguilar-Garavito and Cortina-Segarra, 2023). In addition, invasive species such as *Pteridium aquilinum* (L) Kuhn. are abundant in burned areas, and their cover may increase with recurrent fires (Fernández-Méndez *et al*., 2016; Salazar *et al*., 2020).

Plant communities may show high resilience to fire and even rely on wildfires to persist when fire exerts an evolutionary pressure (Moreno & Oechel, 1994; Bellingham & Sparrow, 2000; Schwild *et al.,* 2016). In contrast, when fire frequency has been historically too low to elicit evolutionary responses, communities may be more vulnerable to fire (Schumacher & Bugmann, 2006; Armenteras *et al.*, 2020). Species' life-history traits, particularly plants' capacity to resprouting and re-establish from seeds after the fire, largely determine their ability to withstand increases in fire frequency and severity (Bond & van Wilgen, 1996; Pausas, 1999; Keeley, 2009; Pausas, 2006). Plants' ability to resprout may be affected by many factors, including the degree of damage (Espelta *et al.*, 2003; Moreira *et al.,* 2007, 2008), plant size, bark thickness, and the occurrence of further disturbances (Ordóñez *et al*., 2005; Silva & Catry, 2006). For example, plants with a higher level of damage have a greater probability of dying or resprouting exclusively from the stump (Miller, 2000; Bond and Midgley, 2003), whereas, at intermediate levels of fire severity, plants may sprout from the crown (Kozlowski *et al*., 1991; Miller, 2000).

Plants may also colonize burned areas by seed. The seed bank and seed dispersal of fire-prone communities and the factors affecting seed abundance and germination, and seedling establishment have been studied (Auld & Denham, 2006; Peppin *et al.,* 2010; Santos *et al.,* 2010; Lipoma *et al.,* 2018; Konsam *et al.,* 2020), including in tropical forests (Cury *et al.,* 2020; Jakovac *et al.,* 2021; Scheper *et al.,* 2021). This study has been carried out in the northern Andes to analyze the impact of other disturbances, but they have not been studied in depth, nor have they been studied for fires (Cardona and Vargas, 2011; Gelviz-Gelvez *et al.*, 2016; López *et al.,* 2016; Velosa *et al.,* 2018).

Colombian Andean forests have been classified as fire-independent ecosystems (Páramo-Rocha, 2011; Armenteras *et al*., 2020) because, historically, they have not been prone to fire and are not fire-adapted. Therefore, many of the plant species of Andean forests may be unable to withstand the current fire regime (Vargas, 2000; 2002; Salazar *et al*., 2020), as the biota of these ecosystems has evolved under another natural disturbance regime. Nevertheless, resprouting is a functional post-fire adaptation, albeit useful under other disturbance regimes more common in the northern Andes, such as frost, hail, and herbivory (Vargas, 2000).

Quercus humboldtii is the only *Quercus* species in South America. It colonized the Northern Andes approximately 250,000-470,0000 years ago (Van der Hammen *et al*., 2008) and currently covers 10 to 40% of its pre-Columbian distribution in the northern Andes (Gentry, 1993; Rangel, 2000; Etter *et al.*, 2006). However, deforestation, agriculture, livestock production, and wildfires have likely caused the decline of this species (Avella, 2016; Fernández-Méndez *et al*., 2016) and its inclusion as Vulnerable (VU) on the IUCN Red List (Salinas & Cárdenas, 2007). Nevertheless, the *Q. humboldtii* forest communities host high levels of biodiversity, including 550 species of vascular plants, 200 species of birds, 55 species of mammals, and 30 species of amphibians (Pulido *et al.*, 2006; Sáenz-Jiménez, 2010), and provide many benefits for people, such as clean water, food, medicinal plants, raw materials for construction, and domestic and industrial fuels, as well as services related to tourism and spiritual landmarks (Bello, 2006; Muñoz and Camacho, 2010).
Like other *Quercus* (Moreira *et al*., 2008; DeSantis *et al.*, 2010; Cooper et al., 2018; Ackerly *et al*., 2019), *Q. humboldtii* is a fire-resilient tree that can resprout up to three years after fire (Salazar *et al.*, 2020). This ability has been associated with dormant buds in the

root collar and stem and thick bark in other species (Avella, 2016; Salazar *et al*., 2020). Additionally, *Q. humboldtii* may have deep root systems, increasing their capacity to withstand post-fire drought (Schwilk *et al.*, 2016; Reyna *et al.*, 2019).

Quercus humboldtii also produce acorns, whose primary dispersal mode is by gravity. Later, acorns can be redistributed or predated by small and medium-sized mammals and birds (Gómez, 2003; Vargas, 2006). Acorn production usually starts in the middle of the dry season and extends during the rainy season (Melo & Parrado-Rosselli, 2010; Pérez *et al.*, 2013). Acorn development takes 4 to 7 months (Gómez & Toro, 2007). Acorns are not dormant and may germinate soon after falling (Sepúlveda *et al.*, 2014). A healthy adult tree may produce 5-8 kg of acorns per year (150 to 500 acorns per kilogram; Galindo *et al.*, 2003; Nieto & Rodríguez, 2004), with field germination rates of up to 20%, and nursery germination rates of 60-80% (Betancur & Cuartas, 2014; Fernández, 2014). A certain tendency to masting every 2 to 6 years has been observed, as well as an increase in the number of abortions and lower germination rates in fragmented populations and populations affected by agriculture and wildfires (Fernández and Sork, 2005; Melo & Parrado-Rosselli, 2010; Fernández, 2014).

We studied the impact of fire on the ability of *Q. humboldtii* to resprout and establish from acorns in a northern Andean Forest affected by frequent wildfires. This knowledge is critical for assessing the effects of changes in fire regimes on this iconic species in north Andean, developing integrated fire management programs, and conserving and restoring the Andean oak forest.

METHODS

Study area

The Iguaque Mountains (22,000 ha) are located in the Northern Andes, on the western slope of the Eastern Mountain range of the Boyacá department, Colombia (-5.60055° to -5.74389° and 73.38250° to 73.52222°, Figure 4.1). The area comprises the protected natural area Santuario de Fauna y Flora Iguaque (SFFI; 2400 to 3890 m asl.; 6750 ha) and is surrounded by a protected buffer zone at lower elevations (from 2200 to 2400 m asl). The landscape is hilly, and the topography is strongly wavy and broken, with slopes steeper than 15%. Soils are shallow, acidic, and moderately evolved, formed by structural sandstones of the Arcabuco Formation (Villarreal *et al.*, 2017). The average annual temperature and precipitation of the whole range are 18°C (average maximum 22°C, average minimum 10°C) and 810 mm, respectively. Rainfall follows a bimodal distribution, with peak precipitation between March-May and September-November. The rainiest months are April-May, with approximately 200 mm, and the driest months are December-February, with about 40 mm. Rainfall decreases toward the southwestern part of the area (Villarreal *et al*., 2017).

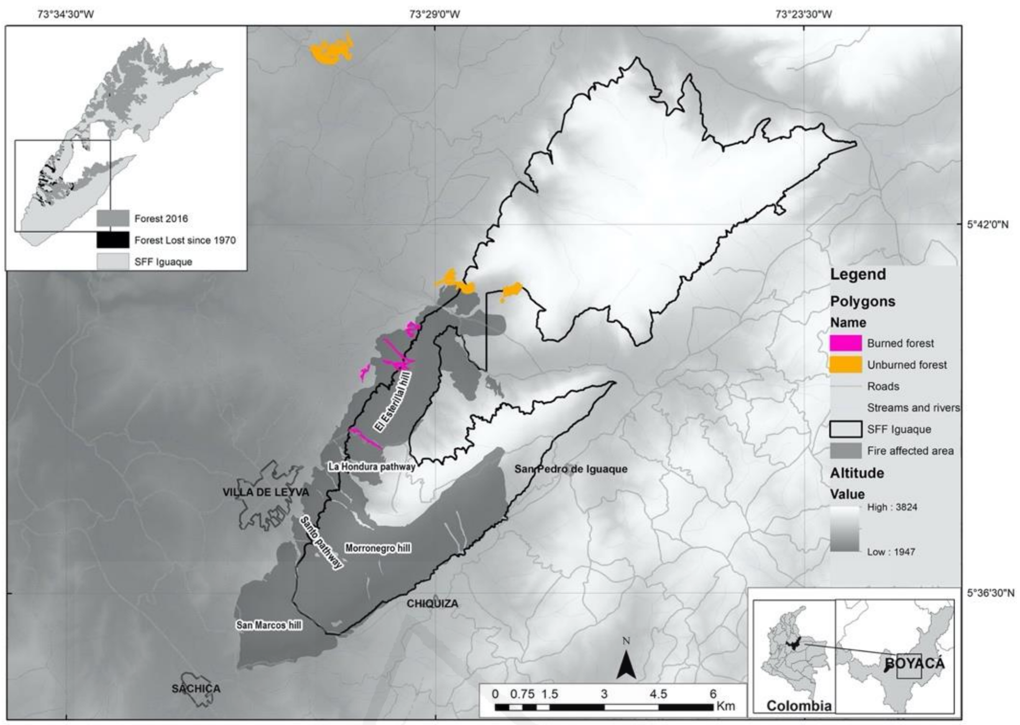

Figure 4.1. Location of the Iguaque Mountains in Boyacá Department, Colombia, northern Andes, and the area affected by wildfires between 1990 to 2016. *Quercus humboldtii* forest patches affected by the fire are inside this area (Burned forest); *Quercus humboldtii* forest patches not affected by the fire are outside (Unburned forest).

Human activity has intensely affected the southern ridges of the Iguaque Mountains. Soils are very degraded in this area, and rock outcrops are common. Recurrent wildfires have historically affected this area (Aguilar-Garavito *et al.,* 2020). It is mainly covered by a mosaic of herbaceous vegetation and shrubs, with a mix of native and exotic species. *Quercus humboldtii* forests can still be found along streams and river canyons. The northern ridge area shows lower anthropogenic disturbances, including wildfires, and is dominated by preserved páramo vegetation and Andean forests (Fernández-Méndez *et al.,* 2016; Mendoza-Cifuentes, 2017). The buffer belt of the protected natural area presents a mosaic of herbaceous and shrubby vegetation mixed with pastures, farmland, and recreational houses.

In a previous study (Aguilar-Garavito *et al.*, 2020), we recorded twenty-five wildfires in the Iguaque Mountains between 1990 and 2017, affecting 28% of the Iguaque Mountains. Fires were commonly small. Wildfire number and size showed substantial interannual variations related to El Niño–Southern Oscillation cycles. As a result, fire recurrence in the area ranges from 1 to 7 events in 30 years. Wildfires contributed to a 45% reduction in *Q. humboldtii* forests and the fragmentation of existing populations (Figure 4.1).

Selection of *Quercus humboldtii* forest patches

We identified burned and unburned *Q. humboldtii* forest patches based on historical Iguaque wildfire maps (Figure 4.1, Appendix A and B; Aguilar-Garavito et al., 2020). We considered criteria such as ease of access and independence between patches (at least 500 m distance between neighboring patches). Also, the patches were similar in altitudinal range, historical use, shape, and size. With these criteria, we sought to identify relatively similar and representative forest patches of the Iguaque mountains.

We chose seven forest patches. We selected the four most extensive forest patches among the ten *Q. humboldtii* forests affected by wildfires in the southwestern of Iguaque (Appendix A). These patches had three fires during the last 30 years. At the time of the study, two and a half years had elapsed since the previous fire (Aguilar-Garavito et al., 2020). They are separated from other patches of *Q. humboldtii* forest of similar shape and size by 0.3-1 km.

We identified some disturbed *Q. humboldtii* forest patches but unaffected by wildfires. Very few met the criteria initially described. However, we selected the two unburned patches of *Q. humboldtii* forest closest to the historical area affected by wildfires in the Iguaque mountains. Then, we set a third unburned patch outside the Iguaque mountains (Figure 4.1; Appendix B and C.). Other *Q. humboldtii* forest patches can be found north of the Iguaque mountains. However, they are larger and much better preserved. The three patch groups were separated by a 2 to 7 km distance. They were also similar regarding the surrounding vegetation, a mixed matrix of scrub and grassland surrounding the burned and unburned forests. The patches were narrow in shape from 3 to 12 ha and distributed from 2,376 to 3,001 m asl. All selected patches are relics of a broader distribution in the past.

The unburnt forest patch outside the Iguaque Mountains belongs to the Iguakan Civil Society Reserve and is located in the Saavedra de Roncancio village, Gachantivá (-5.70958°, 73.48917°). This 33 ha *Q. humboldtii* forest fragment extends from 2440 to 2543 m asl. and is surrounded by shrublands and grasslands mainly established before 1970. According to remote sensing images (Landsat, Rapideye, and Google Earth from 1991, 2010, and 2015) and official fire reports (Unidad Nacional para la Gestión de Riesgos y Desastres, 2018), the forest has not been burned for the last 30 years.

Data collection

We analyzed the influence of individual *Q. humboldtii* tree traits, fire incidence, and forest patch properties as predictors of *Q. humboldtii* resprouting ability and acorn and seedling density. We used the modified methodology of Gentry (1992) and Rangel and Velásquez (1997) to survey vegetation. A sampling of trees and shrubs (diameter at breast height (DBH) > 2.5 cm) was carried out using belt transects. We established five replicated transects of 50 x 2 m (100 m^2) in each forest patch. Transects were separated by at least 150 m, located randomly along the longest forest patch axis, and extended from 20 m inside the patch to 30 m outside it (dimensions were restricted by average patch width). We identified and counted all plants with DBH > 2.5 cm along each transect.

For each *Q. humboldtii* individual, we measured stem DBH, total height, distance to patch edge, and several traits related to fire impact (Dickinson & Johnson, 2001; USDI National Park Service, 2003): a) fire scar area, considering that scars formed isosceles triangles; b) scar number; c) charring height, as a proportion of tree height; d) postfire resprouting ability, and f) postfire resprouting type. The types of post-fire responses were also assessed and classified into two mutually exclusive categories (Moreira *et al.*, 2007, 2008): i) resprouting from the stump and ii) resprouting from the crown.

We used the vegetation survey to analyze the properties of the forest patches. First, we estimated the density of *Q. humboldtii* trees within the patches and the density of woody species outside the patches (individuals/100 m^2). In addition, to estimate the potential fire exposure of adult *Q. humboldtii* individuals within each forest patch, we defined the patch geometry using two metrics, the mean perimeter-to-area ratio (MPAR) and CIRCLE.

MPAR calculates the ratio of perimeter to patch area (McGarigal & Marks, 1995; McGarigal *et al*., 2012). CIRCLE is calculated as one minus the ratio between the patch's area and the circle's area that can be circumscribed within the patch (Matteucci, 1998). Therefore, its value ranges from 0 for circular patches to 1 for thin patches.

The *Q. humboldtii* forest maps of Sierra de Iguaque (Figure 4.1), Google Earth Airbus 2013 image, GIS (ArcGIS 10.3; ESRI, 2015), ArcGIS Path Analyst extension (Rempel *et al*., 2012) and FRAGSTATS V 4.2 (McGarigal, 2015), were used to delineate forest patches and calculate their metrics.

We studied the *Q. humboldtii* acorn and seedling density using ten 1x1 m quadrats located every 5 m along the 50 m transect, where we recorded all acorns and seedlings found. We also measured the distance of acorns and seedlings to the forest edge and the nearest *Q. humboldtii* adult. In addition, we measured the slope using a digital clinometer and the canopy cover with a mirror densimeter. Finally, we estimated the viability of the acorns according to their size, weight, and other physical characteristics described by Gómez and Toro (2007). The vegetation survey was completed between September and December 2017.

Statistical analyses

We used generalized linear mixed models to analyze the effects of predictor variables on post-fire resprouting ability (as a percentage of the adult trees present), resprouting type (as a percentage of the adult trees present), acorn density, the density of healthy acorns (as a percentage of all acorns present), and seedling density. All models were adjusted to include transect as random effects.

We used binomial families (with the logit link function) and negative binomial and Poisson families (with the logit-log and log link functions) to identify the best models. Before modeling, we selected the probability distribution families that best fit the response variables. We used the functions *glmer* and *glmer.nb* from the 'lme4' package (Bates *et al.*, 2015), the *fitDIst* function from the 'gamlss' package (Rigby & Stasinopoulos, 2005), the *r2_zeroinfleted* function from the 'performance' package (Lüdecke *et al.*, 2021) and the *r.squaredGLMM* function from the 'MuMin' package (Barton, 2014) of the R software (R Core Team, 2021).

To reduce the multicollinearity of predictor variables, we evaluated the variance inflation factors (VIFs; Fox & Monette, 1992) using the VIF function of the *car* R package (Fox & Weisberg, 2019). Highly correlated variables (VIF > 2) were gradually removed, and the models recalculated until their VIF was less than 2 (Zuur *et al.*, 2010). Subsequently, a stepwise regression (Venables & Ripley, 2002) was used to select the model with the lowest Akaike information criterion (AIC) using the *stepcAIC* function from the *cAIC4* package (Burnham & Anderson, 2002; Säfken *et al.*, 2018). This approach starts with formulating a series of models that rely on an understanding of e system being studied, followed by an assessment of how different putative models compare to reality (Rushton *et al.*, 2004).

The fit and predictive performance of the models with smaller AICc values were evaluated through the likelihood ratio statistic (full-model ANOVA) and by calculating the area under the receiver operating characteristic (ROC) curve (AUC) (Saveland & Neuenschwander, 1990). This approach has the advantage of assessing model performance in a threshold-independent fashion, independent of the prevalence of several response types. The AUC varies between 0.5 (no discrimination ability) and 1 (perfect discrimination ability; Pearce & Ferrier, 2000). Usually, AUC values of 0.5–0.7 are taken to indicate low accuracy, values of 0.7–0.9 indicate practical applications, and values above 0.9 indicate high accuracy. The calculations of the AUC and the standard error were based on a nonparametric assumption.

Post-fire resprouting: For *Q. humboldtii* post-fire resprouting ability and resprouting type, each variable was modeled separately as a binary variable, taking the value 1 for the specific response type and 0 for the remaining types. A generalized linear model with a binomial error structure and a logit link function (McCullagh & Nelder, 1989) was used to test a group of biologically plausible models, including separate models for each of the three variable groups, namely, *Tree Traits*, *Fire Impact,* and *Patch Properties*, assumed to be biologically significant and all possible combinations of these variables. To account for environmental heterogeneity, we also included the factor *Transect* as a random variable. In addition, one interaction term was added to this list of variables, Burnt or Unburnt. This yielded three groups of 25 models each (one group per response type), resulting from all combinations of these five variables. The model with the smallest AICc value in each group was considered the most parsimonious model (Burnham, 2003) for each response type.

The fit and predictive performance of the models with smaller AICc values were evaluated through the likelihood ratio statistic (full-model ANOVA) and by calculating AUC (Saveland & Neuenschwander, 1990; Pearce & Ferrier, 2000). This approach has the advantage of assessing model performance in a threshold-independent fashion, independent of the prevalence of a response type. A total of 45 models were evaluated for each response variable.

Acorn and seedling density: We analyzed the influence of fire and patch properties on the density of acorns, healthy acorns, and seedlings by employing generalized linear models (GLMER). To account for environmental heterogeneity, we included the factor transect as a random variable in all models and ran mixed-type models. The model with the lowest AIC was selected in each case.

To determine which factors influenced the proportion of healthy and incompletely developed acorns and seedling density in burned and unburned sites, we included transect characteristics (slope and plant cover), the distance to the closest *Q. humboldtii* adult, and patch properties in the model. These factors were included as fixed effects, while we used a polynomial distribution for the response variable. For this analysis, we used a Poisson distribution for the dependent variable.

To determine which factors, influence the presence of *Q. humboldtii* acorns, we used a binary variable, taking a value of 1 for the quadrats where viable acorns were found and 0 for those absent. Finally, using a linear model, we examined whether full and healthy *Q. humboldtii* acorns were influenced by fire and forest patch properties. We first included all possible interactions among the fixed factors in all models and removed nonsignificant ones. The model with the best fit and performance was that with the lowest AICc, and the ROC was calculated for the binomial model for acorns. A total of 73 models were evaluated for each response variable.

RESULTS

We found significant differences in all variables studied for *Q. humboldtii* traits, fire incidence, and forest patch properties between burned and unburned forests (Table 4.1). Tree height and stem diameter were lower in burned than in unburned areas.

Resprouting ability

We sampled 258 *Q. humboldtii* adult trees and found no evidence of completely burned trees. In the burned forests, 92% of the adult trees showed signs of fire (Appendix D). Most trees (80%) were resprouted two years after the last fire. The most common type of response was the simultaneous crown and stumped resprouting (35%), followed by stump resprouting (25%), exclusive crown resprouting, and no resprouting at all (20% each). In the burned forest patches, the number of *Q. humboldtii* individuals showing no signs of fire damage was low (8% of all trees). In unburned forest patches, trees showed no signs of fire damage. Stem and charring heights had a positive and negative non-linear effect on resprouting ability, respectively (Table 4.2, Figure 4.2, and Appendix 4.1). Still, wholly burned small trees showed more than a 60% probability of resprouting.

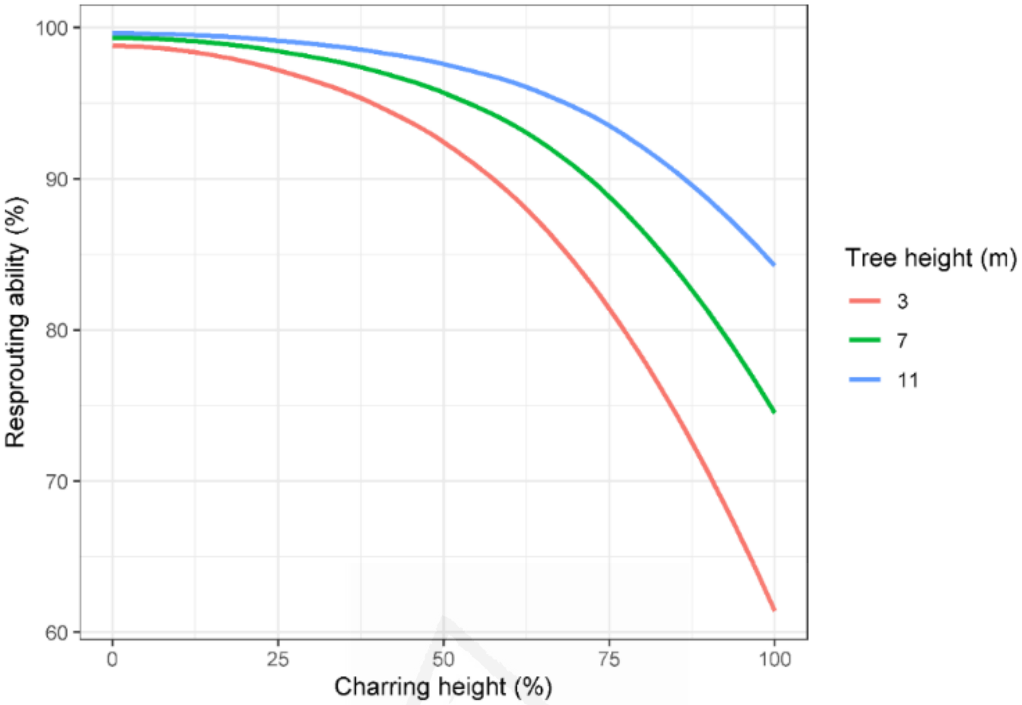

Figure 4.2. Resprouting ability of *Quercus humboldtii* as a function of tree height and charring height (%) in the burned forests of the Iguaque Mountains. Model parameters are described in Appendix 4.1.

Table 4.1. Descriptive statistics are the variables considered in this study. Negative distances to the edge of the forest patch were measured inwards. SE = standard error.

Variable group	**Variable**	**Unburned forest**			**Burned forest**			**t-test**		
		Mean ± SE	**Min.**	**Max.**	**Mean ± SE**	**Min.**	**Max.**	***t***	***df***	***P***
Individual *Q. humboldtii*	Tree height (m)	10.1 ± 0.4	9.4	10.7	6.5 ± 0.7	4.8	8.1	9.9	257	6.2^{-6}
	DBH (cm)	20.6 ± 1.8	0.9	77.0	12.5 ± 0.8	2.0	52.0	17.9	257	2.2^{-16}
Fire incidence	Charring height (%)	0	0	0	0.6 ± 0.1	0	1.0	14.3	257	2.2^{-16}
	Scar number	0	0	0	1.6 ± 0.1	0	8.0	10.4	257	2.2^{-16}
	Scar area (m^2)	0	0	0	0.3 ± 0.1	0	3.0	6.2	257	2.1^{-10}
Q. humboldtii patches	Slope (%)	23.9 ± 13.3	6.2	49.8	16.7 ± 2.3	12.5	23.3	3.7	6	1.0^{-3}
	Canopy cover (%)	29.5 ± 3.4	25.9	36.3	8.4 ± 1.2	6.3	11.8	3.9	6	8.2^{-5}
	Density of woody plants outside the patch (inds./100 m^2)	0.3 ± 0.1	0	0.3	0.2 ± 0.1	0.1	0.2	8.1	6	1.8^{-5}
	Density of *Q. humboldtii* inside the patch (inds./100 m^2)	0.2 ± 0.1	0.1	0.2	0.3 ± 0.1	0.1	0.3	8.4	6	1.6^{-5}
	MPAR	313 ± 60	233	430	550 ± 38	470	644	7.9	6	2.1^{-5}
	CIRCLE	0.7 ± 0.1	0.6	0.8	0.8 ± 0.1	0.6	0.9	13.1	6	1.2^{-6}
Total acorns	Acorn density (acorn/100m^2)	7.2 ± 3.2	0	500.0	170.0 ± 31.5	0	3000.0	5.4	419	9.3^{-8}
	Distance to closest *Q. humboldtii* (m)	1.8 ± 0.3	1.0	3.5	1.9 ± 0.3	0.2	9.7	8.6	59	4.5^{-12}
	Distance to patch edge (m)	-14.0 ± 3.1	-25.0	0	- 13.4 ± 1.5	-25.0	25.0	10.1	59	2.3^{-14}
Healthy acorns	Acorn density (acorn/100m^2)	4.4 ± 1.5	0	1100.0	0.4 ± 0.4	0	100.0	3.1	419	2.6^{-3}
	Distance to closest *Q. humboldtii* (m)	1.8 ± 0.4	1	3.5	1.4	1.4	1.4	5.6	8	4.9^{-4}
	Distance to patch edge (m)	-13.1 ± 3.4	-25.0	0	5.0	5.0	5.0	3.1	8	1.5^{-3}
Seedlings	Seedling density (inds./100m^2)	31.1 ± 4.9	0	500.0	2.5 ± 1.8	0	400.0	6.1	419	2.3^{-9}
	Distance to closest *Q. humboldtii* (m)	2.1 ± 0.3	0.1	10.0	1.8 ± 0.9	0	3.0	7.2	48	3.5^{-9}
	Distance to patch edge (m)	-11.1 ± 1.5	-25.0	- 10.0	-15.0 ± 2.9	-20.0	-10.0	7.6	48	8.1^{-10}

Table 4.2. Final model parameters, the Akaike Information Criterion (AIC), and the Area Under the Curve (AUC) explained by the models for each postfire response type in *Quercus humboldtii* (resprouting ability, resprouting from the stump, and resprouting from the crown). All models, variable coefficients, and AUC values are significant ($p < 0.05$).

Response	**Model**	**Model family**	**AICc**	**AUC**	***df***	**Fixed effects**	**Estimate**	**SE**	***z***	***p***
Resprouting ability	Tree height + Charring height + Site + Transect	binomial (logit)	122	0.93	159	Tree height	0.2	0.1	1.6	0.10
						Charring height	0.04	0.01	-3.3	7.5^{-5}
						Intercept	-4.1	1.3	3.2	1.3^{-4}
Resprouting ability form stump	Tree height + Scar number + Charring height + Scar area + Site + Transect	binomial (logit)	110	0.94	117	Tree height	0.2	0,1	2.2	0.03
						Scar number	0.4	0.2	2.4	0.02
						Charring height	0.06	0.01	4.5	7.8^{-6}
						Scar area	1.	0.6	2.1	0.04
						Intercept	8.5	1.7	-5.1	4.5^{-7}
Resprouting ability form crown	Charring height + Scar number + Density of woody species + Site + Transect	binomial (logit)	136	0.79	117	Charring height	-0.02	0.01	-2.5	0.01
						Scar number	-0.4	0.2	-2.0	0.05
						Density of woody species	7.2	3.3	2.2	0.03
						Intercept	-1.6	0.8	-1.9	0.05

Stump resprouting

The most parsimonious model for estimating *Q. humboldtii* ability to resprout from the stump included variables related to fire incidence and tree size as the most influential explanatory variables (Table 4.2; Figure 4.3). Thus, the proportion of charred stem and the number and surface area of fire scars were positively related to the probability of resprouting from the stump. Similarly, resprouting from the stump was more likely in the tallest trees (Table 4.2, Figure 4.3, and Appendix 4.2).

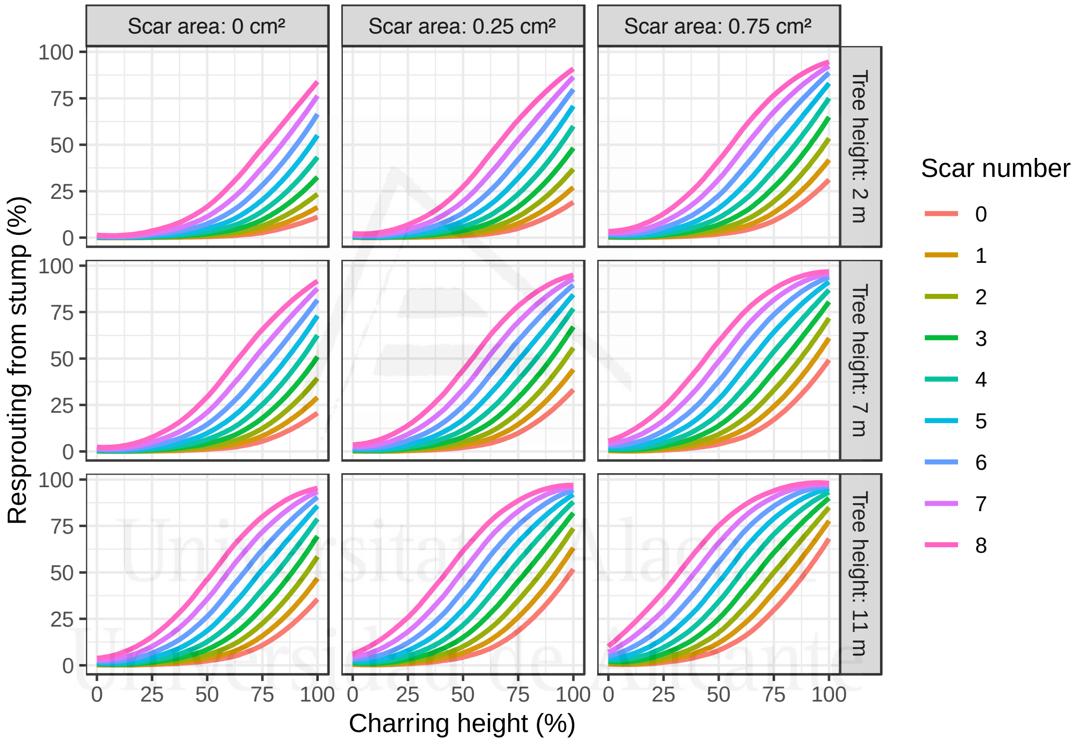

Figure 4.3. The proportion of resprouting *Quercus humboldtii* individuals that resprouted from the stump as a function of the proportion of charring height (%), number of scars, scar area, and tree height. Model parameters are described in Appendix 4.2.

Crown is resprouting

As measured by the number of scars and charring height, fire incidence decreased the probability that trees resprouted from the crown (Figure 4.4, Appendix 4.3). Conversely, the probability of resprouting from the crown increased with the density of accompanying trees. For example, resprouting from the crown was higher than 50% in trees with few scars or a low proportion of charring height and sharing space with 0.3 individuals/m$^{2.}$ In contrast, it was almost null when trees were damaged eight times by fire, or the charring height proportion exceeded 75% of the tree.

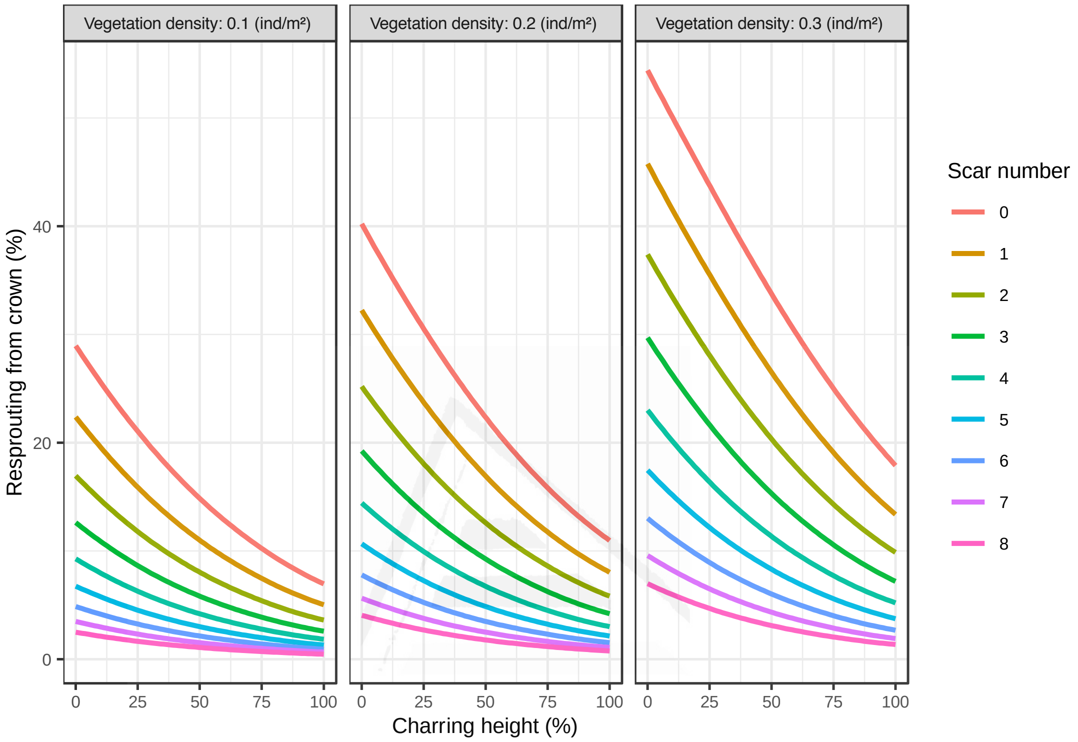

Figure 4.4. The proportion of resprouting *Quercus humboldtii* individuals that resprouted from the crown as a function of charring height (%), number of scars, and the density of woody vegetation outside the *Quercus humboldtii* patch in the Iguaque mountains. Model parameters are described in Appendix 4.3.

Acorn density

The density of acorns (Table 4.3, Figure 4.5, Appendix 4.4) and healthy acorns (Table 4.3, Figure 4.5, Appendix 4.4) was highly heterogeneous in burned and unburned forests, ranging from 0 to 3,000 acorns/100 m^2 (all acorns) or 0-100 acorns/100 m^2 (healthy acorns) (Table 4.1 and Table 4.3). The number of acorns was higher in burned than in unburned *Q. humboldtii* forests. However, most acorns in burned forests were incompletely developed; thus, the number of healthy acorns was low in both types but higher in the unburned forests than in the burned forests.

Acorns were close to adult *Q. humboldtii* individuals in burned and unburned forests, with an average distance between 1.8 and 1.9 m and a maximum distance below 10 m. Results were similar for healthy acorns, as the average distance to the nearest *Q. humboldtii* was 1.4-1.9 m. The average distance to the forest edge was similar in burned and unburned forests, but no acorns were found outside the forest patches in unburned forests. In contrast, acorns were distributed along the whole transect in burned forests.

Four variables, distance to the forest patch edge, distance to the nearest adult, fire, and slope, explained 75% of the variability in acorn density (Table 4.3, Figure 4.5, Appendix 4.4). Acorn density was higher in steeper slopes. The difference in acorn density between burned and unburned forests increased with slope and distance to adult *Q. humboldtii. It decreased* with distance to the forest edge, and thus it was highest in the inner part of steep forest patches, far from the influence of adult *Q. humboldtii*. Only two variables were included in the model to explain the density of healthy acorns: distance to the forest edge and fire. The model explained 85% of the variance in healthy acorn density (Table 4.3, Figure 4.5, Appendix 4.5).

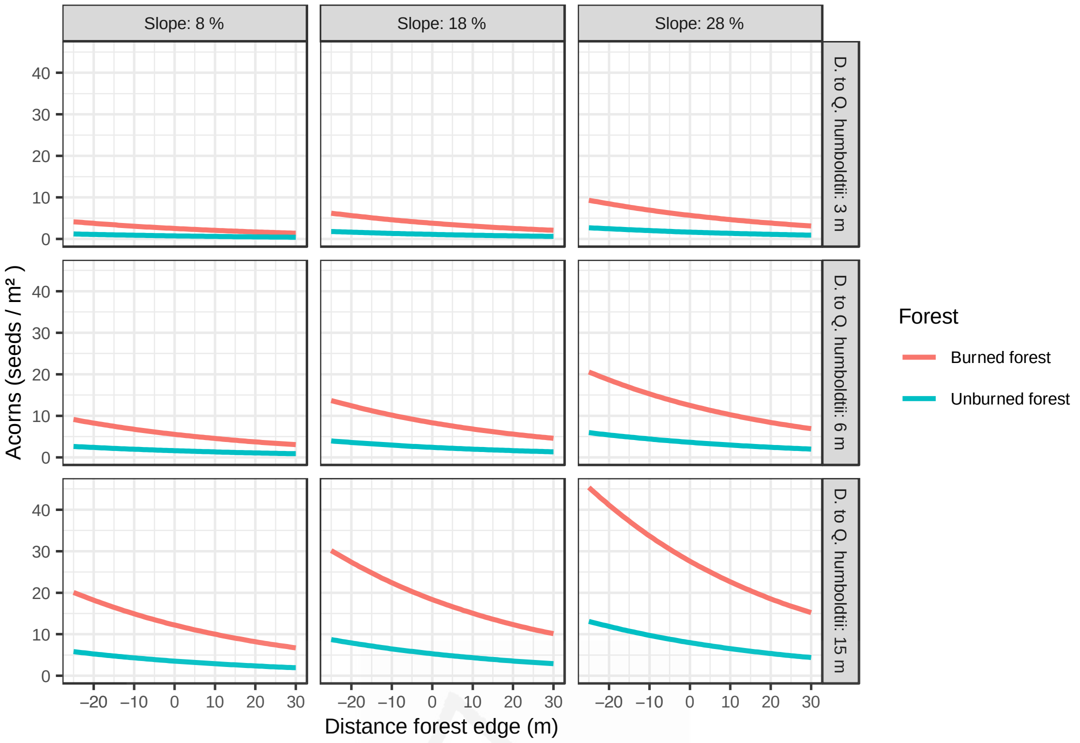

Figure 4.5. Acorn density in burned (Burnt, red line) and unburned (Unburnt, blue line) forests as a function of slope, distance to closest *Quercus humboldtii* adult tree, and distance to the forest edge. Negative numbers represent locations within the forest. Model parameters are described in Appendix 4.5.

Table 4.3. Final model parameters, the Akaike Information Criterion (AICc) and the Area Under the Curve (AUC) explained by the models for each postfire response type in *Quercus humboldtii*: acorn density (acorns/m^2), the proportion of healthy acorns (%), and seedling density (seedlings/m^2). All models, variable coefficients, and AUC values were significant (P < 0.05).

Response	**Model**	**Model family**	**AICc**	**AUC**	***R2***	***df***	**Fixed effects**	**Estimate**	**SE**	***z***	***p***
Acorn density	Burnt/Unburnt + Slope + Distance to closest *Q humboldtii* + Distance to patch edge + Site + Transect	Zero inflated Poisson (log)	841	NA	0.75	420	Zero Burnt	13.1	0.2	8.2	$< 2.0^{-16}$
							Zero Unburnt	13.1	0.4	3.3	9.6^{-4}
							Intercept (Burnt)	0.9	0.2	4.3	2.1^{-05}
							Unburnt	-1.2	0,2	-5.1	4.9^{-07}
							Slope	0.1	0.01	5.2	2.2^{-07}
							Distance to closest *Q. humboldtii*	0.1	0.02	3.8	1.4^{-4}
							Distance to patch edge	-0.01	0.01	-3.8	1.5^{-4}
Healthy acorns (%)	Burnt/Unburnt + Distance to patch edge + Site + Transect	binomial (logit)	80	0.85	NA	420	Intercept (Burnt)	-5.8	1.0	-5.5	3.5^{-8}
							Unburnt	2.4	1.1	2.3	0.02
							Distance to patch edge	-0.1	0.02	-2.2	0.03
Seedling density	Burnt/Unburnt + Distance to closest *Q. humboldtii* + Site + Transect	Poisson (log)	308	NA	0.24	420	Intercept (Burnt)	-5.0	0.7	-6.8	1.0^{-11}
							Unburnt	-3.0	0.7	4.5	1.1^{-5}
							Distance to closest *Q. humboldtii*	0	0	0.8	0.4

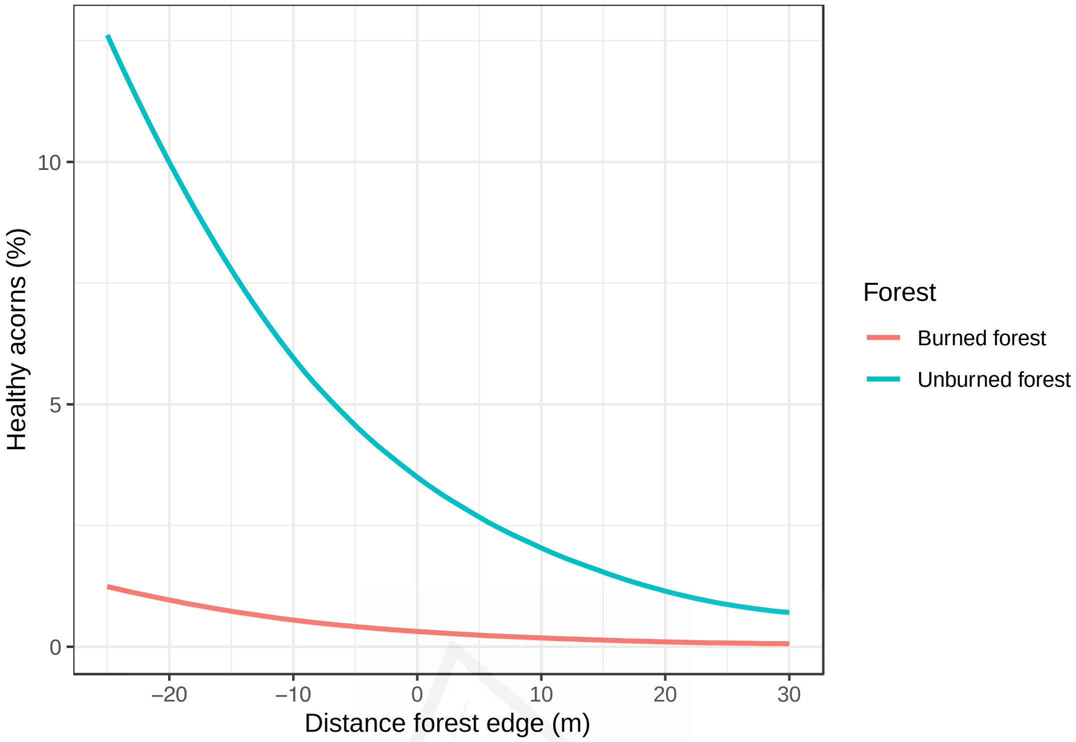

Figure 4.6.The density of healthy acorns in burned (red line) and unburned (blue line) *Quercus humboldtii* forests as a function of distance to the forest edge. Negative numbers represent locations inside the forest patch. Model parameters are described in Appendix 4.5.

Seedling density

Seedling density was spatially heterogeneous, with maximum densities attaining 4-5 seedlings/m^2. The average density was more than 10-fold higher in unburned forests than in burned forests. Seedling density increased as the distance to the nearest *Q. humboldtii* increased. Most seedlings persisted under the forest canopy; thus, the distance to the forest edge was largely negative. Distance to the nearest *Q. humboldtii* adult tree and fire were the only variables included in the model to explain seedling density (Table 4.3, Figure 4.7, Appendix 4.6).

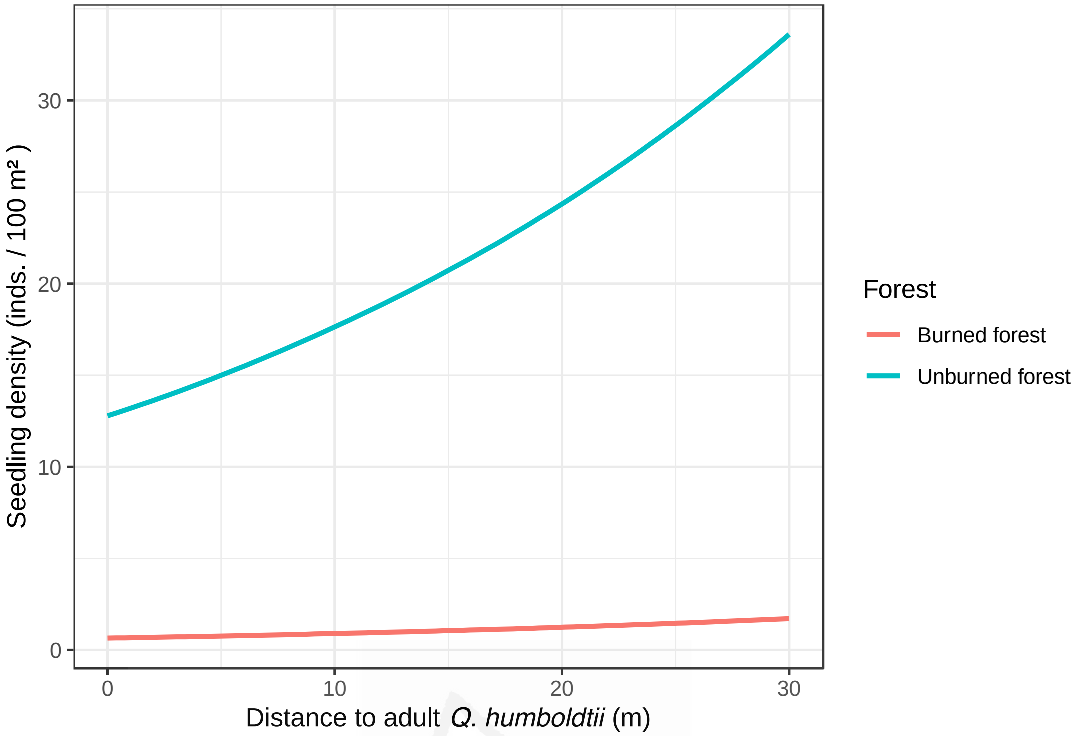

Figure 4.7. The density of *Quercus humboldtii* seedlings in burned (Burnt, red line) and unburned forests (Unburnt, blue line) as a function of distance to closest adult. Model parameters are described in Appendix 4.6.

DISCUSSION

In the Iguaque forests affected by wildfires, the fire triggers post-fire resprouting in *Q. humboldtii* trees. This is an important survival and regeneration mechanism that allows the trees of this species to withstand about three fires in 30 years. Under this fire regime and without other disturbances, *Q. humboldtii* can dominate the forest community. Other tree species of the Andean Forest are intensely affected and are absent in the post-fire communities. However, repeated wildfires affect the *Q. humboldtii* viable acorns density. Although the surviving trees can produce acorns two and a half years after the fire, the fires affect acorn maturation and seedling recruitment.

Resprouting ability

In the Iguaque mountains, most *Q. humboldtii* adult trees resprouted after at least three fires during the previous thirty years. *Quercus humboldtii* can withstand this fire regime and dominate the forest patch community after the fire (up to 30 individuals/ha in burned forests). Other tree species of the Andean Forest are more intensely affected by fire and absent in post-fire communities (Salazar *et al.*, 2020). This result contrasts with our observations of a reduction in the cover of forest patches and increasing patch fragmentation (Aguilar-Garavito *et al.*, 2020) and the scarcity of *Q. humboldtii* seedlings in burned shrublands (Aguilar-Garavito *et al.*, in prep A). Shrinking *Q. humboldtii* patches may thus be a consequence of recruitment limitation in the periphery of forest areas (see below) rather than direct mortality of adult trees.

Resprouting depended on the severity and frequency of fire and tree size. These results agree with previous observations identifying fire regime and tree size as drivers of resprouting ability in woody species (Bellingham & Sparrow, 2000; Bond & Midgley, 2001; Pausas & Keeley, 2017)

Resprouting plants, such as some *Quercus* spp., protect buds in the root collar, meristems, and cambium under a thick bark and other protective structures (Johnson *et al.*, 2002; Pausas & Keeley, 2017). Also, they can store resources in roots, stumps, and stems to support resprouting (Iwasa & Kubo, 1997; Bond & van Wilgen, 1996).

Our results also show that larger trees had a higher resprouting ability and a higher probability of resprouting from the stump, crown, or both than smaller trees. This may be related to the availability of more buds and higher amounts of stored resources, tree architecture, distance to flames and heat, and protecting tissues in large trees (Espelta *et al.*, 2003; Ordóñez *et al.*, 2005). Tree age and a higher probability of large trees experiencing many resource-depleting fires had a minor effect on resprouting (Costa *et al.*, 2004; Silva & Catry, 2006). However, larger or older trees may gradually lose their ability to resprout as dormant buds are depleted during their lifetime (Bellingham & Sparrow, 2000). Despite the positive relationship between tree size and resprouting ability, it is worth noting that even small trees (e.g., 3 m stem height) could resprout.

Patch shape and size were not included in the model to explain tree resprouting ability. In some cases, these variables could not be used in the models because they were collinear with other variables such as burned or unburned forest, charring height, number and area of scars, and density of woody vegetation around the forest patch. This may be related to the limited variability of forest patches.

Quercus humboldtii trees experiencing with higher fire severity (measured as charring height and scar area), and frequency (number of scars) were more likely to resprout exclusively from the stump. Resprouting occurs in the lower parts of the plant when the fire is intense or frequent (Kozlowski *et al.*, 1991; Miller, 2000). Severe fires can kill buds along the stem, and only belowground tissues can remain active after the fire (Bond & Midgley, 2003; Costa *et al.*, 2004). Our results agree with tree regrowth models (Bellingham & Sparrow, 2000; Moreira *et al.*, 2007; 2008). However, it should be noted that severe fires can also trigger extensive regrowth responses in *Q. humboldtii* after a fire. For different species of the genus *Quercus* in North America and the Mediterranean region, the greater the fire severity, the greater the regrowth response (Espelta *et al.*, 2003; Cooking *et al.*, 2014; Cooper *et al.*, 2018; Ackerly *et al.*, 2019).

In the Iguaque Mountains, 55% of the resprouted trees showed crown resprouting. The proportion of trees resprouting from the crown depended on fire severity, tree size, and shrub density around the tree. The higher proportion of trees resprouting from the crown in dense post-fire shrublands seems counterintuitive. If shrubland density was higher before the fire, higher fuel accumulation should release more heat and increase tree damage. On the other hand, competition for resources should result in a trade-off between shrubland growth and tree vitality and resprouting. Thus, lacking more elaborate explanations, we must assume that shrubland density and tree resprouting responded to common environmental factors such as soil fertility.

Acorn density

Quercus humboldtii produced acorns two years and a half after the last fire (Aguilar-Garavito et al. in prep A). Adults of *Q. humboldtii could* produce acorns rapidly because most trees were not completely dead or partially damaged. Thus, *Q. humboldtii* can recover quickly from fire through resprouts and acorns. In the Iguaque mountains, the precipitation has a bimodal regime, with two rainy periods per year (Villareal *et al*., 2017). The 2015 wildfire occurred a few weeks before the start of the second rainy season of that year (Aguilar-Garavito *et al*., 2020). Likewise, the following two years were exceptional because they had abundant rainfall due to the La Niña Phenomenon (NOAA, 2023). In this way, the post-fire humidity conditions could have favored the simultaneous production of acorns and resprout.

In burned forests, acorn density was higher than in unburned forests, suggesting that fire or post-fire conditions stimulated acorn production in some way. Other studies have observed increased seed production in disturbed plants (López *et al*., 2016; Velosa *et* *al*., 2018), including oaks (Guariaguata *et al*., 2006; Jones *et al*., 2015), which has been related to early successional colonization (Howe & Smallwood, 1982). However, unburned forests may have been in a phase of low seed production, while burned forests were in the opposite phase. It has been observed that *Q. humboldtii* shows high interannual variations in acorn production (Gómez & Toro, 2007). In other *Quercus* species, this has been called masting (Guariguata & Sáenz, 2002; Yu *et al.,* 2003; Torres *et al.,* 2004; Carbonero &Fernández-Rebollo, 2014). Therefore, we must be careful when comparing acorn density in different localities in the same year.

Despite the high acorn production in the burned forests, the density of healthy acorns was very low. Ten times lower than in the unburned forests. We only found viable acorns in one of the burned forests sampled (0.4 acorns/100 m^2). Burned trees may prioritize investing their resources in regrowth at the expense of allocating resources to each acorn (Funk *et al*., 2016; Schermer *et al.,* 2019). However, post-fire conditions, including low nutrient availability, predatory insects, direct radiation, and low pollen availability, most likely favored acorn damage and abortion (Diaz *et al.,* 2003; Salazar *et al.,* 2020). In addition, fires by burning the crown reduce the effective area for acorn production (Díaz *et al*., 2003; Melo & Parrado-Rosselli, 2010).

Both incompletely developed and healthy acorns were distributed mainly within forest patches and relatively close to adult trees. This distribution reflects the two main dispersal strategies in oak trees: barochory and zoochory. Squirrels and other acorn dispersers in the Iguaque mountains only reach a few meters outside the forest (Gómez, 2003; López-Barrera & Manson, 2006). This process may be aggravated by the increasing fragmentation of *Q. humboldtii* forests (Aguilar-Garavito *et al.,* 2020). The scarcity of acorns and seedlings outside forest patches suggests that birds do not play a significant role in acorn dispersal in these mountains, unlike in other *Q. humboldtii* forests (Gómez, 2003).

Many studies describe a direct relationship between *Quercus* species productivity and acorn production (Blarer & Doebeli, 1996; Bellingham & Sparrow, 2000). However, in our study, acorn density was higher on steeper and probably less fertile slopes. This may show higher tree density or differences in tree age on these slopes, as *Q. humboldtii* forests have been intensively harvested in the Iguaque mountains, particularly in flat, easily accessible areas (Villareal *et al*., 2017). We cannot exclude the possibility that factors associated with the severity and frequency of wildfires, but not accounted for in the variables measured in our study, affected acorn production on these slopes.

In addition, steeper slopes favored barochory, and acorns may roll beyond the tree canopy (Melo & Parrado-Rosselli, 2010). Under these conditions, the arrival of acorns to the lower parts of the mountains and river canyons is easy. The density of acorns is highest in the forest interior and gradually decreases until the edge. From there, the reduction in density continues up to 30 m outside the edge. This is due to the scarcity of dispersing animals that can transport acorns further away (Lopez-Barrera &Manson, 2006).

Seedling density

Seedling density was lower in the burned forest than in the unburned forest (i.e., <1 seedling/m^2). Their densities were much lower than those reported in Andean oak forests with minor intervention (26 seedlings/m^2; Becerra, 1989) but were close to those in Andean oak forests affected by other disturbances (6 seedlings/m^2; León *et al.*, 2009). Seedlings were mainly located under the canopy of *Q. humboldtii* and in the inner parts of the forest patches. In other oak forests, this pattern has been observed in small and highly disturbed patches (Guerrero *et al.*, 2010). In this study, this distribution is consistent with the distribution of acorns, as reflected by the correlation between acorn density and seedling density. It may also indicate more suitable environmental conditions for seedlings within forest patches.

Seedling density in the unburned forests was twelve times higher in the burned forests than in their periphery or outside. Thus, fire may suppress seed and seedling banks, particularly as fire season in Iguaque largely coincides with peak acorn production (Aguilar-Garavito *et al.*, 2020; in prep B).

The strong relationship between the distribution of healthy acorns and seedlings, the distribution of forest patches, and the passage of fire have important implications for post-fire succession. On the one hand, resprouting and acorn and seedling dispersal inside the forest patches may allow forest regeneration where oaks persist, particularly in the inner parts of forest patches. On the other hand, succession from shrublands to forests may be impeded by natural processes, which agrees with other studies on the effect of fire on vegetation patterns in the Iguaque Mountains (Aguilar-Garavito et al. in prep A).
These seedlings were also found under the canopy and up to 10 m from the nearest *Q. humboldtii* tree. In addition, the seedlings were distributed along the entire plot length. Although mainly in the forest's interior, between 10 and 15 m beyond the edge. In the burned forests, we also observed that the density of *Q. humboldtii* with diameters less than 5 cm is also very low. That is because seedling recruitment has been very low, and that seedling loss also occurred in the fires before the 2015 fire.

Otherwise, recruitment limitation of *Q. humboldtii* may occur in the burned areas of the Iguaque Mountains. First, the low density of viable seeds caused by the fires may be causing source limitation (Pulido & Díaz, 2005), at least during the first post-fire years. On the other hand, there may be dispersal limitations (Palma *et al*., 2021) in the *Q. humboldtii* forest and the shrub matrix. First, due to the location of the forest relicts on slopes and secondly, *Q. humboldtii* dispersing animals, such as squirrels, dare little to go beyond the forest edge (Gómez, 2003; Vargas, 2006). In addition, their populations may be significantly reduced and with significant mobility difficulties due to the fragmentation of the forest. Finally, there may be limitations to establishment and growth (Rey & Alcántara, 2000; Acácio *et al.,* 2007) since the return time of fires is very high (three to seven fires in thirty years) and coincides with times when seeds and seedlings are vulnerable. Therefore, burning contributes to the massive destruction of seedlings recruited between fires.

Management recommendations

The resprouting trees in the Iguaque mountains burned forest are very old or burned repeatedly (between two and eight times). Therefore, their regrowth capacity and resource reserve may have been affected. In addition, the high density of shrubs around the forest patches increases fuel contiguity and fire risk. A highlight is an urgency of developing an integrated fire management program (Moreira *et al.*, 2020) that includes tree and forest protection and control of refined fuel in burned areas, among other measures, to reduce the severity and frequency of fires. In this sense, generating areas with less fuel load or more heterogeneous cover and greater moisture retention around trees and forests can reduce fires. In addition, a species group focus can be exotic species and grasses. The priority sites are the forest interface with other coverages.

As we have seen, *Q. humboldtii* can resprout a few months after fires. Several years after the fire, it could also be recruited by seeds into the forest. However, the density of acorns and seedlings in the burned areas is low, and the fire has affected the other tree species in the forest. Therefore, in the burned areas of Iguaque, assisted population reinforcement programs should focus on reintroducing the acorns and seedlings of *Q. humboldtii* and the other tree species of the Andean Forest no longer found in the burned sites.

CONCLUSIONS

We have shown that fire triggers post-fire resprouting *in Q. humboldtii* trees, which is a crucial tree survival end regeneration mechanism but limits acorn maturation and seedling recruitment. Our results show that *Q. humboldtii* colonization and the expansion of forest patches will be unlikely under the current wildfire regime. This has a significant bearing on the protection of *Q. humboldtii* forests. On the one hand, forest management should reduce wildfire frequency and severity. Moreover, post-fire succession from shrublands to *Q. humboldtii* forests may be arrested. To facilitate the recovery of *Q. humboldtii* forests, this regeneration threshold should be overcome by seeding or planting.

Resprouting is a crucial trait of *Q. humboldtii* to increase its resilience after disturbances like fire. The resprouting ability of this species allows the burned forests of the Iguaque mountains to rapidly recover their biomass during the first two years post-fire, even if they have received simultaneous crown and stump damage. During this period, resprouting is the fundamental strategy of natural regeneration, even more important than recruitment through acorns.

The fire regime of the last 30 years in the Iguaque Mountains has generated *Q. humboldtii* recruitment limitations inside and outside the forest. In the burned areas, reducing the viable acorns' density generates limitations in the source. Similarly, the low seedlings density shows *Q. humboldtii* dispersal and establishment limitations.

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SUPPLEMENTARY MATERIAL 4

Appendix 4.1. Parsimonious resprouting ability model and odds ratios for *Q. humboldtii*.

Appendix 4.2. Parsimonious stump resprouting model and odds ratios for *Q. humboldtii*.

Appendix 4.3. Parsimonious crown resprouting model and odds ratios for *Q. humboldtii*.

Appendix 4.4. Parsimonious acorn density model and odds ratios for *Q. humboldtii*.

Appendix 4.5. Parsimonious healthy acorn density model and odds ratios for *Q. humboldtii*.

Appendix 4.6. Parsimonious seedling density model and odds ratios for *Q. humboldtii*.

CHAPTER 5. Producción y germinación de bellotas de *Quercus humboldtii* en un robledal andino afectado por incendios recurrentes

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Quercus humboldtii acorns production and germination in Andean oak forests affected by wildfires.

ABSTRACT

Anthropogenic disturbances, including wildfires, threaten the diversity of tropical Andean ecosystems. Consequently, 60-90% of Colombia's pre-Columbian Andean oak forests have disappeared. Andean oak forests are dominated by *Quercus humboldtii*, the only South American species of Fagaceae. This species has high socioeconomic and biodiversity interests. The reproductive response of this species will condition its regeneration capacity and the persistence of the forests. However, our knowledge of the effect of fire on the production and germination of acorns in *Q. humboldtii* is incipient. We evaluate the production and germination of *Q. humboldtii* acorns in oak forests affected by wildfires. We monitored (fourteen months) acorn production and germination in *Q. humboldtii* trees from fire and non-fire-affected forests (central Colombia Andes, Boyacá, the Iguaque mountains). We also evaluated fire incidence, tree size, precipitation, temperature, and other site characteristics. The acorn production began 34 months after the fire. In burned oaks, the production of incompletely developed acorns (abortions) was almost nine times higher than viable acorns. In addition, Oaks with larger scar areas or many scars were more likely to produce aborts. Conversely, oaks of larger size, especially in the crown, tend to produce more acorns. The few viable acorns from fire-affected trees had smaller sizes and lower germination rates than unburned trees in the literature. The unburned trees in this study did not produce mature acorns, but abortion production was ten times lower than in the burned trees. Therefore, it is feasible that *Q. humboldtii* presents masting, and the unburned trees are in a low production cycle. The fire, tree size, and masting drive acorn production in the Iguaque oak forests. These could affect the recruitment of the species due to a possible limitation in the source.

KEYWORDS: Andean oak, Fruition, Fruit production, Germination, *Masting*, Reproductive phenology, Wildfires.

El norte de los Andes es una de las regiones biodiversas del planeta Tierra (Meyers *et al.*, 2000; Olson & Dinerstein, 2002). Su riqueza ecosistémica, de especies raras y endémicas proporcionan invaluables beneficios para la humanidad. El agua, las materias primas, los escenarios espirituales, educativos y recreativos, son algunos de ellos. Sin embargo, desde la época precolombina más del 60% de los ecosistemas del norte de los Andes se han alterado (Rodríguez *et al.*, 2006; Etter *et al.*, 2008). La deforestación, el uso agropecuario y los incendios de la vegetación han sido los principales motores de transformación y pérdida de estos ecosistemas (MADS, 2015; Correa-Ayram *et al.*, 2020).

Los robledales andinos son un tipo de bosque Andino, dominado por *Quercus humboldtii* Bonpl. (roble andino), la única especie de *Quercus* Sudamericana (Kapelle, 2006; Avella, 2016). La extensión de estos robledales se ha visto reducida entre un 60-90% de su extensión prehispánica (Rangel-Ch, 2000; Etter *et al*., 2008). A pesar de las medidas de protección (Solano *et al*., 2005; MAVDT, 2006) aún se sigue viendo afectados por los mismos motores de transformación (*Avella et al*., 2015; Fernández-Méndez *et al.*, 2016).

La producción de frutos es un proceso fundamental que sustenta las dinámicas naturales de reclutamiento y mantenimiento de la vegetación, así como para el restablecimiento de esta en los ecosistemas disturbados (Dey *et al*., 2010; Ibarra-Manríquez *et al.*, 2015). Además, a través de las bellotas se da una importante interacción entre muchas especies de *Quercus* y los animales, ya que estas plantas dependen en gran medida la fauna para su dispersión y los animales de la disponibilidad de frutos para mantener sus poblaciones (López-Barrera & Manson, 2006, Ramos-Palacios & Badano, 2014; Delgado-Fernández *et al*., 2017). Sin embargo, las actividades humanas también han intervenido en las interacciones planta-animal, afectando la integridad funcional de los ecosistemas (Barragán *et al*., 2018). Es así como investigar las fases iniciales del ciclo de vida de las plantas contribuye a la identificación de alteraciones dicha dinámica (Jump *et al.*, 2007; Wróbel & Zwolak, 2019). También proporciona información valiosa que pude contribuir al restablecimiento de los robledales (Ramos-Palacios & Badano, 2014).

Estudios fenológicos del roble andino han reportado la producción de bellotas durante dos épocas del año. Estas suelen ocurrir desde finales de la temporada seca y durante la temporada lluviosa (Pacheco & Pinzón, 1997; Pardo & Chiquillo, 2002; Burgos, 2015). Sin embargo, el efecto de los disturbios antrópicos sobre la producción de bellotas en *Q. humboldtii*, así como en otras especies de *Quercus,* ha sido poco estudiado.
En robledales de Norte América, la fragmentación de los bosques afecta la producción de bellotas, haciendo que en los parches de bosque más pequeños, sea frecuente la producción de bellotas con desarrollo incompleto que caen al suelo (abortos; Ramos-Palacios *et al*., 2013). En robledales de Centro América, afectados por deforestación, Guariaguata y Sáenz (2002) encontraron una mayor producción de bellotas en bosques que fueron talados selectivamente con respecto a los que no lo fueron. Por otra parte, en robledales

mediterráneos, Jones *et al.* (2015) obtuvieron una mayor producción de bellotas en los bosques que habían sido incendiados.

En Colombia se ha observado que en los robledales afectados por uso agropecuario, la producción de semillas del roble andino es menor que en los bosques menos disturbados (González & Parrado 2010). De igual forma, en robledales con mayor fragmentación e incidencia antrópica hay una mayor producción de bellotas abortadas (Pérez *et al*., 2013). Sin embargo, la respuesta del roble andino a los incendios forestales sólo se conoce a partir de observaciones anecdóticas (Avella, 2016), desconociéndose el efecto de los mismos sobre su fenología y los mecanismos de regeneración natural

El macizo de Iguaque en Villa de Leyva-Colombia, es un ejemplo de la creciente incidencia de los incendios en la cobertura vegetal de la región Andina (Aguilar-Garavito et al., 2020). Sus laderas, luego de una intensa deforestación, se destinaron durante mucho tiempo para el uso agropecuario. Finalmente se generó un paisaje antropizado dominado por pasturas y matorrales que rodean algunos relictos de robledal y de páramo con distinto tamaño y grado de conservación. Debido a su alto valor socioecológico, desde 1977 gran parte del macizo fue designado como área natural protegida de escala nacional, el Santuario de Fauna y Flora Iguaque-SFFI (Villarreal *et al.,* 2017). A pesar de lo anterior, durante las últimas tres décadas, Iguaque ha sido afectado por incendios recurrentes (siete en 30 años), que han quemado alrededor del 28% del área protegida, reduciendo y fragmentado el 45% los bosques de roble remanentes que existían al suroccidente del macizo en 1970 (Aguilar-Garavito *et al.*, 2020). El conocimiento de la incidencia de los incendios forestales en la producción de semillas es crucial para comprender la dinámica de regeneración del bosque y del reclutamiento del roble, así como para la elaboración de estrategias de gestión para proteger la biodiversidad y mantener el bienestar humano.

Este estudio indaga sobre el papel del fuego en la producción de bellotas del roble andino. Monitoreamos la producción y germinación de bellotas en robles afectados y no afectados por incendios. Lo anterior estuvo dirigido a responder las siguientes preguntas: 1) ¿Cuál es la cantidad de bellotas viables y abortadas que se cosechan de robles andinos afectados y no afectados por incendios?; 2) ¿Existen diferencias en el tamaño, biomasa y tasa de germinación de las bellotas viables provenientes de robles quemados, respecto a las bellotas que provienen de los robles no quemados?; 3) ¿los robles quemados producen una mayor cantidad de bellotas abortadas? y 4) ¿Cuál es la relación entre la temperatura y la precipitación respecto la cantidad de bellotas producidas por robles andinos afectados y no afectados por incendios?

MÉTODOS.

Descripción del roble andino

Quercus humboldtii (Fagaceae) es un árbol de copa globosa, entre 15 y 30 m de altura (Mahecha et al., 2010). Es una especie monoica, sus flores amarrillas, pequeñas y en racimo son polinizadas por el viento e insectos (Palacio & Fernández, 2006). El fruto es una bellota (fruto seco, tipo nuez, característico de las especies de *Quercus*) recalcitrante marrón. Su dispersión primaria es por gravedad y, posteriormente pueden ser redistribuidas o predadas, por ardillas (*Sciurus granatensis* Humboldt), tinajos (*Cuniculus taczanowskii* Stolzmann y *C. paca* Linnaeus), armadillos (*Dasyprocta punctata* Gray), saínos (*Tayassu tajacu* Linnaeus), zarigüeyas (*Didelphys marsupialis* Linnaeus) y aves medianas (Guerrero-Rodríguez *et al.*, 2010). Su fenología varía según la localidad y puede presentar vecería (*masting*), con máximos periódicos separados hasta tres años (Gómez & Toro, 2007). La producción y caída de hojas ocurre durante todo el año, y la producción de flores y frutos es bimodal (Burgos, 2015). La producción de bellotas se suele dar desde mediados de la temporada seca y durante toda la temporada lluviosa (Pérez *et al*., 2013). El desarrollo de la bellota comprende entre cuatro a siete meses (Gómez & Toro, 2007). Éstas no tienen dormancia y germinan de dos a cuatro meses después de caer (Sepúlveda *et al.*, 2014). Un árbol sano puede llegar a producir entre 5 a 8 kg de bellotas (150 a 500 bellotas/kg; Nieto & Rodríguez, 2004), con tasas de germinación en campo que alcanzan el 20%, y el 80% en vivero (Fernández, 2014; Moreno & Cuartas, 2015).

Área de estudio

Este estudio comprende dos relictos de robledal uno afectado por incendios recurrentes y el otro no. Están ubicados sobre la vertiente occidental de la cordillera Oriental, al sur del Corredor de Robles Guantiva-La Rusia-Iguaque (Solano *et al.*, 2015, Armenteras *et al.*, 2003) en la Provincia del Alto Ricaurte-Boyacá (Figure 5.1). Altitudinalmente la provincia comprende entre 2,200 y 3,890 m de elevación.

Climatológicamente presenta un gradiente de temperatura que disminuye con la elevación, así como de precipitación, que incrementa de sureste a noroeste. Presenta una temperatura media de 16,3ºC a 2,200 m de elevación y de 5ºC a 3,800 m. Por su parte la precipitación media anual al sureste alcanza los 683 mm, a la altura del municipio de Villa de Leyva 953 mm y al noreste 1,853 mm. Las lluvias tienen una distribución bimodal, con máximos en marzo-abril y octubre-diciembre. Los meses más lluviosos son los de abril-mayo, con 201 mm de media, y los más secos los de diciembre-febrero, con 40 mm de media. (Villarreal *et al.*, 2017).

Robledal quemado (RQ): es un relicto bosque que hace parte de la Reserva de la Sociedad Civil Robledales, situada en la vereda Sabana Alta del municipio de Villa de Leyva (5º40´21,08” N; 73º29´22” W). Colinda al Oriente con el SFFI, su extensión es de 3 ha. distribuidas en un rango altitudinal entre 2,422 y 2,500 m. de elevación. Este relicto es alargado y estrecho, se encuentra en una matriz dominada por herbazales arbustivos y pasturas, los cuales lo separan entre 0.3 a 1 km de otros robledales de forma y tamaño similar. Este robledal, así como las coberturas vegetales aledañas han presentado una frecuencia de tres incendios en los últimos 30 años, que ocurrieron en 1990, 1994 y 2015 (Aguilar-Garavito et al. 2020).

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El robledal no quemado (RnQ) pertenece a la Reserva de la Sociedad Civil Iguakan, ubicándose en la vereda Saavedra de Roncancio, del municipio de Gachantivá (5º42´34,48”N & 73º29´21”W), a 7 km de RQ. Presenta una extensión de 15 ha, que abarcan un rango altitudinal entre 2,440 y 2,530 m. de elevación. El robledal está inmerso en una matriz agropecuaria y no se evidenciaron incendios en las imágenes de sensores remotos (Landsat, Rapideye y Google Earth de 1991, 2010 y 2015) ni en los reportes Oficiales de Incendio (UNGRD, 2018).

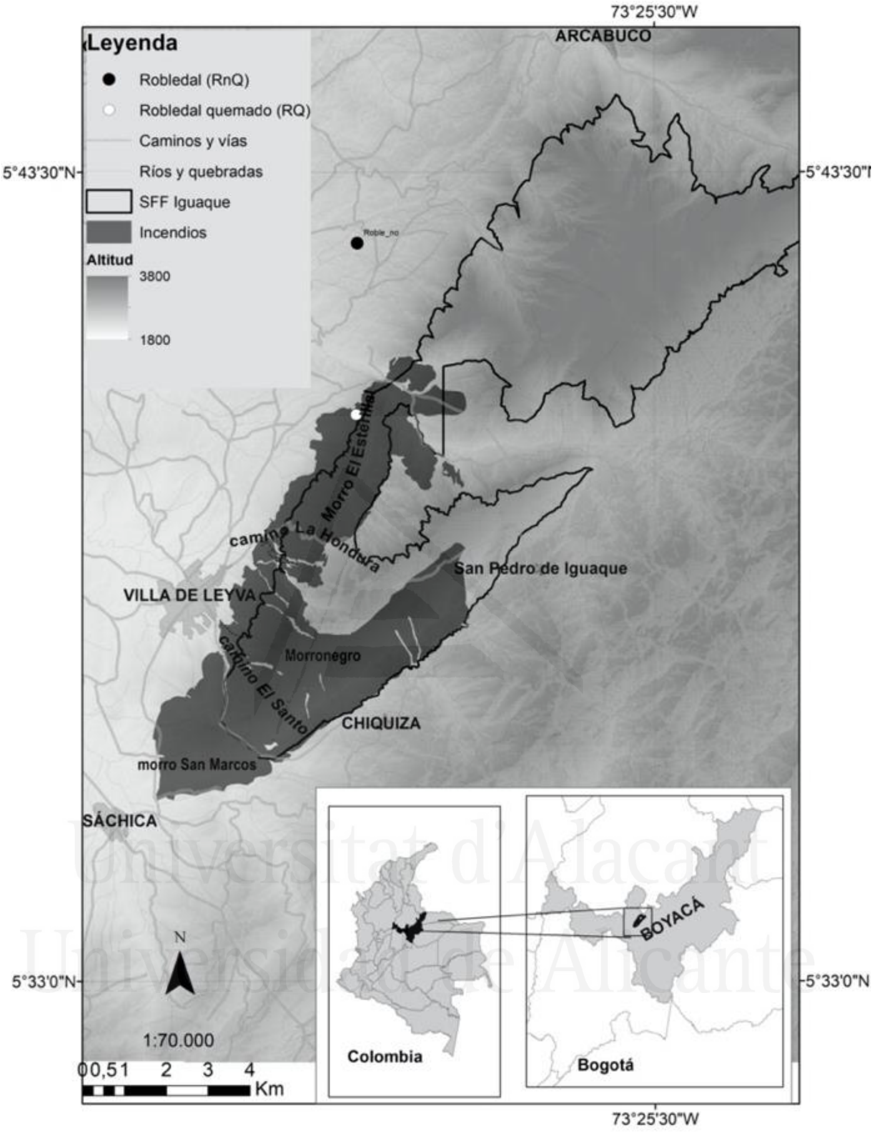

Figure 5.1. Ubicación del robledal no quemado (RnQ) y el robledal quemado (RQ) en la provincia del Alto Ricaurte y del Macizo de Iguaque, departamento de Boyacá, Colombia. Cartografía realizada por: P.J. Isaacs-Cubides.

La selección de estos bosques se realizó a partir de la cartografía de incendios de Iguaque (Aguilar-Garavito et al., 2020) y se tuvieron en cuenta criterios como la facilidad de acceso, un régimen similar de uso histórico (excepto los incendios) y similitud tanto en rango altitudinal como en la relación perímetro-área del parche (0.22 RQ y 0.20 RnQ).

Colecta de Datos

El estudio lo realizamos desde junio del 2018 (fecha en que las bellotas aun no caían en RQ) hasta julio de 2019. La producción de bellotas la evaluamos de acuerdo con los métodos (ajustados) de González y Parrado (2010), Stevenson *et al*. (2005) y Stevenson y Vargas (2008). Para esto, en cada robledal seleccionamos 10 árboles, separados entre sí por una distancia mínima de 100 m. Bajo sus copas distribuimos en triángulo equilátero tres trampas de semilla circulares (1.5 m^2 de diámetro y 1.5 m de alto). Las trampas estaban compuestas por una malla de nylon de 1x1 mm de ojo y 0.8 m de profundidad. Dicha malla era sostenida por un aro metálico y tres tubos de PVC, los cuales clavamos en el suelo, dejando una altura de 1.5 m desde el nivel del suelo hasta el aro.

<u>Características de los árboles productores de bellotas:</u> Medimos el diámetro a la altura del pecho (DAP) de cada árbol estudiado, su altura total, el área proyectada de su copa y su distancia hasta el borde del fragmento de bosque. Adicionalmente, en los árboles del robledal quemado, contamos el número de cicatrices generadas por fuego sobre el tronco y medimos su área. Para esto, asumimos que las cicatrices tenían forma triangular (Apéndice 5.1), por lo que medimos su base y altura para determinar el área del triángulo de la cicatriz. Estas variables dan una aproximación de la frecuencia y severidad de los incendios sobre los árboles (Dickinson & Johnson, 2001; USDI National Park Service, 2003).

Colecta y procesamiento de bellotas: Mensualmente, recogimos y contamos todas las bellotas encontradas en cada trampa, las cuales, transportamos al laboratorio en bolsas de papel debidamente etiquetadas. Allí, clasificamos las bellotas viables o abortos (Ramos-Palacios, et al., 2014) de acuerdo con su coloración, tamaño y diferenciación de estructuras (Pardo & Chiquillo, 2002; Zabala, 2004). También las pesamos (balanza digital 0.1 g de precisión) y medimos cada bellota en su diámetro polar y ecuatorial (calibrador digital 0.01 mm de precisión). Determinamos la producción de bellotas por árbol, considerando la superficie de las trampas. Durante el estudio no se reportaron daños en las trampas. La pérdida de bellotas por rebote la estimamos lanzando 100 bellotas en cinco repeticiones desde una altura de 10 m hacia una trampa idéntica a las utilizadas durante el estudio.

Germinación de bellotas: Determinamos la tasa de germinación de las bellotas viables. Trasladamos las muestras al vivero utilizando bolsas plásticas selladas y etiquetadas. Refrigeramos las muestras a 4 ºC para disminuir la pérdida de viabilidad por desecación (Gómez & Toro, 2007). Como máximo transcurrieron dos días desde la recolección en las trampas hasta la siembra en vivero. Inmediatamente allí, pusimos a germinar las bellotas siguiendo las recomendaciones de Gómez y Toro (2007). En el invernadero, distribuimos y sembramos las bellotas al azar. Utilizamos bandejas plásticas de germinación (30 cm de profundidad) y un sustrato estéril (tierra negra cernida, cascarilla de arroz y hojarasca del robledal en proporción volumétrica 60/30/10). Etiquetamos la procedencia de las muestra en cada bellota sembrada. Ubicamos las bandejas en el centro del invernadero y semanalmente las rotamos entre sí cambiando el sitio de cada bandeja. Con esto buscábamos garantizar que cada bandeja estuviera expuesta a las mismas condiciones de invernadero durante el mismo tiempo. Aplicamos riego diario (07:00 y 17:00 h) manualmente. Semanalmente registramos la germinación de las bellotas y el incremento en altura y diámetro de las plántulas hasta que tuvieron más de cuatro pares de hojas verdaderas y 8 cm de altura. El proceso se completó en nueve semanas (Apéndice 5.2).

Ubicación y condiciones de vivero para la germinación: El vivero se localiza a 30 km al Suroeste (220 º) del RQ. (5º24´49,96"N & 73º42´26,46"W). Su elevación es de 2,550 m. La precipitación, temperatura, humedad relativa y evaporación promedio anual son: 1,108 mm, 15º C, 71 y 76% y 1,180 mm, respectivamente. Consta de un invernadero plástico y estructura en madera (28 m^2 de área y 3.5 m de alto), con malla negra del 45% en el techo, a 2.5 m del suelo.

Procesamiento y análisis de datos

Comparamos la medias y desviación estándar para el número, peso y tamaño de las bellotas viables y abortadas obtenidas de los robles afectados y no afectados por incendios. De igual forma examinamos el DAP, la altura, cobertura de la copa, el número y área de las cicatrices de los árboles seleccionados en cada robledal. Luego, empleamos el test de comparación de medias *Welch* (función *t.test*, paquete "*stats*" del software R; R Core Team, 2023). Previamente comprobamos la normalidad y homocedasticidad de las muestras mediante los test de *Shapiro-Wilk* y *F de Fisher*, con las funciones *shapiro.test* y *fisher.test* del paquete "stats", software R (R Core Team, 2023). Posteriormente, utilizamos la técnica de remuestreo o *boostraping* con un total de 10,000 remuestreos para la media, empleando la función "*boot"*, paquete del software R (R Core Team, 2023).

Adicionalmente, analizamos el efecto de las características estructurales y la incidencia de incendios en los árboles sobre la producción de bellotas abortadas. Aplicamos modelos lineales mixtos generalizados (GLMER). Los modelos los ajustamos para incluir un efecto aleatorio por árbol. Antes de la modelización, seleccionamos la familia de distribución de probabilidad que mejor se ajustaba a la variable de respuesta (Rigby & Stasinopoulos, 2005). También evaluamos los factores de inflación de la varianza (VIF), para reducir la multicolinealidad de las variables predictoras dentro de los modelos (Fox & Monette, 1992).

Eliminamos gradualmente de los modelos las variables altamente correlacionadas (VIF >2) y los volvimos a calcular hasta que su VIF fue inferior a 2 (Zuur et al., 2010). Posteriormente, utilizamos una regresión por pasos (Venables & Ripley, 1992) para seleccionar el modelo con el criterio de información de Akaike (AIC) más bajo (Burnham & Anderson 2002, Burnham, 2003, Säfken et al., 2018). Finalmente, mediante el estadístico de razón de verosimilitud (ANOVA del modelo completo). Estos procedimientos los realizamos con el software R, paquetes: 'cAIC4', 'BiodiversityR', 'carR', 'funrar', 'ggplot2', 'gamlss', 'lm4', 'reshape', 'tidyr', y 'vegan' (R Core Team 2023). Para el GLMER se utilizaron las funciones glmer (Bates et al., 2015), fitDIst (Rigby & Stasinopoulos 2005), stepcAIC, (Burnham & Anderson 2002; Säfken et al., 2018) y VIF (Fox & Weisberg 2019).

<u>Condiciones climáticas y cosecha de bellotas:</u> Empleamos los registros de temperatura media mensual y precipitación mensual de los años 2 018 y 2 019 (24 observaciones) de la estación climatológica del IDEAM número 24015300 (la más cercana a los robledales de estudio). Esta estación se ubica en el municipio de Villa de Leyva, Boyacá (5º39´21”N & 73º32´38.2”W), a 2,215 m de elevación (IDEAM, 2020). Comparamos la producción de bellotas con los datos de temperatura y precipitación media mensual. Con esta información calculamos el Coeficiente de Correlación de Spearman (Bratsas et al., 2018; R Core Team

2023) utilizamos las funciones *cor.test* y *spearman*, paquete "*gginference*" del software R. Como los datos pueden estar auto-correlacionados en el tiempo, indagamos si las series eran estacionarias (la media y varianza no cambian con el tiempo ni siguen una tendencia). Para esto, se realizamos un análisis de series de tiempo incluyendo el cálculo de la Función de Auto correlación (ACF), la Función de Auto Correlación Parcial (PACF) y la prueba de estacionalidad de Dikey-Fuller (Said & Dickey, 1984; Banerjee et al., 1993). De acuerdo con lo anterior, no fue necesario realizar ningún tratamiento a los datos originales y se continuó con la estimación de la Función de Correlación Cruzada (CCF). Para realizar estos análisis utilizamos las funciones adf.test, acf, pacf y Dikey-Fuller en el paquete "*tseries*" del software R (Trapletti et al., 2018; R Core Team 2023).

RESULTADOS

Producción de bellotas y germinación

Cosecha de bellotas y germinación: La pérdida de bellotas por fuera de las trampas fue del 10%. Es decir que, de cada 100 bellotas que caían en una trampa se perdían 10 por rebote. En el robledal quemado la cosecha total fue de 41.2 bellotas/m^2 (1,855 en total), de las cuales 35.5 bellotas/m^2 (86.1 %; 1,598 total) fueron abortos y 5.7 bellotas m^2 fueron viables (13.9 %; 257 total; Tabla 5.1). En este robledal la cosecha de bellotas abortadas inició en junio y las viables en agosto de 2018 (Fig. 5.2).

La cosecha principal de bellotas abortadas en el robledal quemado comprendió seis meses (junio a diciembre) y tuvo su pico máximo en agosto (el 35% de la cosecha total y el 42% bellotas abortadas). Desde noviembre la cosecha se mantuvo por debajo de 0.6 abortos/m^2 por mes (28 abortos en total, 1.5% de cosecha total y 1.8% y de los abortos) y fue decreciendo hasta llegar a 0.1 abortos/m^2 (cuatro abortos en total) al finalizar el estudio

(Fig. 5.2). Las bellotas viables se cosecharon durante cinco meses (julio a diciembre), tuvo su pico máximo en septiembre (2.6 bellotas/m^2, 117 bellotas viables en total; 6.3% de cosecha total y 45.5% de bellotas viables) y finalizó en diciembre de 2018 con 0.6 bellotas viables/m^2 (28 bellotas viables en total; 1.5% de la cosecha total y 10.9% de bellotas viables), posterior a este periodo no se obtuvieron más bellotas viables.

Por otra parte, en el robledal no quemado no se cosecharon bellotas viables durante el periodo de estudio. La cosecha de bellotas abortadas fue de 3.5 abortos/m^2 (158 abortos en total; Tabla 5.1). El periodo de producción en este robledal inició en julio de 2018, agosto de 2018 fue el mes de máxima cosecha (1.2 abortos/m^2, 56 abortos o el 34.5 % de la producción total). En los meses siguientes la cosecha fue descendiendo hasta a diciembre de 2018 donde se cosecharon 0.2 abortos/m^2 (siete abortos en total). En enero incrementó ligeramente la cosecha a 0.2 abortos/m^2, 11 abortos en total, pero decreció nuevamente en febrero de 2019 a 0.02 abortos/m^2 (un aborto en total). Esta cantidad mensual de bellotas se mantuvo hasta julio de 2019, cuando ocurrió un nuevo incremento (0.4 abortos/m^2, 19 abortos en total; Fig. 5.2).

Encontramos que la producción total y la media mensual de bellotas viables y con desarrollo incompleto entre los robledales quemados y no quemados es distinta (Tabla 5.1). Mientras el robledal quemado produjo bellotas viables (18,6 ± 9,9) y muchos más abortos (114,1 ± 51,1) el robledal no quemado solo presentó bellotas abortadas (11,3 ± 3,6). De acuerdo con el test de Welch existen diferencias estadísticamente significativas (Welch t-test, t-5.7029, df = 188.83, p = 4.45^{-08}) en la producción de ambos robledales.

Adicionalmente, encontramos que la producción promedio de bellotas viables y abortadas por árbol en los robledales de estudio se encuentra en el rango de producción de otros robledales no quemados, dónde se realizaron estudios similares (Tabla 5.2; Figura 5.3). Sin embargo, en este caso la producción de bellotas maduras en el robledal no quemado es notablemente inferior (18.7 ± 9.9) a la de los robledales no afectados por fuego estudiados por González & Parrado (2010) (Cachalú, C: 206 ± 2.8, Alto de Patios, AP: 54.7 ± 2.5), pero superior en la producción de bellotas con desarrollo incompleto (RQ: 114.4 ± 51.1, Cachalú C:131.5 ± 15.4, Alto de Patios AP: 47.1 ± 5.4).

Table 5.1. Densidad total (m^2) y promedio de bellotas viables y abortadas de *Quercus humboldtii* en el robledal quemado y no quemado de este y otros estudios. En el número de bellotas por árbol se reporta la media y la desviación típica.

Estudio	**Total de bellotas m^2**		**Media de bellotas m^2 por árbol**		**No de árboles**	**Trampas árbol**	**Total trampas**	**Área trampa (m^2)**	**Meses estudio**
	Viables	**Abortos**	**Viables**	**Abortos**					
Robledal quemado RQ **(este estudio)**	5.7 (13.9%)	35.5 (86%)	0.4±0.2	2.5±1.1	10	3	30	1.5	14
Robledal no quemado RnQ **(este estudio)**	0	3.5 (100%)	0	0.3±0.1	10	3	30	1.5	14
Robledal no quemado Fernández, 2014	3.1 (100%)	No reportó	0.2±0.1	No reportó	11	4	44	1	12
Robledal no quemado AP. González & Parrado, 2010	11.3 (68.3%)	5.2 (32%)	0.6 ±0.1	0.5±0.1	11	No reportó		1.5	5
Robledal no quemado C. González & Parrado, 2010	27.5 (72%)	10.7 (28%)	1.5± 0.1	1.0± 0.1	15			1.5	5

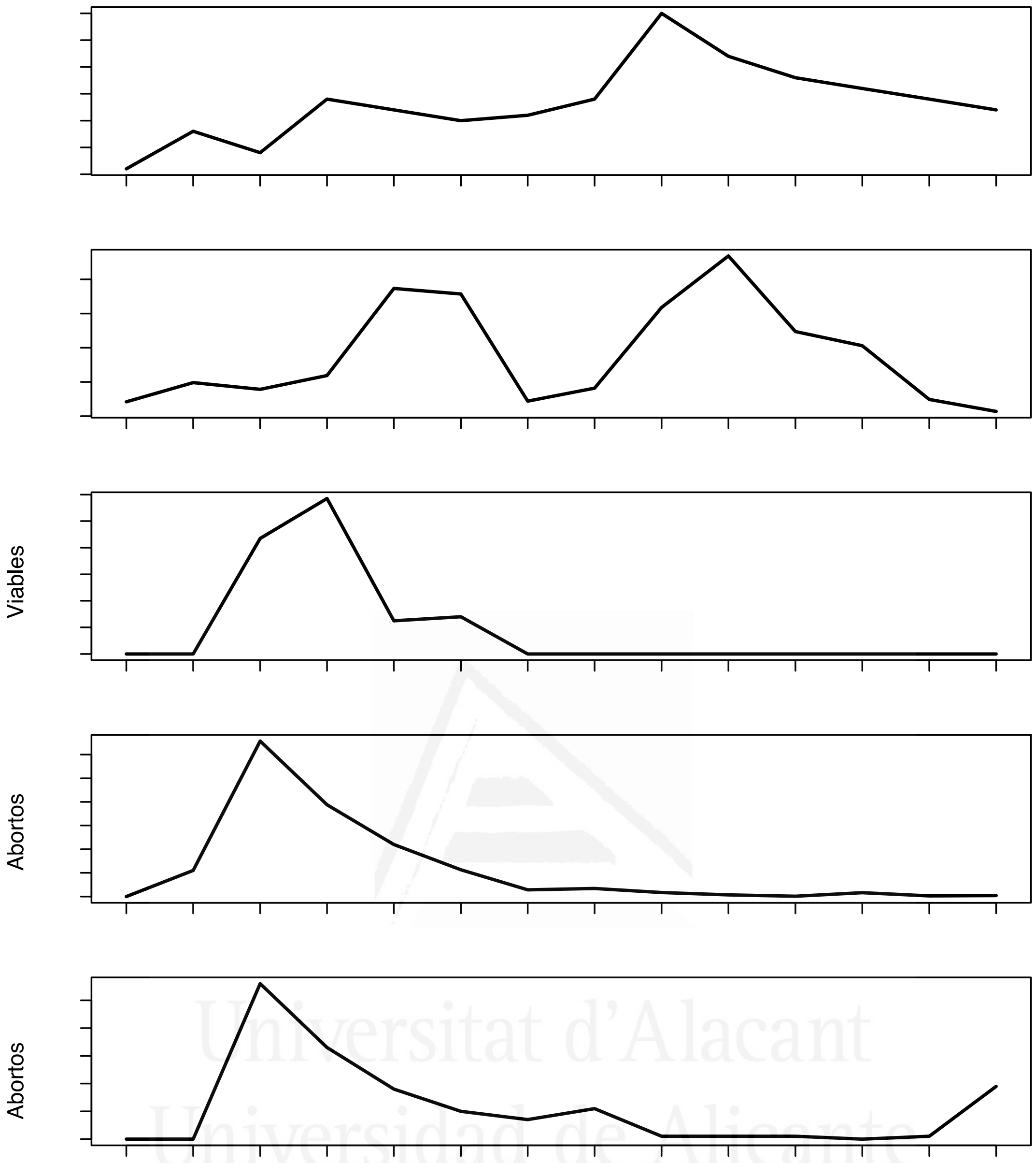

Figure 5.2. Temperatura y precipitación en Villa de Leyva y número total de bellotas viables y abortos por individuo de *Quercus humboldtii*, producidos mensualmente en un robledal quemado (RQ) y otro no quemado (RnQ) durante el periodo junio 2018 y julio 2019.

También, encontramos que es mayor el peso y tamaño promedio de las bellotas con desarrollo incompleto del robledal no quemado (peso: 1.6 g ± 0.1, diámetro ecuatorial: 1.5 mm ± 0.1 y diámetro polar: 1.4 mm ± 0.02) que las del robledal quemado (peso: 1.1 g ± 0.1, diámetro ecuatorial: 0.8 mm ± 0.1 y diámetro polar: 0.7 mm ± 0.1). Según el test de

Welch existen diferencias en el peso fresco *(Welch t-test*, t-5.2968, d*f* = 234.8, $p = 2.709^{-07}$), así como en el tamaño *ecuatorial (Welch t-test*, t-12.733, *df* = 338.8, $p = 2.2^{-16}$) y polar (*Welch t-test*, t-18.551, *df* = 357.8, $p = 2.2^{-16}$) de las bellotas con desarrollo incompleto entre ambos robledales.

Table 5.2. Porcentaje de germinación, peso y tamaño de bellotas maduras de *Quercus humboldtii* de robledales quemados y no quemados.

Estudio	**Germinación (%)**	**N**	**Tipo bellota**	**Peso (g) media**	**Tamaño (mm)**	
					Polar	**Ecuatorial**
Robledal quemado RQ (este estudio)	15	257	Pequeña	5± 0.9	20.5± 0.4	21.3± 0.5
Robledal no quemado (Vivero el Nativo, datos no publicados).	78	300	Grande	15.6± 0.7	34.1± 0.9	28.6± 0.6
Robledal no quemado (Moreno & Cuartas, 2014).	64	600	No reportó			
Robledal no quemado (Fernández, 2014).	63	800	Pequeña	10	23.3	24.4
Robledal no quemado (Paz & Paz, 2012).	893	300				
Robledal no quemado (Gómez & Toro, 2007).	75		No reportó		25	22
Robledal no quemado lote Bogotá (Hernández, 2006).	64	1.330	Pequeña			
Robledal no quemado lote Arcabuco-Villa de Leyva (Hernández, 2006).	50	236	Pequeña	No reportó		
Robledal no quemado lote Santander (Hernández, 2006).	100	484	Grande			
Robledal no quemado (CAR, 1984).	80	No reportó				

Finalmente, todas las bellotas maduras (257) del robledal quemado fueron llevados al vivero, de las cuales solo germinaron 38 bellotas, es decir el 14,8 % de las bellotas maduras o el 2 % de la producción total. Esta tasa de germinación es inferior a las tasas reportadas en bibliografía (entre el 60 y 95 %), pero también lo es el peso y tamaño de las bellotas (Tabla 5.2).

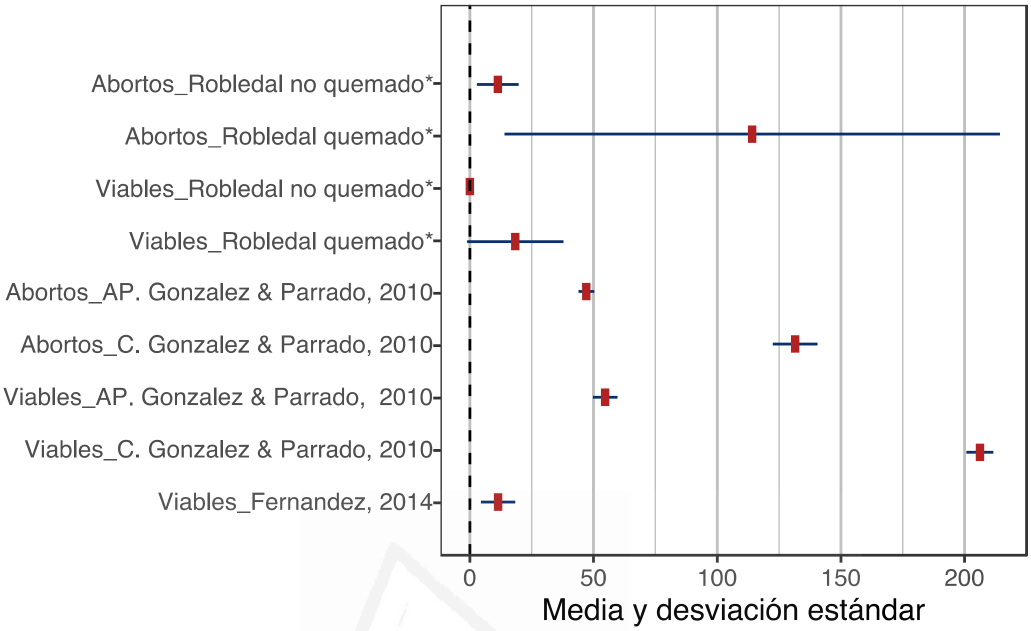

Figure 5.3. Producción de bellotas de *Quercus humboldtii* por árbol en un robledal quemado y otros no quemados. AP: Alto de Patios y C: Cachalú. Se presenta la media y desviación estándar para la media *boostrap* del número de bellotas abortadas o viables.

Características de los árboles estudiados y producción de frutos

Encontramos un mayor tamaño en los robles no quemados. El área de copa promedio y desviación estándar para la media *bootstrap* en los árboles no quemados del bosque no quemado (131 ± 14,5 m^2) fueron mayores que los robles quemados en el bosque quemado (114 ± 9,3 m^2; Figura 5.4). La altura de los árboles no quemados (RnQ 23 ± 1,5 m, RQ 13 ± 1 m) y su diámetro (RnQ 137±15,1 cm, RQ 106,1 ± 13,4 m) también fueron mayores. Por otra parte, el número de cicatrices (1,1 ± 0,3) y área de cicatriz (0,1 ± 0,1 cm^2) fueron parámetros exclusivos de los robles quemados.

El modelo más parsimonioso (Tabla 5.3) para la producción de bellotas muestra que el número de bellotas con desarrollo incompleto (abortos) se relaciona positivamente con los bosques quemados, así como con los robles que tengan una mayor área de cicatriz (mayor severidad o frecuencia de incendios) y una menor área de copa. Por el contrario, el número de abortos disminuye en los bosques no quemados o si los árboles tienen un mayor tamaño en copa, diámetro y altura (Apéndice 5.3).

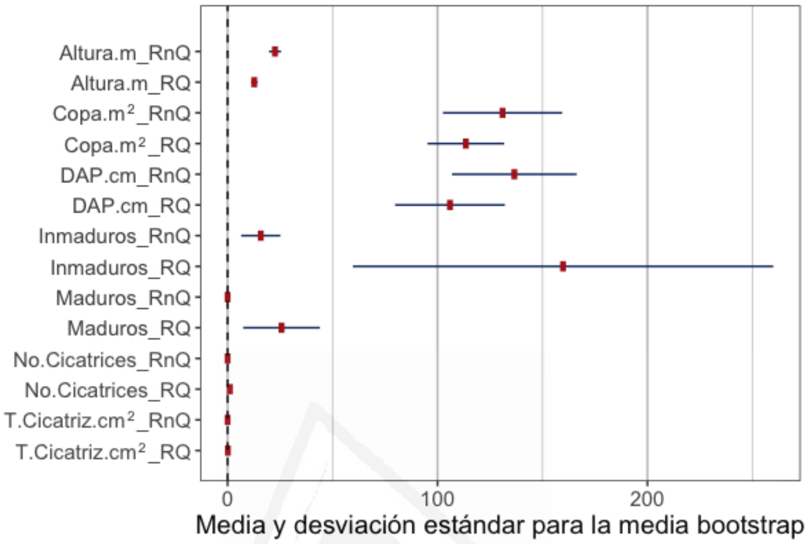

Figure 5.4. Producción de bellotas y características de los árboles productores de semilla de este estudio (DAP, Altura, área de la copa, número y área de cicatrices producidas por fuego). Se presenta la media y desviación estándar para la media *bootstrap* del número de frutos.

Table 5.3. Parámetros del mejor modelo para la producción de bellotas inviables (abortos) y criterio AIC explicada. El modelo y los coeficientes de las variables son significativos ($p < 0.05$).

Respuesta	**Modelo**	**Familia modelo**	**Modelos testeados**	**AIC**	***df***	**Efectos fijos**	**Estimación**	**SE**	***z***	***p***
Número bellotas inviables (abortos	Robledal + DAP + altura + área de la copa + Tamaño cicatriz + (1|árbol)	GLMR Poisson (log)	12	195	13	RQ	7,6	0,6	13,8	$3,6^{-43}$
						RnQ	-1,3	0,2	-5,7	$1,1^{-8}$
						DAP	-0,03	0,01	-7,7	$2,1^{-14}$
						Altura	-0,2	0,03	-6,6	$3,4^{-11}$
						Área Copa	0,01	0,01	7,8	$6,9^{-15}$
						Área cicatriz	1,2	0,1	9,9	$3,3^{-23}$

Clima y producción de frutos

La producción en ambos robledales ocurrió principalmente durante la segunda temporada seca y la segunda temporada lluviosa del año (entre julio y noviembre de 2018). El inicio de producción de bellotas con desarrollo incompleto coincidió con la mitad de temporada seca, pero la producción de bellotas maduras y el pico máximo de bellotas con desarrollo incompleto ocurrió en el mes de agosto, es decir, durante la transición hacia la temporada de lluviosa. A partir de aquí la empezó a decrecer hasta finalizar esta temporada (Figura 5.2).

En el robledal quemado no encontramos correlación entre la producción media mensual de bellotas y la temperatura (rho: -0,21, p = 0,46), pero respecto a la precipitación, encontramos una correlación de Sperman moderada y negativa (rho: -0,56, p = 0,04). En el robledal no quemado no se encontró correlación significativa entre la producción de bellotas y la temperatura (rho: 0,24, p = 0,40) o la precipitación (rho: -0,36, p = 0,20). Adicionalmente, la Función de Auto Correlación Cruzada (CFF; Figura 5.5) mostró un patrón estacional en la producción de bellotas de ambos robledales y en los parámetros climáticos, confirmando obtenido con la correlación de Sperman.

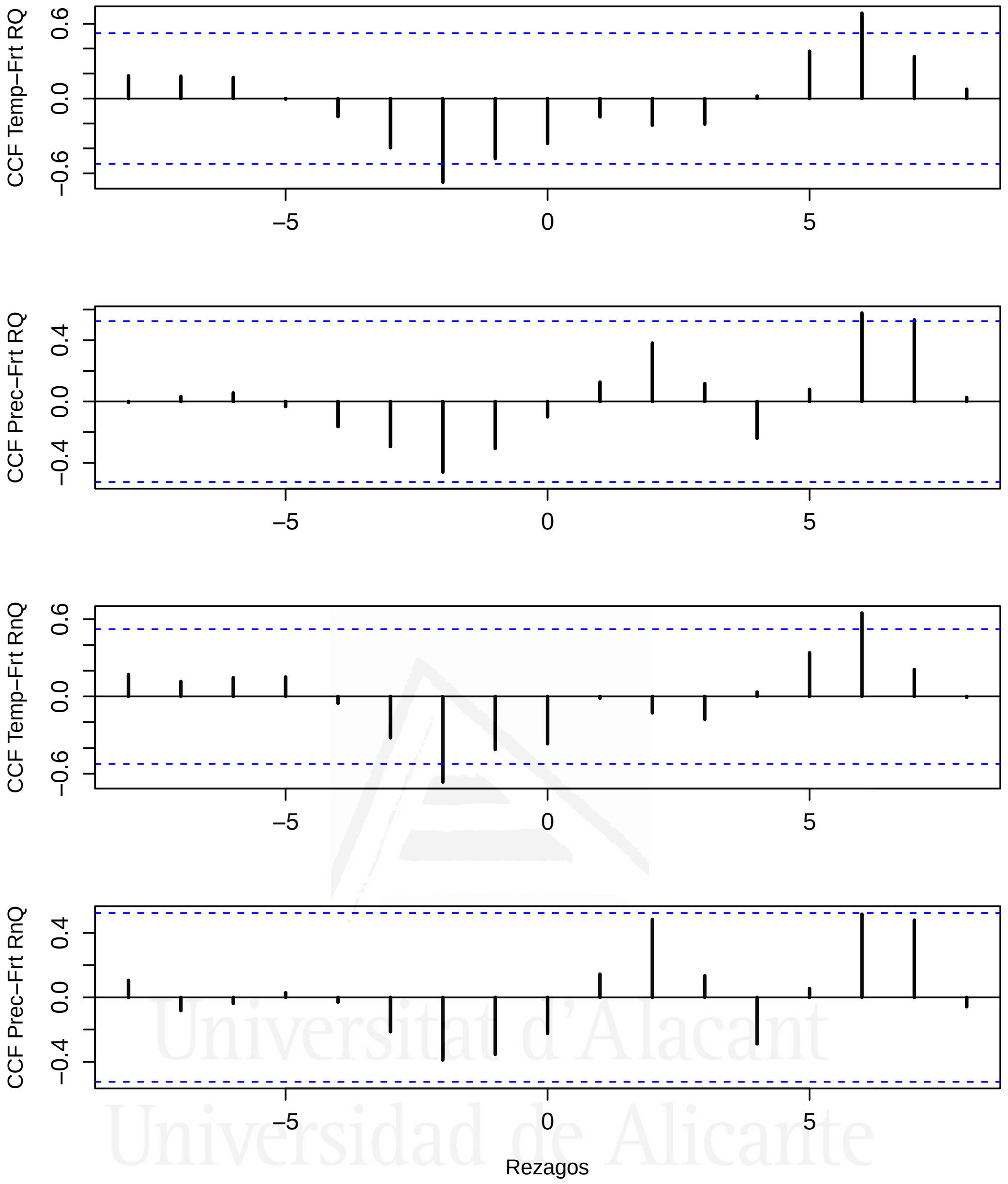

Figure 5.5. Valor de la Función de Correlación Cruzada (CCF) para comparar el número de bellotas (Frt) de un robledal quemado (RQ) y otro no quemado (RnQ) y parámetros climáticos (Temp: temperatura y Prec: precipitación).

Para el caso del robledal quemado, la producción y la temperatura no mostraron correlación durante ni en los meses anteriores o posteriores, mientras que para la precipitación mostró una correlación débil y negativa durante los meses anteriores. Por su parte el CCF para el robledal no quemado no se encontró correlación significativa entre la producción de bellotas y los parámetros climáticos durante el mes anterior o posterior.

DISCUSIÓN

La cosecha de bellotas en los robles de este estudio se concentró en cuatro meses para los bellotas viables y seis meses para las bellotas abortadas. Inició durante la época de transición de la temporada seca a lluviosa, manteniéndose hasta la mitad de la temporada de lluvias. Durante la primera fase se cosecharon exclusivamente bellotas abortadas. Estos resultados coinciden con otros estudios fenológicos de *Q. humboldtii* (Tabla 5.1; Fig. 5.4; Pacheco & Pinzón, 1997; Pardo & Chiquillo, 2002; Gómez & Toro, 2007; Gonzales & Parrado, 2010; Pérez et al., 2013; Fernández, 2014; Ramos-Palacios et al., 2014; Burgos, 2015), así como de otros robles del género *Quercus* (López-Barrera & Manson, 2006; Nixon, 2006). Sin embargo, en el robledal quemado la cosecha promedio de bellotas viables por árbol es notablemente inferior (0.4±0.2 bellotas/m^2) a la de los robledales no afectados por fuego estudiados por González y Parrado (2010) (Cachalú, C:1.5 ± 0.1 bellotas/m^2, Alto de Patios, AP: 0.6 ± 0.1 bellotas/m^2), pero superior en la cosecha de abortos (RQ: 2.5 ± 1.1 bellotas/m^2, Cachalú C:1.0±0.1 bellotas/m^2, Alto de Patios AP: 0.5 ± 0.1 bellotas/m^2). Adicionalmente, la tasa de germinación de las bellotas de los robledales quemados de este estudio es inferior a las tasas reportadas en bibliografía (entre el 60 y 95 %), pero también lo es el peso y tamaño de las bellotas (Tabla 5.2).

La baja cosecha de bellotas viables de los robles afectados por incendios en el bosque quemado de este estudio, comparada con la cosecha y germinación de bellotas obtenidas en otros bosques no quemados, podría explicarse en parte por el régimen de incendios (tres en 30 años); de acuerdo con Funk et al. (2016), los fuegos de alta frecuencia e intensidad influyen negativamente en la disponibilidad de semillas. De igual forma, los incendios pueden reducir el número de robles adultos, en ese sentido una menor cantidad de árboles, repercute en que la población no pueda producir el número suficiente de flores femeninas o que la donación de polen sea de pocos individuos. Por lo anterior, podría haber una mayor proporción de flores no polinizadas, que no completan su desarrollo o que ocurra un menor éxito e intensidad en la fecundación (Schermer et al., 2019a). Esto se traduce en menos bellotas viables y más abortos. Estos fenómenos también se han observado en pequeños relictos de bosques andinos fragmentados (Fernández & Sork, 2005), así como en robledales de Norte América (Ramos-Palacios et al., 2014; Barrgán et al., 2018).

Otras explicaciones para la baja cosecha de bellotas viables, la baja tasa de germinación y la alta producción de abortos en los árboles del bosque quemado frente a los reportes en literatura pueden ser: 1) una baja fertilidad del suelo, 2) la reducción del tamaño de la copa y del área foliar por el incendio y 3) una alta incidencia de insectos defoliadores. En efecto, Gonzales & Parrado (2010) reportan una mejor producción de bellotas en robledales cuyo suelo tenía una mayor disponibilidad de fósforo (P) y potasio (K). En ese sentido, es posible que debido a los incendios recurrentes y al uso histórico, este robledal presente déficit en la fertilidad y los árboles no dispongan de nutrientes suficientes como para producir una cosecha en calidad y cantidad. A pesar que los incendios pueden mejorar la fertilidad a corto plazo, varios estudios (Valdés et al., 2016; Mogollón et al., 2017; Gómez-Sánchez et al., 2019) han encontrado que los incendios reducen la fertilidad de los suelos e incrementan el riesgo de erosión.

De igual forma, los incendios al quemar o chamuscar las copas de los árboles reducen el área foliar y de copa, de esta manera los árboles no pueden producir el número suficiente de ramas y de follaje, lo que reduce la producción de bellotas en los años siguientes al incendio. También, una reducción en el tamaño de hojas y la copa podría afectar la capacidad fotosintética del árbol, con esto disminuye la posibilidad de transferir los recursos necesarios para un buen desarrollo de las bellotas (Stephenson, 1981; Nakajima, 2015; Canelo et al., 2018).

Adicionalmente, el elevado número de abortos en los árboles del bosque quemado pudo verse influenciado por un posible incremento poblacional de insectos defoliadores que se beneficiaron por el incendio de 2015. Si bien es natural que el roble andino produzca una buena proporción de abortos (Gonzáles & Parrado, 2010; Pérez et al., 2013), como lo hacen otras especies de *Quercus* (Stephenson, 1981; Diaz et al., 2003), se ha encontrado en robledales con incidencia antrópica, que las hojas son atacadas durante la fenofase reproductiva por la larva de un lepidóptero de la familia Geometridae, género *Alsophyla* (Paz, 2004; Fernández, 2014), lo que generaría una menor capacidad foliar para la asimilación de nutrientes y como consecuencia la producción de abortos (Nakajima, 2015; Tiberi et al., 2016; Canelo et al., 2018). Esto guardaría relación con los estudios que han demostrado un incremento de plagas en bosques afectados por incendios (Catry et al., 2014; Botella-Martínez & Fernández-Manso, 2017; Catry et al., 2017; Mezt et al., 2017).

El menor tamaño y peso de las bellotas viables y su baja germinación también puede deberse a que estas semillas tengan una menor reserva de almidones (Rubio-Licona et al., 2011). La producción de bellotas grandes puede ser costosa en términos de agua o nutrientes, y debido al estrés que genera el fuego, los árboles quemados pueden estar produciendo semillas más pequeñas mientras se sobreponen a esas condiciones, tal y como lo menciona Bartlow et al. (2018) en su investigación. De igual forma, varios estudios han obtenido una mayor tasa de germinación cuando las semillas son de mayor tamaño

(Hernández, 2006, Huerta-Paniagua & Rodríguez-Trejo, 2011; Rodríguez-Trejo & Pompa-García, 2016; Pandey et al., 2017).

Por otra parte, los robles del bosque quemado presentaron un mayor número de bellotas viables y abortadas que los árboles en el bosque no quemado. Esto puede deberse a la mayor incidencia de la radiación solar que se puede presentar después del incendio y de esta manera estimular la producción de bellotas; tal como ha ocurrido en otros estudios en robledales afectados por tala (Guariguata & Saenz, 2002), uso agropecuario y fragmentación (Gonzales & Parrado, 2010; Fernández, 2014; Barragán et al., 2018) e incendios (Jones et al., 2015).

También la baja cosecha de bellotas de los árboles no quemados puede deberse a características reproductivas naturales de *Q. humboldtii* y no al régimen de fuego, a variables estructurales o del clima. Dado que los árboles de este robledal presentaron mejores áreas de copa que los del robledal quemado y ninguna evidencia de fuego (Fig. 5.4), es factible que durante los meses estudiados la población podría haberse encontrado en una fase no reproductiva de bellotas viables y que en los años anteriores haya tenido una alta producción. Esto lo suponemos por que observamos en campo plántulas de seis meses, uno y dos años de edad en el sotobosque. Adicionalmente, Sesquilé (2019) reporto una densidad de 1 plántula/m^2 en dicho robledal.

Este ciclo de producción y no producción de bellotas es factible que ocurra en los bosques de roble andino, ya que otros árboles del género *Quercus* presentan el fenómeno de vecería o *masting*. En donde la producción de bellotas varía considerablemente de un año a otro con pulsos de producción (año de *masting*) entre 2 a 6 años (Sork, 1993). La vecería ha sido reportada en robledales templados (Jensen, 1982; Crawley & Long, 1995; Yu et al., 2003; Torres et al., 2004; Carbonero & Fernández-Rebollo, 2014) y tropicales (Guariguata & Saenz, 2002) y en el roble andino se ha propuesto por observaciones anecdóticas (Gómez & Toro, 2007).

Para Colombia, este el primer estudio en evidenciar un posible comportamiento de vecería en *Q. humboldtii.* Nixon (2006) ha propuesto que los picos de producción de bellotas en árboles del subgrupo *Erytrobalanus* puede ser de dos años. Sin embargo, esto debe comprobarse en otras poblaciones de *Q. humboldtii*, con estudios fenológicos con datos entre cinco a diez años (Torres et al., 2004). Estudios fenológicos en otros robledales del género *Quercus* han realizado cosecha de bellotas con resultados concluyentes durante tres años (Díaz-Pontones & Reyes Jaramillo, 2009), seis años (Hirayama et al., 2017), 19 años (Parmenter et al., 2018), 13 años (Schermer et al., 2019b) y ocho años (Vergotii et al., 2019).

Diferentes estudios en roble andino (Pacheco & Pinzón, 1997; Pérez et al., 2013, Fernández, 2014; Burgos, 2015) y del género *Quercus* (Koenig et al., 2015; Bogdziewicz et al., 2017; Caignard et al., 2017; Pearse et al., 2017; Nussbaumer et al., 2018; Parmenter et al., 2018, Bogdziewicza et al., 2019; Schermer et al., 2019b; Vergotti et al., 2019), han encontrado una relación positiva de la producción de bellotas con la temperatura o la precipitación. Sin embargo, en este estudio como en González & Parrado (2010), no fue así. Lo que nos lleva a pensar que la producción de bellotas en *Q. humboldtii* no solo debe relacionarse con las variables climáticas, sino también con otros aspectos biofísicos o propios de la biología y genética del roble andino; como por ejemplo: 1) los ciclos de vecería, 2) la fertilidad del suelo, 3) la fragmentación, y 4) el impacto de fuegos recurrentes, tal y como se ha atribuido en estudios de otros robledales (Nixon, 2006; López-Barrera & Manson, 2006; Gonzáles & Parrado, 2010; Funk et al., 2016). En todo caso, un tamaño de muestra mayor y un periodo de estudio más amplio serían necesarios para identificar efectivamente algún tipo de correlación entre el clima y la producción de frutos.

CONCLUSIONES

Los árboles del bosque quemado produjeron bellotas dos años y diez meses después del último incendio. Estos árboles en relación con otros estudios fenológicos de roble andino y del género *Quercus* presentaron una baja producción de semillas maduras y una alta producción de abortos. De igual forma, el tamaño, peso y germinación de las bellotas maduras provenientes de árboles quemados es notoriamente inferior a las bellotas maduras de robledales no quemados. Esto puede atribuirse a disturbios como los incendios, el uso agropecuario y la fragmentación, que en su conjunto pueden haber generado una posible disminución de la fertilidad del suelo, la reducción del tamaño de las hojas y del área de la copa, reducción del tamaño poblacional del roble y el incremento eventual de insectos defoliadores. Lo anterior, incidiría en una menor capacidad de los árboles en la distribución de recursos para el desarrollo de la bellota.

Por otra parte, encontramos que la producción de bellotas maduras puede depender de aspectos intrínsecos del roble andino, como lo es la vecería o *masting*, siendo factible que los robledales de este estudio presenten ciclos de alta, baja o nula producción de bellotas a lo largo del tiempo (de acuerdo con las observaciones empíricas y este estudio puede ser de cada dos a tres años). En ese sentido, este trabajo es el primero en reportar este posible comportamiento reproductivo en *Q. humboldtii*. Sin embargo, es necesario probar dicha hipótesis haciendo estudios fenológicos con un mayor tamaño de muestra, involucrando distintas poblaciones de roble y durante al menos cinco años.

El reclutamiento de *Q. humboldtii* en los robledales quemados de Iguaque puede verse afectado por la baja producción y germinación de las bellotas maduras, generando limitación en la fuente. Esto puede ser particularmente grave en el macizo de Iguaque ya que ha presentado de tres a siete incendios recurrencias en las últimas décadas y además estos incendios suelen ocurrir entre agosto y septiembre (Aguilar-Garavito *et al.,* 2020), fecha en este estudio registró la producción de bellotas. Entonces, los incendios recurrentes además de afectar por quema directa el follaje y la producción de bellotas en el año en el que ocurre el incendio, retrasa la producción de semillas maduras al menos tres años, alterando posiblemente el ciclo de vecería. Además, la primera cosecha de bellotas viables después del incendio puede ser de baja cantidad y calidad, y las bellotas maduras presentan una baja germinación.

Recomendamos realizar estudios fenológicos de largo plazo (de cinco a 10 años), esto permitiría confirmar el patrón de vecería en *Q. humboldtii* y establecer los efectos de los disturbios en la producción de frutos, así como el tiempo que toman los árboles en tener nuevamente un fructificación óptimo. De igual forma, es necesario incluir otras variables climáticas (humedad relativa y la radiación solar), variables físico-químicas del suelo y otras relacionados con el régimen de incendios (severidad, frecuencia), proporción y partes del árbol quemadas y también incluir el proceso de floración, polinización y tasa de herbívora después de los incendios.

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SUPPLEMENTARY MATERIAL 5

Apéndice 5.1. Cicatrices casi triangulares sobre troncos de *Q. humboldtii*

Apéndice 5.2. Curva de germinación para las bellotas viables colectadas en el bosque quemado durante nueve semanas.

Apéndice 5.3. Modelo parsimonioso de producción de bellotas inmaduras (abortos) y razones de probabilidad.

CHAPTER 6. *Quercus humboldtii* germination and establishment in Andean forests affected by recurrent wildfires.

Quercus humboldtii **germination and establishment in Andean forests affected by recurrent wildfires.**

ABSTRACT

Quercus humboldtii is the only South American oak species that covers certain high and mid-mountain areas of the northern Andes. Historically, oak forests have been used for firewood and replaced by crops. As a result, their pre-Hispanic extension was reduced to 28%. Recently, their persistence has been threatened by wildfires. In recent decades, oak forest cover has been reduced as the frequency of forest fires has increased, and oak regeneration after fires is limited. Following agricultural use and recurrent wildfires, oak forests are replaced by dense shrublands with a high cover of shrubs and exotic invasive herbaceous species. This study evaluates the limiting factors for oak germination and establishment and seedling growth in fire-affected oak forests and shrublands in the Iguaque mountains of central Colombia. In a manipulative experiment, we measured the germination and rooting of acorns and the development of seedlings planted under oak forests, intact shrublands, and shrublands where exotic invasive species had been removed. We found that *Q. humboldtii* can germinate, survive and grow in high proportions in both forests and shrublands. However, surprisingly were significantly lower in the oak forest. Environmental conditions intrinsic to oak forests, such as steeper slopes, high canopy cover, and acorn predation, impeded germination and establishment. On the other hand, our results of germination, survival, and growth demonstrate that if the availability and dispersal limitations are overcome, Andean oak acorns and seedlings can establish in fire-affected oak forests and shrublands with or without exotic invasive species. Although exotics are not directly affecting the recruitment of *Q. humboldtii*, we consider that

indirectly the high biomass density of invasive exotic species functions as fuel for wildfires, influencing the wildfire frequency and magnitude and thus destroying *Q. humboldtii* seeds and young recruits. Recruitment of *Q. humboldtii* in this system then requires simultaneous alleviation of the restriction on seed availability and dispersal but also sufficient time without fire so that established recruits can grow and develop fire protection structures and activate their regrowth capacity. Developing these strategies requires comprehensive fire management and assisted reintroducing of *Q. humboldtii* seeds and seedlings.

KEYWORDS: Acorn; Andean Forest; Relative growth rate; Forest regeneration; Seed germination; Seedling establishment; Sapling establishment

The northern Andes is a global biodiversity hotspot and plays an essential role in carbon sequestration, hydrological processes, and biodiversity conservation (Meyers *et al.*, 2000; Olson & Dinerstein, 2002). However, approximately 60% of Andean ecosystems have been altered in Colombia by deforestation, wildfire, agriculture, and livestock grazing (Etter 2006, 2008, Galindo *et al.*, 2014; Minambiente, 2015; Avella, 2016). Under these conditions, fire may act as an ecological filter, favoring invasive species and excluding native species that cannot cope with the current fire regime (Vargas 2000, 2002, Schaffhauser et al. 2012).

Andean oak (*Quercus humboldtii* Bonpl.) is the only *Quercus* species in South America and was once widespread in the northern Andes (Nixon 2006, González et al. 2011). Under certain conditions, the Andean oak develops as the dominant species in the Andean Forest (Avella, 2016). However, only 28% of the Andean oak forest persists nowadays. Once covered with oak forests, now the landscape is small patches of oak forests alongside patches of shrublands, pastures, and cultivated areas (González et al. 2011, Avella 2016).

After land abandonment use, shrublands and tree species colonize disturbed areas and reassemble oak forests (Ramírez-Marcial *et al.,* 2006; Fernández-Méndez *et al.,* 2016). However, frequent wildfires often arrest successional trajectories (Zahawi & Augspurger, 1999; Hobbs *et al.,* 2009; Palma *et al.,* 2021). Under recurrent fires, landscapes shift from diverse, resilient oak forests to a species-depleted mosaic of shrublands and grasslands, which may be prone to fire, following auto-successional trajectories (Schaffhauser *et al.,* 2012; Zouhar *et al.,* 2008).

In the Iguaque mountains of the eastern cordillera of Colombia, frequent wildfires trend toward reductions in the richness, density, and cover of woody species. In addition, they facilitated the establishment of exotic species, particularly *Andropogon lehmannii, Melinis minutiflora,* and *Pteridium aquilinum* (Aguilar-Garavito & Cortina, in press).

Understanding the drivers of oak establishment in burned areas is crucial to assessing wildfire regimes' impact on forest dynamics and protecting and restoring oak forests. Oak recruitment may be limited by various factors, including reduced acorn availability, poor acorn dispersal, high levels of acorn predation by wild and domestic animals, low acorn germination, and low seedling survival (Pulido & Díaz, 2005; Acácio *et al.,* 2007).

Andean oak trees can resprout vigorously after the fire (Salazar *et al.,* 2020). Conversely, acorn density, and particularly the density of healthy acorns, is low and negatively affected by the fire. Acorn and seedling density is lower outside the forest patches and decreases from the path center to the periphery (Aguilar-Garavito *et al.*, in press). These results suggest that oak recruitment may be limited by acorn availability and dispersal. Furthermore, limitations in acorn germination and seedling establishment cannot be excluded, as various studies suggest that acorn germination may be limited by drought and predation (Pulido & Díaz, 2005; Acácio *et al.,* 2007). The seedling establishment may be strongly hampered by competition with exotic species, weather conditions, and herbivory (Schupp *et al.,* 2002; Palma *et al.*, 2021).

In the Iguaque mountains wildfire landscape, we established a manipulative field experiment. We measured the germination and rooting of acorns and the development of seedlings planted under oak forests, intact shrublands, and shrublands where exotic invasive species had been removed. We tested the following hypotheses: (1) conditions for acorn germination and seedling establishment are better in the forest than in the shrubland, (2) predation negatively affects acorn germination, and (3) acorn germination and seedling establishment are both hampered by exotic species.-To our knowledge, no previous study has explored the drivers of *Q. humboldtii* establishment in the Northern Andes.

METHODS

Study site

The Iguaque Mountains cover 22,000 ha and are located on the western slopes of the Eastern Mountain range of Colombia in the northern Andes (Figure 6.1). The area comprises the protected natural area Santuario de Fauna y Flora Iguaque (SFFI; 2,400 to 3,890 m; 6,750 ha) and is surrounded by a protected buffer zone at lower elevations (from 2,200 to 2,400 m). The landscape is hilly, and the topography is strongly wavy and broken, with slopes greater than 15%. Soils are shallow, acidic, moderately evolved, and formed by structural sandstones of the Arcabuco Formation (Villarreal *et al.*, 2017). Across the range, the average annual temperature is 18°C (average max. 22ºC, average min. 10ºC), and the average yearly precipitation is 810 mm. Rainfall follows a bimodal distribution, with peak precipitation occurring during March-May and September-November. The rainiest months are April-May, approximately 200 mm, and the driest months are December-February (40 mm). Rainfall decreases toward the area's southwest (Villarreal *et al.*, 2017).

Human activity has intensely affected the southern ridges of the Iguaque Mountains. Soils are highly degraded in this area, and rocky outcrops are widespread. This area has historically experienced recurrent wildfires (Aguilar-Garavito *et al.*, 2020) and is mainly covered by a mosaic of herbaceous vegetation and shrubs, including native and exotic species. Patches of *Q. humboldtii* forests are mostly found along streams and river canyons. In contrast, the northern ridges, which historically lack wildfires and have been subjected to lower human pressure, are dominated by preserved páramo vegetation and Andean forests, including Andean oak (Fernández-Méndez *et al.*, 2016; Mendoza-Cifuentes, 2017). The buffer area presents a mosaic of herbaceous and shrubby vegetation mixed with pastures, farmland, and recreational areas.

A previous study (Aguilar-Garavito *et al.*, 2020) recorded twenty-five wildfires in the Iguaque Mountains between 1990 and 2017, affecting an accumulated area of 6,236 ha (28.4% of the region). Fires were relatively small, but the extent of land affected by fires increased with time. Fire recurrence in the area currently ranges from 1 to 7 events in 30 years. Wildfires affect the structure and composition of the native forest, suppressing *Q. humboldtii* and favoring the establishment of shrubby grasslands with a significant presence of páramo and exotic species such as *Pteridium aquilinum* (Aguilar-Garavito *et al.,* 2020). As much as 45% of the *Q. humboldtii* forests existing 30 years ago now vanish.

Experimental area

The experimental area is located in the Robledales Civil Society Reserve, in the Sabana Alta district of the municipality of Villa de Leyva (5°40'21.08" N; 73°29'22" W), a buffer zone of the SFFI. In this area, the altitude ranges between 2422 and 2500 m. The site burned thrice in the last thirty years (1990, 1994, and 2015; Aguilar-Garavito *et al.,* 2020). As a result, in the study area, fragmented oak forests are surrounded by a matrix of shrubland and pastures with a significant cover of invasive species, as in other regions burned by the Iguaque Mountains (Aguilar-Garavito *et al.,* 2020).

The oak forest patch under study covers a narrow 3-ha strip along the banks of the upper watershed of Roble Creek. The forest canopy is open (40 ± 2% projected cover) and dominated by *Q. humboldtii* individuals, with an average height of 6.5 ± 0.3 m and a density of 43 ± six individuals/ha. Scars from old fires can be observed on all trees (on average, 1.6 ± 0.1 scars per tree). This forest also presents a 2.1 ± 0.1 m high woody understory, dominated by *Q. humboldtii, Viburnum tinoides* (L.f.), *Symplocos theiformis* (L. f.) Oken and *Bejaria resinosa* Mutis ex (L. f.). The herbaceous layer is poor and covered mainly by ferns of the species *Serpocaulon levigatum* (Cav.) A.R. Sm., *Niphidium crassifolium* (L.) Lellinger, *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf and seedlings. The forest floor covers 84 ± 3% and is dominated by oak litter. The vegetation adjacent to the forest patch is open shrubland (1.3 individuals/m^2, 1.2 ± 0.1 m tall). Common species are *B. resinosa, Pentacalia corymbosa, Morella parvifolia, Palicourea angustifolia, Viburnum triphyllum*, and *Dodonaea viscosa*. The herbaceous layer covers 77 ± 2% and includes *Pteridium aquilinum, Heteropogon contortus, Puya bicolor, Andropogon lehmanii, Melinis minutiflora, Calea peruviana, Rubus bogotensis*. Bare soil and rocky outcrops are frequent (29 ± 2% cover).

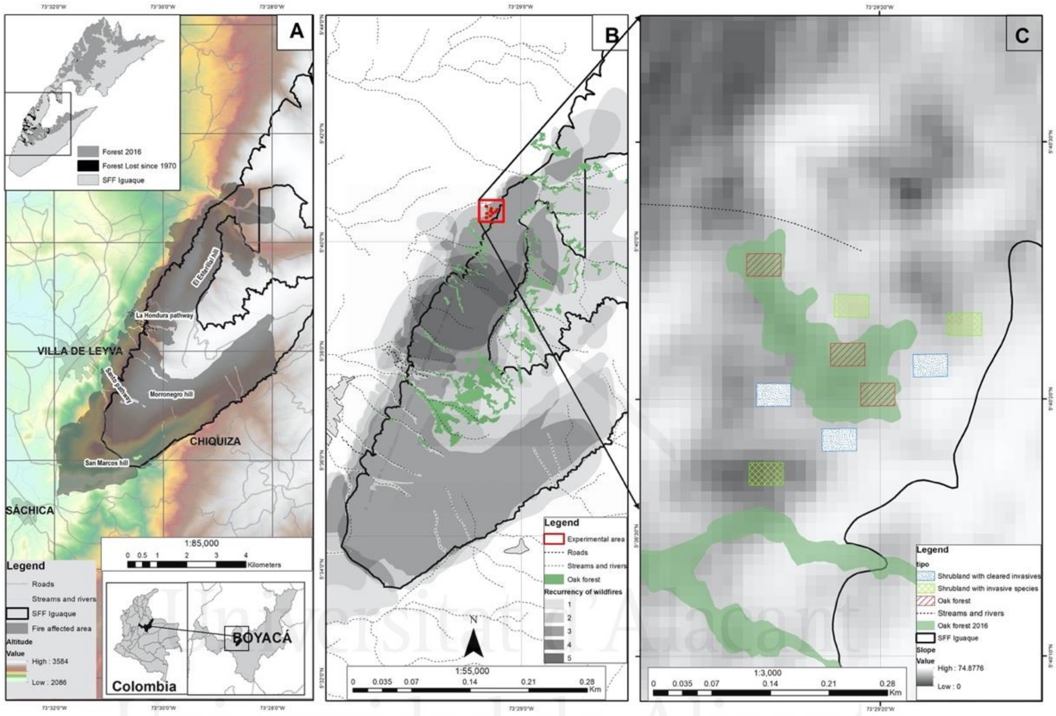

Figure 6.1. Location of the experimental areas in the Iguaque Mountains. 5°36'02"- 5°44'38" N and 73°22'57"- 73°31'20" W. (A) Location of the Iguaque Mountains in the Department of Boyacá, northern Andes in Colombia, including the historic areas affected by wildfires, oak forests, and the natural protected area (Santuario de Fauna y Flora Iguaque). (B) Wildfire frequency between 1990 and 2016. (C) Location of the experimental plots.

Plot characterization

We measured air temperature and humidity in each plot at 1 m above the ground between 30 March 2018 and 30 November 2019, using Holden et al. (2013) methodology.

Temperature and humidity Dataloggers sensors (DT-171; CEM) were located in the center of each plot. Data was stored hourly in a Datalogger and downloaded every two weeks. A spherical crown densiometer Model-A was used to assess canopy cover in the center of each planting plot and quadrat (Forestry Suppliers). The slope and penetration resistance of the surface soil (R) were also recorded, following the method of Cimmyt (2013). We used a Suunto Pm-5/66 Pc optical clinometer to determine soil slope, and penetration resistance was measured with a dynamic soil penetrometer inserted on the soil surface. This variable was calculated for all quadrants on a single morning from 6:00 am to 9:00 am. Finally, the phytomass of invasive species was assessed after harvesting five 20-cm^2 samples randomly distributed within each plot. Samples were immediately taken to the lab, dried in an oven at 76°C for 6 hours (until constant weight), and weighed.

Experimental setting

We established nine 1-ha plots separated by at least 300 m from each other, with similar slopes and topography (20°-35°) in the oak forest patch (three plots) and the adjacent shrubland (six plots). The latter was separated from the edge of the oak forest by 150 to 200 m. We randomly selected three plots in the shrubland to remove the exotic species manually *P. aquilinum, H. contortus, P. bicolor, A. lehmanii,* and *M. minutiflora*. The removal was repeated quarterly for one year. Thus, we created three replicates of experimental plots for each of the three vegetation types: oak forest (OF), shrubland with exotic invasive species (SI), and shrubland cleared of alien invasive species (SC).

Experiment 1: acorn germination and seedling survival. In 2018 and 2019, we collected acorns directly from 50 healthy trees spaced at least 300 m apart and located at least 500 m inside two forest patches in the El Robledal Forest Reserve. These 400 ha patches are a protected oak forest, with no fire reports, and located 30 km from the experimental area (5°27'48" N, 73°39'45" W) at an altitude of 2800 to 3200 m in the municipality of Guachetá-Cundinamarca. Approximately 1,600 acorns were measured (length and width), weighed, and placed in water for 24 hours. Acorns that floated after 24 hours and those showing physical damage were discarded. Six hundred healthy acorns were used to test germination in the nursery, and the remaining (810 acorns) were used in field experiments. In the field, acorns were sown in ten 1 x 1 m quadrats distributed around nine 23 × 39 m subplots located 2 m from their edge and separated by at least 5 m from each other. Two seeding years were sown in adjacent quadrats, one in March 2018 and one in March 2019, corresponding to peak dispersal dates. Nine acorns were sown in each quadrat on each date, for a total of 90 acorns per site and year (810 in total). In 2018, acorns in five randomly selected quadrats were individually protected by a ten × 10 × 10 cm cube made with wire mesh (1 cm mesh diameter). In 2019, five randomly selected quadrats were protected by enclosing the whole quadrat with the same mesh (30 cm height). Acorns were introduced into 5 cm deep holes and covered with soil. In the nursery, they were sown within a 10-cm peat layer.

Acorn germination was recorded in the field when cotyledons emerged. Field surveys were carried out every week between May and July, every three months between May 2018 and October 2019 (2018 seeding year), and from May 2019 to October 2019 (2019 seeding year). After germination, each seedling was tagged, and its survival, stem height, diameter at the root collar, and canopy cover were recorded for the sampling period. We used the same methodology for monitoring acorn germination in the nursery.

Nursery location and conditions: The nursery (Vivero el Nativo de Ticha) is located in the municipality of Guachetá, Department of Cundinamarca (5°24'49.96" N, 73°42'26.46" W). It is located 30 km and 220° SW of the Iguaque mountains, at an elevation of 2550 m asl. The average annual precipitation, temperature, relative humidity, and evaporation are 1,108 mm, 15ºC, 71%, and 1,180 mm, respectively. In the nursery, acorns were placed in 60 x 20 cm trays within a 5 cm layer of peat and rice fiber and kept in the darkroom at 20°C and 80% air humidity content for three months. The trays were watered daily in the morning with 250 cm3 of fresh water.

Experiment 2: oak seedling establishment and growth. Five hundred and forty 8-month-old oak saplings were obtained from the El Nativo de Ticha nursery in March 2018. They were grown in a 30 X 50 cm black polyethylene container with a substrate of 50:50 organic soil and compost humus mix. Their average height by the end of the nursery period was 41.1 ± 0.47 cm. Planting was performed in March 2018, following a 1 x 1 m regular pattern within the 23 × 39 m plots. Seedlings were planted in manually dug 30 × 30 × 30 cm holes, and 500 g of organic soil and compost humus mix was added to the bottom of each planting hole. No irrigation or fertilization was used.

Each sapling was monitored quarterly between May 2018 and October 2019 (five surveys). Sapling height was measured from the root collar to the apical bud. Additionally, we measured basal stem diameter and canopy cover (estimated as a diamond with diagonals corresponding to the maximum length of the orthogonal axes of the projected canopy). Saplings were considered dead if their aboveground biomass was missing or dry for four months. Relative growth rates between consecutive sampling dates (RGRs) were estimated according to Hunt (1990).

Identification of potential seed predators

In 2019, we randomly selected one protected and one unprotected seeding quadrat under each plant cover type and established one camera trap focused on each (Reconyx® PC800 Professional). Phototrapping was run four months following sowing (April-July 2019), with an effort of 736 days/camera (n = 6 quadrats). The cameras took three images per shoot and were active 24 hours daily. Thus, data on a total of 736 trap days were collected. The recorded animals were identified to the species level, and their relative abundance was related to the vegetation cover type and protection level of the acorn's quadrats. Relative abundance was calculated from the number of independent photos of a species over the total number of images sampled per sampling effort (tra $Ar = \left(\frac{Xi}{Yi}\right) \times 92$ (Díaz-Pulido & Payan, 2012).

Statistical analyses

A one-way analysis of variance (ANOVA) was used to assess the impact of the type of plant cover, protection against herbivory, seeding year, and their interactions on the proportion of seeds that germinated and the proportion of seedlings that survived at the end of the period. It was also used to analyze the following plot variables: tree canopy cover (%), elevation (m asl), slope, monthly average temperature (°C), monthly average air relative humidity (%), resistance to soil penetration (MPa), Dry weight exotics invasive species (g/m2) in the first elimination and dry weight exotics invasive species (g/m2) after four eliminations. Proportions were transformed using the arcsine of the square root of the raw data before the analyses to meet the assumption of normality (Mangiafico, 2016). Other variables were transformed by calculating the square root of the original datum to correct for deviations from normality and homoscedasticity (Shapiro-Wilk and Bartlett-

Levene tests, respectively). Significant ANOVA results were followed by Tukey's post-hoc tests for pairwise comparisons.

We used generalized linear (GLM) and mixed models (GLMER) to analyze the effects of predictor variables on acorn germination, seedling and saplings' survival, and growth. All models were adjusted to include a random plot or seeding and sapling year as random effects. We used one of the following three family probability distributions: namely, binomial (with the logit link function), Gaussian (with the identity link function), and gamma (with the log link function). Before modeling, we selected the probability distribution families that best fit the response variables (Rigby & Stasinopoulos, 2005). We used the functions *glmer* and *glmer.nb* from the ‘lme4’ package (Bates *et al.*, 2015), the *fitDIst* function from the ‘gamlss’ package (Rigby & Stasinopoulos, 2005), the *r2_zeroinfleted* function from the ‘performance’ package (Lüdecke *et al.,* 2021) and the *r.squaredGLMM* function from the ‘MuMin’ package (Barton, 2014) of the R software (R Core Team, 2021).

We evaluated the variance inflation factors to reduce the multicollinearity of predictor variables within the models (VIFs; Fox & Monette, 1992). First, highly correlated variables (VIF>2) were removed from the models and recalculated until the VIF was less than 2 (Zuur *et al.,* 2010). Subsequently, we used stepwise regression to select the model with the lowest Akaike information criterion for small sample sizes (AICc). We used the R software's stepcAIC function from the cAIC4 package (Burnham & Anderson, 2002; Säfken *et al.,* 2018). This approach starts with formulating a series of models that rely on understanding the studied system, followed by assessing how different putative models compare to reality (Rushton *et al.,* 2004).

The fit and predictive performance of models with smaller AICc values were assessed using the likelihood ratio statistic (full model ANOVA) and by calculating the area under the receiver operating characteristic curve (AUROC) (Saveland & Neueschwander, 1990). This method can assess model performance in a threshold-independent manner, independent of the prevalence of the various response types. AUROC values vary between 0.5 (no discriminatory ability) and 1 (perfect discriminative power) (Pearce & Ferrier, 2000). AUROC values of 0.5-0.7 generally indicate low accuracy, whereas values of 0.7-0.9 indicate practical applications, and values greater than 0.9 indicate high accuracy. The calculations of AUROCs and standard errors were based on a nonparametric assumption.

All statistical procedures were performed using the R Studio App statistical computing software packages ‘cAIC4’, 'Biodiversity’, ‘carR’, ‘funrar’, ‘ggplot2’, ‘gamlss’, ‘lm4’, ‘reshape’, ‘tidyr’, and ‘vegan’ (R Core Team 2020). For GLMs and GLMER, we used the functions *glmer* and *glmer.nb* (Bates et al. 2015), *fitDIst* (Rigby & Stasinopoulos 2005), *stepcAIC*, (Burnham & Anderson 2002; Säfken et al. 2018), and *VIF* (Fox & Weisberg 2019).

RESULTS

Plots conditions and biomass accumulation of exotic species

Plots were similar in terms of average altitude and slope. The tree canopy cover was high in oak forest (64%) and the cero for the other coverages. Soil resistance to penetration presented significantly lower values in the oak forest than in the other two coverages. These had the same value for this variable. The air temperature was lower in the forest than in the shrublands, but the opposite was true for relative humidity. (Table 6.1; Appendix 6.1 and

6.2). The biomass of exotic invasive species was lower in the forest than in the shrubland. We removed 95% of the biomass of alien invasive species in intact shrublands plots through quarterly extractions.

Table 6.1. Climatic conditions and biomass accumulation of exotic species *in Quercus humboldtii* forests (OF), shrubland with exotic invasive species (SI), and shrubland cleared of alien invasive species (SC) in the Iguaque Mountains of Colombia. Data correspond to averages and standard deviations of N=9 measurements.

Plots indices	**Coverage type**			**ANOVA**		***Tukey homogeneous groups***
	OF	**SI**	**SC**	***f***	***p***	
Tree canopy cover (%)	64 ± 6	0	0	2667	$<2.0^{-16}$	OF>SI=SC
Elevation (m asl)	2456 ±2	2485 ± 15	2477 ± 15	3.4	6.0^{-2}	OF<SI=SC
Slope (°)	29 ± 2	22 ± 2	26 ± 2	0.92	0.4	OF=SI=SC
Monthly average temperature (°C)	15 ± 0.1	16 ± 0.1	17 ± 0.1	838	$<2.0^{-16}$	OF<SI=SC
Monthly average air relative humidity (%)	81 ± 0.1	76 ± 0.1	73 ± 0.1	1598	$<2.0^{-16}$	OF>SI=SC
Resistance to Soil Penetration (MPa)	0.8 ± 0.1	1.2 ± 0.1	1.2 ± 0.1	7.35	6.0^{-3}	OF<SI=SC
Dry weight exotics (g/m^2) First elimination.	497 ± 106	8778 ± 734	6227 ± 186	92.4	$<2.0^{-16}$	SI<SC<OF
Dry weight exotics (g/m^2). After four eliminations.	451 ± 96	8880 ± 766	290 ± 12	122	$<2.0^{-16}$	SI<OF<SC

Acorn germination and early seedling performance

Acorn germination percentage in the nursery was 91 ± 1% for 2018 and 89 ±3% for 2019. The average germination percentage in the field was 45% in 2018 and 53% in 2019, from that measured in the nursery. The germination rate was lower in the forest than in the shrubland, whereas removing exotic species did not affect this variable (Table 6.2). The magnitude of this difference was different in 2018 and 2019 (Figure 6.2, Appendix 6.2). Acorn protection increased germination, regardless of the plant cover and seeding year (Table 6.2., Appendix 6.3).

Table 6.2. Acorn germination and early seedling survival of *Quercus humboldtii* seeded and planted in 2018 and 2019 as a function of plant coverage and acorn protection in the Iguaque Mountains.

Variable	Factor	*df*	*Sum Sq*	*Mean Sq*	*f*	*p*	*Tukey homogeneous groups*
Acorn Germination (%)	Plant cover	2	49066	24533	37	1.2^{-13}	OF < SC = SI
	Protection	1	5932	5932	9	0.004	-
	Seeding year	1	1681	1681	2	0.120	-
	Plant cover × Protection	2	836	418	1	0.547	-
	Plant cover × Seeding year	2	15572	7786	11	2.5^{-5}	OF2018 < OF2019 < SC2018 = SC2019 = SI2018 = SI2019
	Protection × seeding year	1	302	302	0.4	0.509	-
	Residuals	170	117154	389			
Early Seedling Survival (%)	Plant cover	2	3.5	1.7	8	6.9^{-4}	OF > SC = SI
	Seeding year	1	14.3	14.3	63	5.0^{-13}	-
	Plant cover × Seeding year	2	2	1	4	0.01	SI2019 = SC2019 > OF2018 = OF2019 > SC2018 = SI2018
	Residuals	145	32.1	0.2			

The survival of seedlings sowed in the oak forest was higher than those sowed in the shrubland in 2018, but not in 2019, when survival rates were very high (Figure 6.2; Table 6.2). Removing exotic invasive species did not affect seedling survival in 2018 or 2019. Survival also depended on the local planting conditions (Table 6.2).

Seedlings in OF showed a lower RGR stem height (OF 2018: 1 ± 0.1 mm/month; OF 2019 4 ± 1 mm/month) than shrublands, which showed the same value for this variable in 2018 (6 ± 1 mm/month) and relatively higher in SI for 2019 (SI: 7 ± 1 mm/month, SC: 5 ± 1 mm/month). Removing exotic invasive species did not affect the RGR stem height in 2018 or 2019 (Figure 6.3., Appendix 6.3). RGR Root collar diameter showed a similar pattern to height. According to the GLMM, seedling RGR stem height (Table 6.3) was positively related to SI and SC cover types and negatively associated with increasing slope and OF cover (Table 6.3, Appendix 6.4). According to the GLMM, the seedling's RGR

Root collar diameter was positively related to SI and SC cover types and increasing canopy cover (Table 6.3).

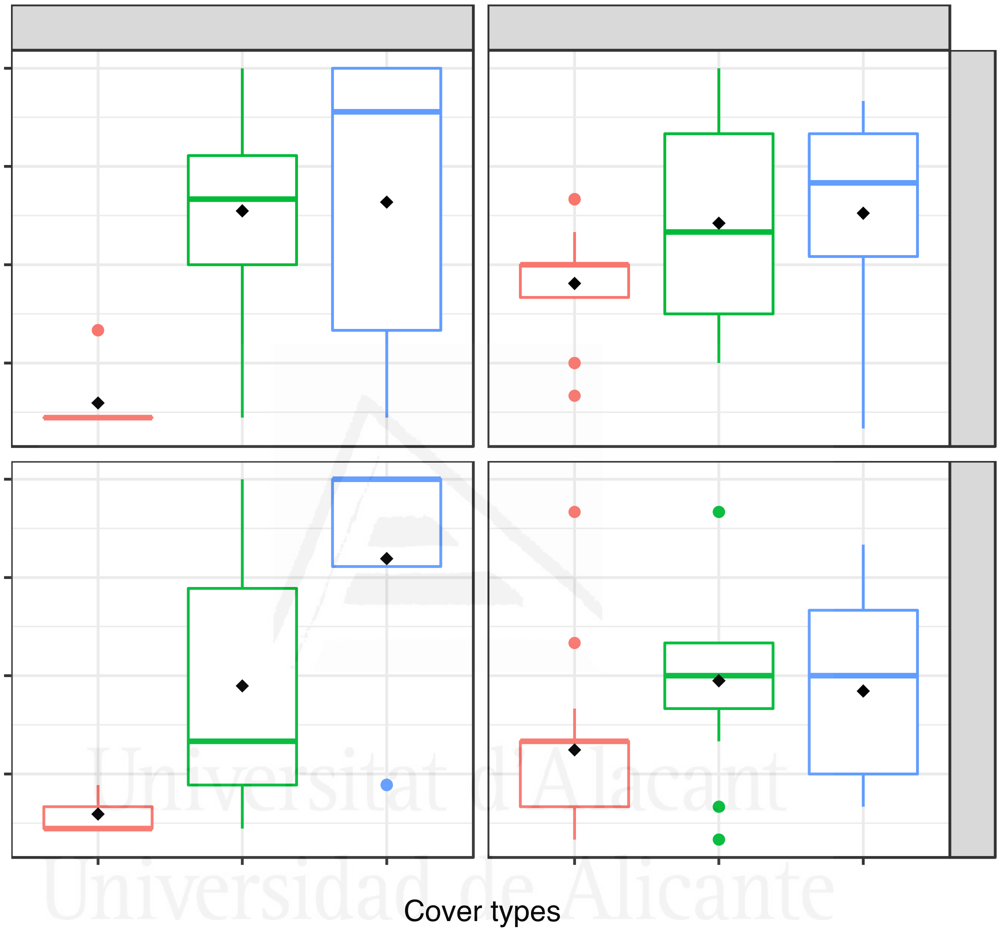

Figure 6.2. Effect of plant cover, seeding year, and seed protection on the germination rate of *Quercus humboldtii* in the Iguaque Mountains. OF, SI and SC correspond to oak forests, unaltered shrubland, and shrubland where exotic invasive species had been removed.

Table 6.3. Generalized Linear Models including at least one independent variable and the null model of acorn germination, early and later seedling survival, and relative growth rate of the stem height and root collar diameter of *Quercus humboldtii* seedlings after germination in the Iguaque Mountains. OF, SI and SC correspond to oak forests, unaltered shrubland, and shrubland where exotic invasive species had been removed. SE= Standard error.

Variable	Model	Model family	Tested models	AIC	R^2	AUROC	Fixed effects	Estimate	SE	*z/T*	*p*
Germination (%)	Plant cover + Protection + Slope + (1| seeding year)	GLMM Gaussian (identity)	16	1.7	0.3	-	OF	27	72	4	NA
							SI	35	5	6	NA
							SC	32	5	7	NA
							Protection	7	4	2	NA
							Slope	-0.3	0.2	-2	NA
Early seedling survival (%)	Plant cover + (1| seeding year)	GLM binomial (logit)	17	145	0.4	83%	OF	1.2	1	1	0.3
							SI	-0.1	1	-0.1	0.9
							SC	-0.5	1	-0.1	0.4
Later seedling survival (%)	Plant cover+ soil penetration resistance + (1| seeding year)	GLM binomial (logit)	4	329	0.2	80%	OF	2	0.4	5	5.8^{-6}
							SI	3	1	6	3.2^{-10}
							SC	3	0.5	6	4.9^{-10}
							Soil penetration resistance	-1	0.4	-3	4.5^{-3}
Seedlings RGR stem height	Plant cover + Slope + (1| seeding year) + (1|Site)	GLMM Gaussian (identity)	18	51	0.6	-	OF	-1	0.4	-0.3	2.0^{-3}
							SI	0.6	0.3	2	2.0^{-3}
							SC	0.5	0.3	2	0.1
							Slope	-0.1	0.1	-2	0.1

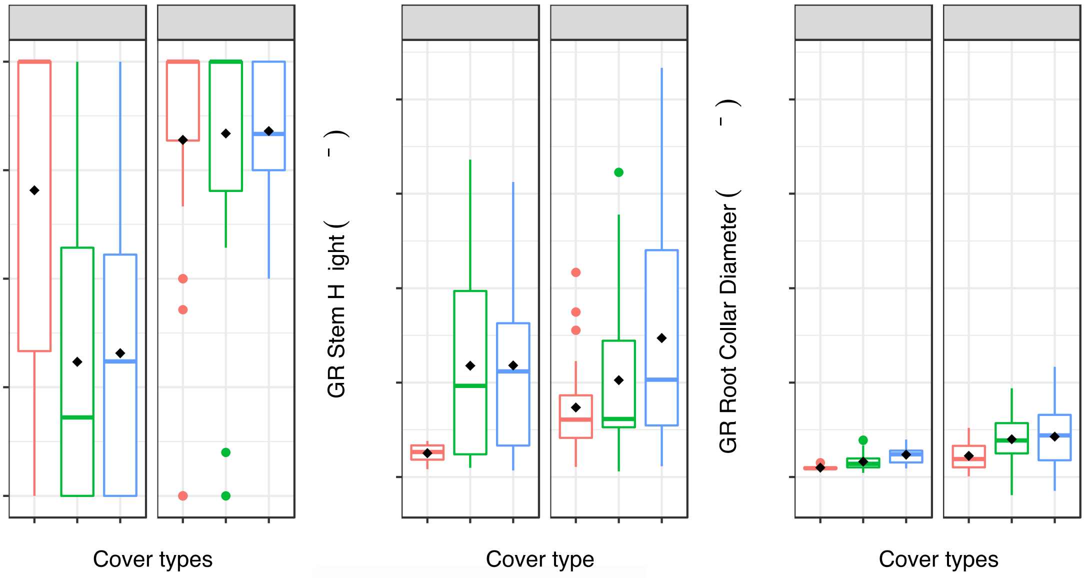

Figure 6.3. Effect of plant cover on the survival and relative growth rate of the stem height and root collar diameter of *Quercus humboldtii* seedlings after germination in the Iguaque Mountains in 2018 and 2019. OF, SI and SC correspond to oak forests, unaltered shrubland, and shrubland where exotic invasive species had been removed.

Acorn predators

We identified four acorn predator species in the experimental plots: *Didelphis peregrina* Allen (Andean white-eared opossum), *Mus musculus* Linnaeus (home mouse), *Notocirius granatensis* Humboldt (red-tailed squirrel), and *Sylvilagus andinus* Thomas (Andean rabbit) (Appendix 6.5, 6.6). The most abundant species was *N. granatensis*, followed by *D. peregrina*. *Notocirius granatensis* and *D. peregrina* were foraging and extracting seeds in the planting sites (Appendix 6.6). The species with the highest abundance in all coverages were *N. granatensis*, *D. peregrina*, and *S. andinus*. In the forest, *N. granatensis* was the most abundant species (AR: 13 in protected, AR 9 in unprotected), while this species in the shrublands was 130 times less in the protected plots and 90 times less in the unprotected. *Didelphis peregrina* was not recorded in the protected forest plots (AR= 5) but in both SC (AR= 0.02 in protected, AR= 0.03 in unprotected) and SI (AR=0.03 in protected, AR= 0.07 in unprotected). Like *D. peregrina*, in the forest, *S. andinus* was only recorded in unprotected plots (AR=0.4). In the case of shrublands, it was also present in both plots' types. We found a negative effect of protection on the abundance of visiting fauna.

Survival of planted saplings

The survival of planted saplings was consistently high (Figure 6.4, Appendix 6.7, 6.8), mainly when buried under shrubland. Removing exotic invasive species did not affect saplings' survival. Similarly, the growth rate was lower in the forest and similar in saplings planted in SI and SC plots. Again, the GLM for the sapling survival rate found that it was positively related to SI and SC coverage and negatively related to OF coverage and soil penetration resistance (Table 6.4, Appendix 6.8). The aboveground growth rate was similar in saplings and seedlings growing from seeded acorns.

Quercus humboldtii **sapling growth**

The saplings exhibited a similar RGR stem height among the three coverage types (Figure 6.4, Appendix 6.9); however, a higher height SI achieved RGR (8 ± 0.4 mm/month) and SC saplings (7 ± 0.4 mm/month) than by OF saplings (5 ± 0.3 mm/month). According to the GLMM, the RGR stem height for saplings (Table 6.4) was positively related to SI and SC coverage types and negatively associated with increasing slope and OF coverage (Appendix 6.9). Additionally, saplings showed a higher RGR root collar diameter (Figure 6.4) in SC (0.3 ± 0.01 mm/month) and SI (2 ± 0.1 mm/month) than in OF (1 ± 0.1 mm/month; Figure 6.5). According to the GLMM, saplings' RGR root collar diameter was positively related to the SI and SC coverage types and increased slope and soil penetration resistance;

the RGR root collar diameter was negatively associated with increasing temperature and OF coverage (Table 6.4).

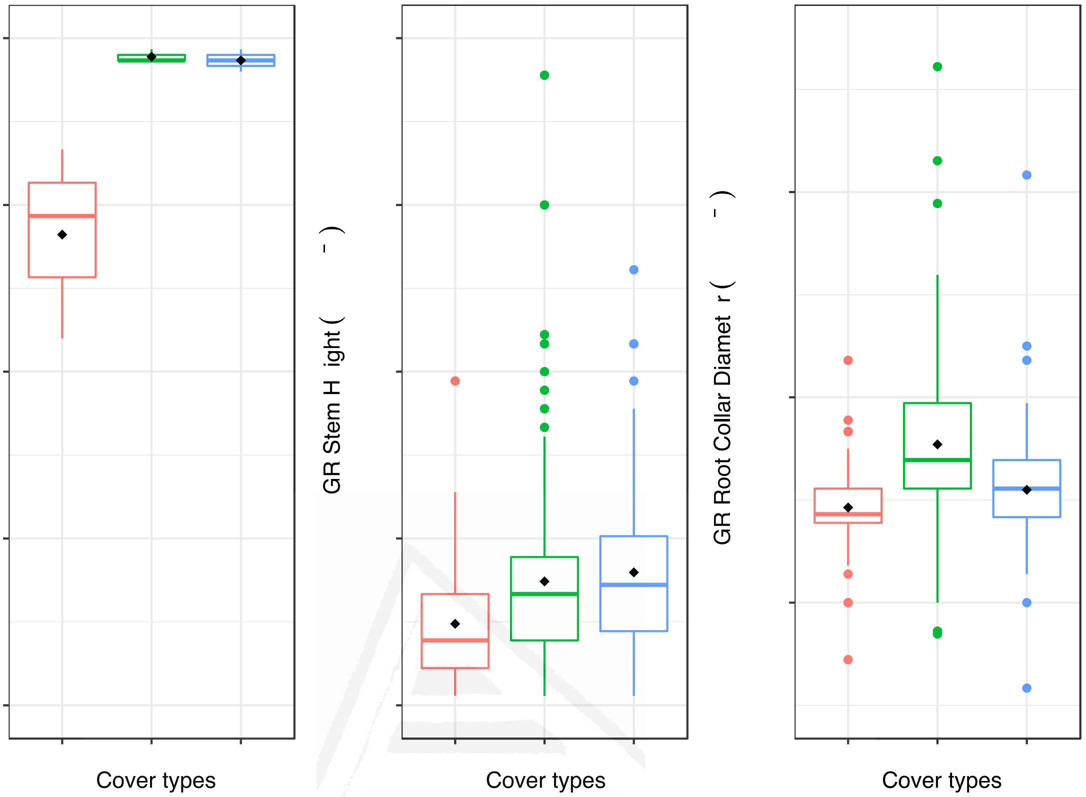

Figure 6.4. Effect of plant cover on the survival and relative growth rate in stem height and root collar diameter of *Quercus humboldtii* saplings planted under oak forest (OF), unaltered shrubland (SI), and shrubland where exotic invasive species had been removed (SC). in the Iguaque Mountains.

Table 6.4. Generalized Linear Models including at least one independent variable and the null model of saplings survival rates and relative growth rate of the stem height and root collar diameter of *Quercus humboldtii* saplings in the Iguaque Mountains. SPR = soil penetration resistance. SE= Standard error.

Variable	Model	Model family	Tested models	AIC	R^2	ROC	Fixed effects	Estimate	SE	*z/ T*	*p*
Sapling survival	Plant cover + soil penetration resistance + (1|site)	GLM Binomial (logit)	10	329	0.17	80%	OF	1.9	0.4	4.5	6.0^{-6}
							SC	2.8	0.5	6.3	3.0^{-10}
							SI	2.9	0.5	6.2	5.0^{-10}
							SPR	-1.1	0.4	-2.8	5.0^{-3}
Relative height growth for saplings	Plant cover + slope + (1|site)	GLMER Gamma (log)	8	323	0.15	-	OF	-0.6	0.3	-2.2	0.03
							SC	0.4	0.2	1.7	0.09
							SI	0.3	0.4	1.6	0.10
							Slope	-0.1	0.1	-0.5	0.60
Relative cover growth for saplings	Plant cover + (1|site)	GLMER Gamma (log)	8	2594	0.07	-	OF	2.2	0.2	13.9	1.5^{-44}
							SC	0.3	0.2	1.1	0.26
							SI	0.1	0.2	0.4	0.68
Relative diameter stump growth for saplings	Plant cover + temperature + Soil penetration resistance + slope + (1|site)	GLMER Gamma (log)	7	3023	0.25	-	OF	-1.6	1.2	-1.3	0.78
							SC	0.5	0.1	3.9	9.0^{-05}
							SI	0.2	0.1	1.7	0.09
							Temperature	-0.2	0.1	-2.1	0.03
							SPR	0.2	0.1	1.1	0.28
							Slope	0.1	0.1	1.9	0.06

DISCUSSION

Acorn germination

The number of healthy acorns, as estimated by the number showing no external damage, those that sank in the water, and those that germinated under the benign conditions of the nursey, was 89 to 91%. This percentage is relatively high compared to acorns of other species and populations (Jhonson *et al.*, 2002; Gómez & Toro, 2007; Kapelle, 2006; Sepúlveda *et al.*, 2014; Granger *et al.*, 2018), suggesting that acorn germinability may not deter oak recruitment. The germination rate in the field was lower than in the nursery, particularly under the oak forest in 2018. However, it was sufficiently high in the shrubland in 2018 and under all cover types in 2019 to suggest sufficient germinability under field conditions. On the other hand, the high proportion of selected acorns germinating in the nursery shows that choosing healthy acorns is suitable for nursery and field management.

Lower germination rates in the forest may be attributed to differences in microclimate, mainly reduced radiation caused by dense canopies and the forest floor (Asbjorsen *et al.*, 2006; Díez *et al.*, 2017). Slight differences in air temperature and moisture content between the forest and the shrubland point to this possibility. Also, the leaf litter of Andean oaks has relatively high tannin concentrations (Lozano & Torres, 1965), and low seed germination rates have been documented under trees of the same species (Avila *et al.*, 2010). An additional reason for the low germination in oak forests can be attributed to the slope, which is more significant in the forest than in the shrublands. A steeper slope facilitates the downslope movement of acorns, preventing their germination in the place where they are sown or dispersed.

Predation of acorns by mammals can also be a relevant element in their germination, as could be observed experimentally in the germination rate between protected and unprotected acorns, where the former had a higher germination rate. Predation in the oak forest may occur with greater incidence due to the greater abundance of these mammals. However, the role of mammals should be studied in detail depending on their behavior and acorn satiation. They could become acorn dispersers rather than predators (Nathan & Muller-Landau, 2000; López-Barrera & Manson, 2006; Bonfil, 2006; Bogdziewicz *et al.*, 2018). For example, red squirrels (the most abundant species in all vegetation covers) tend to redistribute acorns in the forest to store them in good hiding places. Many of these acorns reach ideal microenvironments to germinate and are forgotten by these animals. Therefore, squirrels have been cataloged as good dispersers of oak trees (Garcés-Restrepo & Saavedra-Rodríguez, 2013; López-Ramírez *et al.*, 2020). A study that allows us to see the rate of re-spreading, final destination, and germination of acorns after sowing can contribute to understanding the extent to which acorn redistribution occurs in the three covers. Finally, differences in invertebrate predator activity and soil microflora may also have reduced acorn germination in the forest (Sepúlveda *et al.*, 2014).

Seedling and saplings survival

The survival of seedlings established from acorns and planted saplings were relatively high. However, oak seedlings and saplings face much higher mortality in the oak woodland than in the shrubland, whether or not the shrubland has exotic species present. It must be noted that in 2019, almost all seedlings planted in the shrubland survived the first year. Thus, field conditions do not deter oak establishment. Survival was higher than other *Q. humboldtii* plantations or many plantations of different oak species (López-Barrera & Manson, 2006; Ramírez-Marcial *et al.*, 2006; Sepúlveda *et al.*, 2014; Granger *et al.*, 2018).

It has been suggested that saplings growing in nursery containers may be less suited for field conditions because of changes in biomass allocation patterns and root architecture (Leverkus *et al.,* 2021; Villar-Salvador *et al.,* 2021). However, in our study, the negative effect of nursery culture may be absent or may show in the later stages of the saplings' establishment. Indeed, variability in the survival of seedlings developing from acorns that germinated in the field was higher than in the survival of planted saplings, which may reflect the vulnerability of young seedlings. However, early survival was highly variable and very high.

The effect of cover type on seedling survival depended on the type of seedling, the type of cover, and the seeding or planting year. Thus, in 2018, which was colder and wetter, early survival was low, particularly in the shrubland, whereas the survival of planted seedlings was high, particularly in seedlings planted in the shrubland. Furthermore, variability was increased in early survival but lowered in planted saplings. Finally, the survival of seedlings emerging from seeded acorns in 2019 was high under all types of plant cover. These results suggest different early vs. late survival drivers, which depend on the site and the climate conditions. Thus, early survival is spatially heterogeneous under harsh climatic conditions and somewhat higher in the forest. Unfortunately, we can provide a consistent mechanistic explanation for this response but may assume that acorns are highly vulnerable at this stage, and forest sometimes provides a microclimatic buffer. On the contrary, planted saplings were more resistant to adverse climatic conditions but more sensitive to interference by the forest.

Seedling and saplings growth

Growth of seedlings established from acorns and saplings was relatively high, but RGR for tall stumps and diameter in the shrublands was higher than in the oak forest. Field conditions and removing invasive exotic species did not impede the growth of *Q. humboldtii* seedlings or saplings. Growth was similar to other *Q. humboldtii* plantations (Sepúlveda *et al.,* 2014; Díez et al., 2017) and many plantations of different oak species (Jhonson *et al.,* 2002; Granger *et al.,* 2018; López-Barrera & Manson, 2006; Kapelle, 2006; Ramírez-Marcial *et al.,* 2006). The environmental conditions of the shrublands, such as direct light incidence (Rey & Alcántara, 2000; Palma *et al.,* 2021; Roque *et al.,* 2021) and a lower slope, favor more significant growth in seedlings and saplings in these cover types. The seedlings or saplings under these conditions can present a more substantial development of the stem as a possible strategy for obtaining and reserving resources (Barrera *et al.,* 2010; Davis & Pinto, 2021; Villar-Salvador *et al.,* 2021). Also, the condition of a moderate slope favors better rooting and better retention of resources in the soil for the seedlings (Jhonson *et al.,* 2002; Villar-Salvador & Oliet, 2021). In addition, a possible allelopathic effect of *Q. humboldtii* trees and high litter density in the forest could reduce seedling and sapling growth rates (Lozano & Torres, 1965; Avila *et al.,* 2010).

Moreover, the low light conditions in oak forests may stimulate seedlings and saplings to remain in that state, forming a seedling stock (García *et al.,* 2001; Ramírez-Marcial *et al.,* 2006). The formation of this seedling bank is very positive for the population dynamics and long-term maintenance of the oak population. However, recurring wildfires in the Iguaque mountains can destroy it.

Exotic interference of acorns and seedlings' performance

A low richness and density of tree species characterize the post-fire vegetation community in the mountains of Iguaque. It is dominated by small native shrubs, herbs, and resprouting grasses, most of which are invasive exotic species such as *Andropogon lehmannii, Melinis minutiflora,* and *Pteridium aquilinum*. Our experimental plots presented this type of vegetation. However, through recurrent eliminations in the SI plots, we guaranteed the control of the aerial biomass of these species during the whole experiment. Thus, acorn germination and seedlings establishment comparisons between SC and SI plots (with and without invasive aliens) allow us to assume that invasive aliens did not directly interfere with oak germination, establishment, and growth.

In contrast, some specific benefits of invasive exotic cover on germination and development can be attributed to microclimatic improvements, such as reduced ground-level temperatures and improved moisture conditions. This cover may also stimulate oak growth because seedlings must outcompete grasses and other weeds for light or other resources. This was largely unexpected, as invasive exotic species have been attributed as potential competitors capable of excluding native species (Baptiste *et al.*, 2010; Cárdenas-López *et al.*, 2017).

However, exotic invasive species can indirectly limit *Q. humboldtii* recruitment. High biomass accumulations generated by these species will act as fuel, affecting the fire regime (Vargas, 2000; Zouhar *et al.,* 2008) (Shaffhauser *et al.,* 2012; Bianchi *et al.,* 2014). In the long term, even if the oaks have been recruited in these thickets, their survival will be reduced if they are not large enough to resist and resprout after a fire (Salazar *et al.,* 2020). Therefore, it should be ensured that the fire return time is longer than when the

Andean oak exceeds 6 cm in diameter or 10 m in height. According to studies, Andean oaks or other species of these sizes can survive a fire and resprout from the crown or stump (Johnson *et al.,* 2002, Aguilar-Garavito *et al.,* in prep. B). In this way, the accumulation of biomass of invasive exotic species affects the fire regime and could affect *Q. humboldtii* recruitment.

Quercus humboldtii **germination and establishment limitations**

Our results show that the three potential mechanisms of recruitment limitation (seed germination, seedling, sapling survival, and growth) are comparable between oak forests and shrublands and contribute to a more or less equivalent final density of established seedlings after eighteen months of experimental observation. However, germination and growth in the shrublands were much higher than those in the oak forests, implying more significant obstacles to tree recruitment in oak forests. Other studies have pointed to seed dispersal as the critical process limiting tree recruitment due to the difficulty dispersing acorns at a distance and in open sites (Acácio *et al.,* 2007; Granger *et al.,* 2018; Palma *et al.,* 2021; Roque *et al.,* 2021). Our experiment shows that seeds can germinate and establish as seedlings and saplings in shrublands–if they can reach them. Additionally, microhabitat conditions play an essential role in germination, survival, and growth (Johnson et al. 2002, Moreno & Cuartas 2014;). This highlights the importance of seed dispersers; for example, squirrels can transport and forget acorns in microenvironments suitable for oak recruitment (Nathan & Muller-Landau, 2000; Kapelle, 2006; López-Barrera & Manson, 2006).

Suppose the source and dispersal limitation in the Iguaque Mountains is overcome (Aguilar-Garavito et al. in prep B, C). In that case, many occurring acorns arriving in oak forests and shrublands with or without exotic species can germinate, establish and grow. In the oak forest, seedlings and saplings will constitute a seedling bank (García *et al.,* 2001; Ramírez-Marcial *et al.*, 2006), while in the shrubland, seedlings and saplings will continue their development. Based on the above, it can be hypothesized that the vegetation that dominates the shrublands do so not because they are superior competitors in the given environmental conditions but because the best competitors, such as *Q. humboldtii* and other tree species, can never establish themselves in those sites due to source limitation and dispersal, rather than because of germination or establishment limitation. This situation has been reported in other ecosystems with arrested successions (Acácio *et al.*, 2007; Rey & Alcántara, 2000; Palma *et al.*, 2021; Werden *et al.*, 2021) or under disturbances such as fire (Jhonson *et al.*, 2002; Schaffhauser *et al.*, 2012).

Implications for management

Overcoming acorn availability and dispersal is done through direct seeding and planting assistance. Both repopulation techniques can show good results in survival and growth in forests and shrublands affected by fires in the mountains of Iguaque. However, containerized seedlings from nurseries have better results than directly planting acorns. Primary care in the nursery contributes to better plant quality and possible better establishment in the field (Ramírez-Marcial *et al.*, 2006; Haase & Davi,s 2017; Leverkus *et al.,* 2021; Villar-Salvador *et al.*, 2021). In a reforestation program in the Iguaque Mountains, it would be advisable to use both techniques for oak establishment. Direct seeding of acorns can be prioritized for areas with more difficult access, introducing a more significant number of individuals in better micro-sites at a lower cost. According to our experience, one worker can plant around 450 acorns in one day. On the other hand, planting container seedlings, although more time-consuming and complex (140 saplings for a worker, day 1), can be prioritized in areas of easy access, guaranteeing better plant quality and possibly a better establishment (better survival and larger seedlings).

Reducing the frequency and severity of wildfires is a priority for managing the Iguaque mountains. On the one hand, a lower fire frequency would allow the large shrubs and trees in the thickets to develop, generating continuous canopies fully. These canopies would allow seed dispersers, such as squirrels, to use these canopies more reliably and contribute to an excellent biomass accumulation number of seeds. On the other hand, the lower frequency and intensity of fires would allow seedlings and saplings recruited in the thickets to reach adequate sizes to withstand fires and produce viable acorns. In the same way, the seedling bank of the forest could be maintained in the long term, guaranteeing the replenishment and permanence of *Q. humboldtii.* In this sense, reducing the biomass accumulation of invasive exotic species could influence the control of the fire regime (Baeza et al. 2002, 2006, Keeley et al. 2005a, 2005b) and ultimately improve the recruitment of *Q. humboldtii*. Based on our field experience, four manual removals of invasive species carried out every four months for a year and a half reduce invasive biomass in invaded shrublands by up to 95%.

Management plans must simultaneously alleviate low seed availability and dispersal and reduce fire frequency and severity to allow sapling growth. Specific actions could include a combination of reducing fuel loads in oak forests, shrublands, and edges and developing a comprehensive fire management plan (Moreira *et al.*, 2020); additionally, adding acorns and *Q. humboldtii* seedlings, planting shrubs and nurse trees (e.g., *Bejaria resinosa* Mutis ex (L. f.), *Clethra fimbriata* Kunth, *Clusia multiflora* Kunth, *Pentacalia corymbosa* (Benth.) Cuatrec., *Palicourea angustifolia* Kunth, *Viburnum tinoides* (L.f.), *Dodonaea viscosa* Jacq., *Miconia squamulosa* (Sm.) Triana, *Myrsine guianensis* (Aubl.) Kuntze, and *Myrsine coriacea* (Sw.) R. Br. Ex Roem. & Schult.) can facilitate the germination, survival, and growth of Andean oak seedlings and saplings.

CONCLUSIONS

Our results demonstrate that the Andean oak does not appear to experience strong germination and establishment limitations in the shrublands of the Iguaque Mountains. Instead, the strongest limitations may be the source and dispersal limitations. Succession in shrublands appears to be arrested and unable to progress into forests. *Quercus humboldtii* recruitment is rare in forests and shrublands, although the shrubland patches are contiguous with oak forests. However, the shrublands represent an unstable vegetation type that could transform into a forest if oak seeds or seedlings can reach it and if fire recurrence is considerably reduced until the oak saplings reach an adequate size to resist fire and to resprout.

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SUPPLEMENTARY MATERIAL 6

Appendix 6.1. Temperature and relative humidity differences between the experimental plots.

Appendix 6.2. Germination, survival, and growth rate for *Quercus humboldtii* acorns sown.

Appendix 6.3. Generalized Linear Mixed-Effects Model for the relative germination of protected and unprotected *Quercus humboldtii* acorns from two years sown in three vegetation types.

Appendix 6.4. Relative seedlings height growth model on tree different coverages.

Appendix 6.5. Species, number of individuals, and relative abundance of potential-seed predators' mammals among cover and protection levels.

Appendix 6.6. Camera traps in experimental plots detected the most abundant seed dispersers/predatory mammals.

Appendix 6.7. Survival and growth of saplings in three experimental cover types.

Appendix 6.8. Relative saplings survival model on tree different coverages.

Appendix 6.9. Relative height growth rate model on different tree coverages.

RESUMEN Y DISCUSIÓN GENERAL

1. Pérdida y fragmentación de los robledales del norte de los Andes

En los Andes colombianos, *Quercus humboldtii* tiene una amplia distribución, abarcando gradientes altitudinales y climáticos que abarcan elevaciones bajas (900 m s.n.m.) y altas (3.200 m s.n.m.), ambientes húmedos y secos (623 mm/año - 6.978 mm/año) y temperaturas (media anual) en el rango de 4ºC a 27°C. Esta distribución se ajusta estrechamente a los patrones generales de la distribución natural descrita en otros estudios (Lozano & Torres, 1974; Avella *et al*., 2017; Rangel, 2017). Según nuestro modelo, *Q. humboldtii* ocupa el 28% de su distribución potencial, lo que está dentro del rango de las estimaciones hechas por otros autores (González *et al.,* 2006; 2011; López, 2014). Consideramos que nuestra estimación proporciona más detalles, pues utilizamos umbrales de discriminación, realizamos un ajuste riguroso de los hábitats que podría ocupar esta especie, y utilizamos una base de datos con un mayor número de observaciones. La reducción en su área de distribución es superior a la observada en bosques andinos de Colombia (ca. 60%; Etter *et al.,* 2008).

Los incendios se han añadido a la serie de impulsores antrópicos de transformación, que están influyendo en la pérdida de hábitat de esta especie. Nuestros resultados muestran que, durante los últimos 30 años, se han producido numerosos incendios dentro del hábitat potencial de *Q. humboldtii*. Adicionalmente, encontramos que la incidencia de los incendios sobre el área de distribución remanente es baja, y los incendios parecen concentrarse en su periferia. Muchas de las áreas consideradas en nuestros modelos como hábitat remanente forman parte de áreas naturales protegidas, en las que la regulación de usos y la gestión de incendios deberían ser prácticas comunes (León-Parra & Vilardy, 2022). Sin embargo, en algunas áreas naturales protegidas de Colombia, los incendios ocurren mayormente en su periferia y, en algunos casos en su interior lo que coincide con estudios previos (UNGRD, 2018, Armenteras, et al. 2019, Aguilar-Garavito, et al. 2020). Actualmente los incendios en el norte de los Andes presentan una mayor frecuencia que los regímenes prehispánicos y su origen es principalmente antrópico. La gestión se ha fundamentado en la supresión, dejando de lado la prevención y la restauración ecológica (Rodríguez-Buriticá *et al.*, 2017, Aguilar-Garavito et al., 2018, Armenteras, 2020).

Los incendios están afectando a extensas áreas del hábitat potencial del roble andino y la periferia del hábitat remanente. Esta presión, a la que podrían estar contribuyendo las variaciones ENSO, estaría provocando una reducción del hábitat remanente de la especie. De acuerdo con López (2014), la combinación de incendios y cambio climático podría causar una reducción adicional del 13% del hábitat remanente del roble andino para 2080. A nivel regional, en algunos hábitats incluidos en la distribución potencial y remanente de *Q. humboldtii*, la frecuencia de incendios ha incrementado en los últimos 30 años (UNGRD, 2018, Aguilar-Garavito 2020). En el Macizo de Iguaque, los incendios forestales han supuesto una reducción del 45% de la superficie de robledales.

Los datos existentes, han permitido realizar una primera aproximación a la ocurrencia de incendios en el norte de los Andes, sus posibles impulsores, y su relación con la superficie de robledal. Sin embargo, es necesario profundizar en el registro y caracterización de la distribución de fuegos a múltiples escalas. Esto permitiría determinar las principales causas de su distribución, y su relación con la presencia de *Q. humboldtii*. Además, ayudaría a priorizar los lugares donde es necesario implementar planes para el manejo integral de incendios y la restauración de robledales en regresión. De acuerdo con los resultados obtenidos, podemos proponer algunas medidas de gestión a escala nacional y regional:

1) Establecer normatividad para la gestión integral de incendios.
2) Mejorar la gestión de los incendios en las áreas protegidas.
3) Fortalecer la normatividad sobre la conservación del roble andino.
4) Promover acciones de conservación de la biodiversidad en remanentes de bosque no protegidos, y en las áreas productivas circundantes.

En este sentido, Moreira y colaboradores (2020) propusieron una serie de medidas para la gestión de incendios en la región Mediterránea, con aplicabilidad en el norte de los Andes, incluyendo acciones encaminadas a la prevención y mitigación de incendios, y evitar o minimizar los daños sociales y ecológicos.

2. El creciente protagonismo del fuego en el norte de los Andes

Los incendios son cada vez más frecuentes en el norte de los Andes (Figura II; Pabón-Caicedo, 2011; Earl & Simmonds, 2018; Aguilar-Garavito *et al.*, 2019). Sin embargo, la escasa comprensión de la dinámica de los incendios y de la respuesta de los ecosistemas en esta región, limita la toma de consciencia sobre la magnitud del problema, y dificulta el diseño de estrategias apropiadas de gestión.

En muchos países Andinos los informes sobre incendios son escasos (Armenteras *et al.*, 2020) y a veces contradictorios (Anaya-Acevedo & Chuvieco-Salinero, 2010). Con nuestro estudio hemos demostrado que utilizando una combinación de técnicas de teledetección, informes oficiales, entrevistas y mapas sociales, se pueden delimitar los incendios, estimar su extensión y determinar su dinámica en lugares con registros inexistentes o no estandarizados. Sin embargo, se debe hacer un esfuerzo por desarrollar un sistema unificado de recolección, procesamiento y custodia de dicha información. Técnicas complementarias, como el análisis de las cicatrices de incendios en los anillos transversales de los troncos, podrían ayudar a afinar estas aproximaciones.

A nivel regional, los incendios están asociados a la dinámica climática, especialmente a los ciclos ENSO, y a las actividades humanas, tal y como se ha observado en otras regiones (Fuller & Murphy, 2006; Mariani *et al.*, 2017). La frecuencia y extensión de los grandes incendios han mostrado relaciones consistentes con la dinámica ENSO en regiones tropicales, donde se le atribuyen al menos el 30% de los incendios (Chen *et al.*, 2017). En Iguaque, los incendios se concentraron en los periodos de sequía estacional, altas temperaturas y mayor afluencia turística (Villarreal *et al.*, 2017; Google Trends, 2020).

Durante más de 500 años, la tala de árboles, las prácticas de roza y quema, la agricultura intensiva y el pastoreo han modelado el paisaje del norte de los Andes (Fals Borda, 2006; Etter, *et al.*, 2008, Mora, 2012). Tras la designación de áreas naturales protegidas para la conservación de la biodiversidad, como en el macizo de Iguaque, el abandono de los usos tradicionales del suelo puede favorecer la colonización de especies herbáceas, gramíneas y arbustos, promoviendo la acumulación y continuidad del combustible (Fernández-Méndez *et al*., 2016; Salazar *et al*., 2020). Hay que tener en cuenta que, por lo general, en áreas protegidas de Colombia no se permite realizar labores agrícolas o de pastoreo. Paralelamente al abandono rural, el turismo no regulado ha ido en aumento (Villareal *et al.*, 2017, León-Parra & Vilardy, 2022). Como consecuencia, ha disminuido la población residente y se han originado conflictos relacionados con la tenencia de la tierra y el uso de la biodiversidad. Esta compleja situación favorece la ocurrencia de incendios forestales.

Las entrevistas realizadas en Iguaque revelaron la existencia de dichos conflictos socioambientales. Los entrevistados identificaron los conflictos sociales con los gestores de la biodiversidad y la mala gestión de las actividades humanas en la zona de amortiguamiento del área natural protegida como una de las causas más importantes en dar origen a los incendios. Determinar la importancia relativa de los factores sociales en el aumento de los incendios forestales es crucial para diseñar programas de gestión eficaces. Estos programas deben implicar el fortalecimiento de la capacidad de prevención, vigilancia y extinción de incendios, así como la ampliación de los esfuerzos de educación y sensibilización ambiental. Además, los programas de gestión pueden promover acuerdos de conservación entre el área protegida, los propietarios de predios, los agricultores y el gobierno, reforzando así el marco de gobernanza.

3. La resiliencia de la vegetación del norte de los Andes y del roble andino a los incendios

La creciente frecuencia de incendios en la región Andina puede superar la resistencia de los bosques al fuego. En los paisajes del norte de los Andes severamente transformados, y ahora afectados por incendios recurrentes, existen al menos dos tipos de coberturas vegetales post-incendio con dominancia de especies nativas. Los matorrales y los bosques (Parra, 2011; León-Parra & Vilardy, 2022). En los matorrales quemados, la vegetación herbácea y arbustiva rebrotadora (obligadas y facultativas) es capaz de responder rápidamente después de la quema, conformándose una comunidad que guarda más similitud con la vegetación del páramo que con el bosque andino. La persistencia de matorrales de este tipo ha sido descrita en paisajes andinos y tropicales fuertemente modificados (Lippok *et al.*, 2013; Arroyo-Rodríguez *et al.*, 2017). Probablemente, la larga historia de uso y transformación del macizo de Iguaque, aunado al actual régimen de incendios han contribuido en la selección de especies herbáceas y arbustivas resilientes a los cambios en el régimen de incendios, como ha ocurrido en otros ecosistemas (Lippok *et al.*, 2013; Arroyo-Rodríguez *et al.*, 2015; Palma *et al.*, 2021). Aunque esta vegetación protege el suelo e inicia el ensamblaje de la comunidad, la elevada frecuencia de incendios representa un obstáculo para el reclutamiento de arbustos grandes y árboles.

La expansión de las comunidades vegetales del páramo hacia menor altitud se ha observado en otras regiones disturbadas de alta montaña de los Andes septentrionales (Sarmiento, 2002, Vargas, 2011). Esto ocurre paralelamente con la migración en altura del páramo como resultado del calentamiento climático (Sklenář *et al.*, 2021). La vegetación de páramo desciende en paisajes transformados, debido a su alta capacidad de adaptación a las nuevas condiciones biofísicas creadas por perturbaciones antropogénicas (Hernández-Camacho, 1997; Velásco & Vargas, 2007).

La cobertura de especies herbáceas exóticas invasoras es relativamente alta poco después del incendio y no se ve afectada por la frecuencia de éste. Tres especies exóticas invasoras encontradas en Iguaque, *A. lechnianii, M. minutiflora* y *P. aquilinum*, son altamente invasoras en Colombia (Cárdenas et al. 2010), y están ampliamente distribuidas en todo el continente americano (CABI, 2019a; 2019b). *Pteridium aquilinum* fue la especie más abundante y estuvo presente bajo todos los regímenes de fuego. El fuego contribuye al establecimiento de dichas especies invasoras al suprimir la competencia y aumentar el pH del suelo (Brooks & Lusk, 2008; Zouhar et al., 2008). El fuego también estimula el rebrote de sus yemas y rizomas, y puede promover la germinación de sus semillas (Cárdenas-López *et al.*, 2017). Además, la necromasa en pie de dichas especies es el combustible de nuevos incendios (Pinzón *et al.*, 2012; Mora-Goyes & Barrera-Cataño, 2015). Este patrón se ha encontrado en áreas donde los incendios eran históricamente raros, pero que han aumentado su frecuencia en las últimas décadas (van der Wal *et al.*, 2008; Keeley & Brennan, 2012).

Las especies herbáceas exóticas invasoras de Iguaque se remplazaron unas a otras en las primeras etapas de sucesión post-incendio, siendo *P. aquilinum* muy abundante durante el primer año, y *A. lechnianii* y *M. minutiflora*, seis años después. Las evidencias de esta investigación señalan que estas especies no están frenando la sucesión y los experimentos de germinación apuntan a que esta vegetación tampoco afecta la germinación y crecimiento inicial de *Q. humboldtii.* Sin embargo las especies invasoras pueden favorecer el incremento de los incendios (Brooks & Lusk, 2008; Zouhar et al., 2008; Pinzón *et al.*, 2012; Schaffhauser et al., 2012a). La presencia de un estrato herbáceo denso y seco, aumentaría la continuidad vertical y horizontal del combustible, facilitando la quema de las bellotas y robles juveniles, impidiendo su reclutamiento.

En los matorrales incendiados del macizo de Iguaque, es notable la ausencia de especies forestales, como *Q. humboldtii*, que son comunes en bosques cercanos no quemados. Esto sugiere que la mayoría de las especies forestales serían incapaces de colonizar los matorrales bajo las condiciones ambientales actuales y el actual régimen de incendios. Las especies forestales andinas se desarrollaron en ambientes donde los incendios eran poco comunes y son vulnerables a los incendios (Páramo-Rocha, 2011; Armenteras, *et al.*, 2020). Además, en paisajes modificados por el hombre, la sucesión a menudo progresa hacia una vegetación arbustiva autosucesional persistente, es decir, el fuego selecciona un conjunto de especies herbáceas y arbustivas propensas al fuego que se establecen con éxito tras incendios recurrentes (Zouhar *et al.*, 2008; Arroyo-Rodríguez *et al.*, 2017). Sin embargo, observamos un aumento en la riqueza de especies y la densidad de tallos de especies leñosas de gran porte seis años después del último incendio. Esta observación sugiere que la protección de matorrales frente al fuego podría facilitar el desarrollo de las especies arbustivas y la colonización de algunas especies arbóreas.

En los bosques incendiados de Iguaque, *Q. humboldtii* resiste hasta tres incendios en un periodo de 30 años. Después de un incendio, los robles son capaces de sobrevivir y los árboles quemados pueden rebrotar en una alta proporción (alrededor del 80%). En estos bosques, *Q. humboldtii* puede llegar a dominar la comunidad forestal bajo este régimen de fuegos. Otras especies arbóreas del bosque andino se ven intensamente afectadas y están ausentes en las comunidades post-incendio (Fernández-Méndez, *et al.*, 2016; Salazar *et al.*, 2020).

Según la severidad y la frecuencia del incendio, y el tamaño del árbol, *Q. humboldtii* responde con tres tipos de rebrote: tocón, copa o simultáneo. Cuando la frecuencia o severidad de incendios aumenta, especialmente en árboles pequeños, se reduce la capacidad de rebrote, y ésta se localiza progresivamente en las partes más bajas del árbol. Esto probablemente se relaciona con el nivel de protección de los brotes, del cambium y los tejidos epicórmicos, así como la cantidad de reservas disponibles para que la planta invierta en rebrotes. Estos resultados concuerdan con observaciones previas que identifican el régimen de incendios y el tamaño de los árboles como factores determinantes de la capacidad de rebrote en especies leñosas (Bellingham & Sparrow, 2000; Moreira, *et al*., 2007; 2008; Pausas & Keeley, 2017).

Gran parte de los robles que rebrotan en los bosques incendiados de Iguaque son muy viejos o se han quemado repetidamente (entre dos y ocho veces). Por lo tanto, su capacidad de rebrote y sus reservas de recursos pueden verse afectadas en el futuro por nuevos incendios u otros disturbios recurrentes. A su vez los relictos de robledal se harán cada vez más pequeños y fragmentados. También, la alta densidad de arbustos y hierbas pirófilas alrededor de las manchas forestales aumenta la continuidad del combustible y el riesgo de incendio. Estas condiciones reafirman la urgencia de desarrollar un programa de manejo integrado de incendios (Moreira *et al.,* 2020) que incluya la protección arbórea, el refuerzo poblacional y el control del combustible fino en las áreas incendiadas. (Baeza *et al.,* 2002; 2006; Lloret, 2004). Con el fin de proteger los bosques remanentes y las fuentes semilleras, los lugares prioritarios para el control del combustible vegetal serían las zonas de interface entre los bosques con las otras coberturas.

Finalmente, la gestión de incendios forestales en Iguaque, y en el norte de los Andes, debería considerar un cambio de paradigma (Aguilar-Garavito *et al.,* 2019; Moreira *et al.,* 2020), ya que históricamente se ha centrado en la supresión. Nuestros resultados sugieren que estos enfoques de gestión pueden ser insuficientes y deberían complementarse con otras medidas, como mejorar los programas de prevención de incendios, y educar a la población local y a los turistas sobre el riesgo, la prevención y el manejo de incendios en las montañas de Iguaque. También es necesario ser más eficientes en la identificación y penalización de quienes infrinjan la normativa ambiental en materia de incendios (Prestemon *et al.*, 2019).

4. La difícil recuperación del robledal andino

En los bosques quemados de Iguaque, la densidad de bellotas viables es diez veces menor que en los bosques no quemados. También la germinación de estas bellotas es significativamente menor (64 veces) que lo reportado para robledales no quemados (Gómez & Toro, 2007; Fernández, 2014). Dos años y medio después del incendio, los árboles suelen producir una alta densidad de bellotas con desarrollo incompleto que caen al suelo antes de madurar (abortos). Pueden existir diferentes causas para explicar este déficit de bellotas viables. Por un lado, los árboles quemados podrían estar priorizando la inversión de sus recursos en el rebrote, a expensas de los recursos asignados a cada bellota (Funk *et al.,* 2016; Schermer *et al*, 2019). Por otro lado, las condiciones post-incendio, incluyendo el estrés hídrico, los insectos depredadores y la radiación directa, pueden haber favorecido el daño y aborto de las bellotas (Díaz *et al.,* 2003; Salazar *et al.,* 2020).

Finalmente, la quema del dosel y reducción del área efectiva de copa también pudo haber afectado negativamente la calidad de las bellotas (Díaz *et al.,* 2003; Melo & Parrado-Rosselli, 2010).

La densidad de bellotas fue mayor en el interior del bosque que en el borde de éste. También observamos mayores densidades de bellotas cerca de los árboles adultos. Esto puede reflejar la escasez de animales dispersores, dentro y fuera de los parches forestales (Gómez, 2003; López-Barrera & Manson, 2006). Esta ausencia de dispersores se puede ver agravado por la creciente fragmentación de los bosques de *Q. humboldtii* (Aguilar-Garavito *et al.,* 2020), que afecta al tamaño poblacional y la movilidad de los dispersores de semillas (Howe & Smallwood, 1982; Delgado-Fernández *et al.,* 2017).

La baja producción y germinación de las bellotas en el robledal quemado podría estar afectando al reclutamiento de *Q. humboldtii*. Esto sería particularmente grave en el macizo de Iguaque, dada la estacionalidad de los incendios. Éstos suelen ocurrir entre enero-febrero, y agosto-septiembre, fechas que coinciden con la máxima producción de bellotas en Iguaque. Entonces, los incendios, además de afectar por quema directa el follaje y la producción de bellotas de ese año, retrasaría la producción de bellotas maduras al menos tres años. Además, la primera cosecha de bellotas viables post incendio es de baja cantidad y calidad, y presenta baja germinación.

La densidad de plántulas en los bosques quemados de Iguaque fue doce veces menor que en los bosques no quemados. Las plántulas se localizaron principalmente bajo el dosel de *Q. humboldtii* y en el interior de las manchas forestales. Esto es coherente con la distribución de las bellotas anteriormente descrita. Por lo tanto, el fuego podría suprimir las plántulas.

Primero, por la coincidencia temporal entre la temporada de incendios y el pico de producción de bellotas (Aguilar-Garavito *et al.,* 2020), como se indicaba con anterioridad. Luego, por la baja producción de semillas viables y la mala dispersión hacia lugares adecuados. El rebrote, la dispersión de bellotas y el reclutamiento de plántulas en el interior de las manchas forestales podría permitir la regeneración donde persistan los robles y particularmente en el interior de los parches. Mientras que por el contrario, el reclutamiento del roble en el matorral podría verse impedido por la baja disponibilidad de bellotas (limitación por la fuente, Pulido y Díaz, 2005), y su pobre dispersión (limitación por la dispersión, Palma *et al.,* 2021), dentro y fuera de la mancha forestal.

Nuestro análisis de la producción de bellotas ha sido breve. Existen evidencias de variaciones interanuales sustanciales en este proceso. Por ello, sería recomendable realizar estudios fenológicos a largo plazo (no menos de 5-10 años), lo que permitiría confirmar los efectos observados de los disturbios en la producción de bellotas, así como el tiempo que toman los árboles en recuperar una fructificación óptima. También, si existe un patrón de vecería en *Q. humboldtii* y si ésta se ve afectada por el régimen de incendios. De igual forma, sería necesario considerar el impacto de variables climáticas (como humedad relativa y radiación solar), propiedades edáficas, (Gonzáles & Parrado, 2010), características de los incendios (como severidad y frecuencia), el grado de afección del árbol, y la herbivoría post-incendio, sobre las diferentes fases fenológicas del roble, para comprender la dinámica de producción de bellotas y determinar de qué manera se ve alterada por el fuego.

5. La siembra y la plantación como opciones para superar la limitación al reclutamiento de *Q. humboldtii*

La siembra de bellotas y el establecimiento de plántulas y brinzales en los robledales y matorrales incendiados de Iguaque demuestran que los incendios no limitan significativamente el reclutamiento de *Q. humboldtii*. Sin embargo la germinación y crecimiento de plántulas y brinzales en el interior del robledal es inferior que en el matorral con o sin herbáceas exóticas invasoras. Esto puede atribuirse al microclima, principalmente la reducción en la radiación solar causada por las copas de los robles (Asbjorsen *et al.*, 2006; Díez *et al.*, 2017). Además, la hojarasca del robledal contiene altas concentraciones de taninos (Lozano & Torres, 1965).

La depredación de bellotas por mamíferos también parece incidir en su germinación. En nuestro estudio, la depredación ocurrió con mayor incidencia en los robledales que en los matorrales, posiblemente por la mayor abundancia de mamíferos. Sin embargo, el papel de los mamíferos debe ser estudiado detalladamente. En función de su comportamiento y saciedad de alimento, estos pueden convertirse en dispersores de bellotas más que depredadores (Nathan & Muller-Landau, 2000; López-Barrera & Manson, 2006; Bonfil, 2006; Bogdziewicz *et al.*, 2018). Por ejemplo, las ardillas tienden a redistribuir las bellotas en el bosque para almacenarlas en “buenos escondites”, pero luego olvidan algunas. De esta manera muchas especies de *Quercus* logran que sus bellotas alcanzan microambientes ideales para germinar (Nathan & Muller-Landau, 2000; Kapelle, 2006; López-Barrera & Manson, 2006). Investigaciones que permitan analizar la tasa de re-dispersión, destino final y germinación de las bellotas de *Q. humboldtii* tras la dispersión primaria o siembra puede contribuir a entender en qué medida y en dónde se produce la redistribución de las bellotas.

Las hierbas y gramíneas exóticas invasoras más comunes en el macizo de Iguaque no interfirieron en la germinación, establecimiento y crecimiento de *Q. humboldtii*. Por el contrario, estas especies podrían ser beneficiosas para la germinación y el desarrollo de las plántulas de roble. Por ejemplo, podrían generar mejoras microclimáticas, como la reducción de la temperatura a nivel del suelo y la mejora de las condiciones de humedad. Dicha vegetación también podría estimular el crecimiento del roble, porque las plántulas deben superar al estrato herbáceo en la competencia por la luz u otros recursos. La ausencia de un efecto negativo fue en gran medida inesperado, ya que las especies exóticas invasoras son consideradas como competidores, capaces de excluir a las especies autóctonas (Baptiste *et al.*, 2010; Cárdenas-López *et al.*, 2017). Sin embargo, las especies exóticas invasoras pueden limitar indirectamente el reclutamiento de *Q. humboldtii*. Las altas acumulaciones de biomasa generadas por estas especies pueden actuar como combustible, afectando al régimen de incendios (Vargas, 2000; Zouhar *et al.*, 2008 Shaffhauser *et al.*, 2012; Bianchi *et al.*, 2014). A largo plazo, aunque los robles hayan sido reclutados en estos matorrales, su supervivencia se verá afectada si no tienen el tamaño suficiente para resistir y rebrotar tras un incendio. Por lo tanto, se debe asegurar que el tiempo de retorno del fuego sea mayor como para que el roble andino supere los 10 m de altura. Según estudios, los árboles del algunas especies del género *Quercus* y de otras especies resistentes a los incendios, sobreviven y rebrotan solo cuando superan ciertos tamaños (Johnson *et al.*, 2002; Salazar *et al.*, 2020).

En las áreas afectadas por incendios de Iguaque, si se supera simultáneamente la limitación en la fuente y a la dispersión de bellotas, estas serían capaces de germinar y crecer, tanto en robledales como en matorrales afectados por fuego, con o sin especies exóticas invasoras. La limitación en la fuente es originada por la incapacidad de los robles quemados para producir bellotas viables y en cantidades suficientes. La limitación a la dispersión de bellotas podría ocurrir por dos razones: i) los dispersores no salen completamente hacia los matorrales, por tanto, las bellotas quedan bajo el progenitor o solo llegan 5 m fuera del borde del robledal, y ii) la dispersión primaria de los robles ocurre ladera abajo y en cañones estrechos, dada la pendiente dominante en la mayoría de robledales remanentes, y no en la dirección opuesta, donde se encuentran las zonas quemadas. Otros estudios han señalado la dispersión de semillas como el proceso crítico que limita el reclutamiento de árboles (Acácio *et al.,* 2007; Granger *et al.,* 2018; Palma *et al.,* 2021; Roque *et al.,* 2021).

La liberación de la sucesión cíclica en los matorrales y los bosques de Iguaque requiere el alivio simultáneo de la restricción a la disponibilidad de bellotas y de su dispersión, pero también del tiempo suficiente sin fuego como para que los reclutas de roble puedan crecer, desarrollar estructuras de protección contra el fuego y activar su capacidad de rebrote. Con base en lo anterior, se puede plantear la hipótesis de que la vegetación que domina los matorrales lo hace, no porque sean competidores superiores en las condiciones ambientales dadas, sino porque los mejores competidores, como *Q. humboldtii* y otras especies arbóreas, nunca pueden establecerse en esos sitios debido a la limitación en la fuente y en la dispersión de sus semillas, más que por la limitación de germinación o establecimiento. Esta situación ha sido reportada en otros ecosistemas con sucesiones detenidas (Acácio *et al.,* 2007; Rey & Alcántara, 2000; Palma *et al.,* 2021; Werden *et al.,* 2021) o bajo disturbios como el fuego (Johnson *et al.,* 2002; Schaffhauser *et al.,* 2012).

Un aumento de la disponibilidad de bellotas y plántulas o brinzales se puede conseguir mediante la siembra y la plantación. Ambas técnicas de repoblación forestal podrían mostrar buenos resultados, en términos de supervivencia y crecimiento, en los bosques y matorrales afectados por incendios de Iguaque. Las plantas en contenedores procedentes de vivero presentaron mayor supervivencia que la siembra directa de bellotas. Los cuidados primarios en el vivero contribuyen a generar plantas menos vulnerables a las condiciones ambientales, superando los primeros y más drásticos filtros ecológicos para el establecimiento (Leverkus *et al.,* 2021; Villar-Salvador *et al.,* 2021). Sin embargo, en un programa de revegetación en el macizo de Iguaque, sería recomendable utilizar ambas técnicas para mejorar el reclutamiento del roble. La siembra de bellotas puede priorizarse en zonas de difícil acceso, introduciendo un número significativo de individuos en los mejores micrositios y a un costo relativamente menor que una plantación. Por su parte, la plantación de plantas en contenedor, aunque más costosa y compleja, puede priorizarse en zonas de fácil acceso, donde los individuos pueden alcanzar una mayor supervivencia y crecimiento que en una siembra. Según nuestra experiencia, en un jornal, una persona puede sembrar 450 bellotas. En el mismo terreno, pero en el caso de la plantación, una persona requirió de un jornal para plantar 140 plántulas de aproximadamente 50 cm de altura. Finalmente es importante garantizar en la plantación, que las plántulas hayan sido producidas con criterios de calidad (Villar-Salvador & Oliet, 2021; Villar-Salvador et al., 2021), evitando problemas genéticos, fitosanitarios o de formación, como por ejemplo sistemas radiculares muy confinados.

Reducir la frecuencia y la severidad de los incendios forestales es una prioridad para la gestión en el macizo de Iguaque. Por un lado, una menor frecuencia de incendios permitiría el desarrollo de los grandes arbustos y árboles en los matorrales, generando heterogeneidad de estratos y doseles. De esta manera, los dispersores de semillas podrían utilizar estos espacios de forma más fiable, incrementando la posibilidad de dispersión de las bellotas. Por otro lado, la menor frecuencia e intensidad de incendios permitiría que las plántulas y los brinzales reclutados en los matorrales alcancen tamaños adecuados para resistir a los incendios y producir bellotas viables. Del mismo modo, el banco de plántulas del bosque podría mantenerse a largo plazo, garantizando la reposición y permanencia de *Q. humboldtii.* En este sentido, la reducción de la acumulación de biomasa de especies exóticas invasoras podría influir en el control del régimen de incendios, como ha ocurrido en otros ecosistemas (Baeza, *et al.* 2002, 2006, Keeley *et al.* 2005a, 2005b). Sin embargo, primero será necesario realizar ejercicios piloto en robledales y otros ecosistemas Andinos para comprobar los riesgos y beneficios de estas acciones.

Basándonos en nuestra experiencia de campo, cuatro eliminaciones manuales de las especies invasoras, incluyendo su biomasa epigea e hipogea, realizadas cada tres meses durante un año y medio reducen hasta en un 95% la biomasa de dichas especies en los matorrales invadidos. Debido a las condiciones biofísicas y su costo, la implementación de dichas eliminaciones debe priorizarse en lugares donde históricamente se han iniciado los incendios. Por otra parte en los espacios recientemente incendiados, pues los incendios en cierta medida controlan la biomasa y allí fácilmente puede mantenerse en una baja cobertura y densidad. También, otros sitios de control son los alrededores de caminos, quebradas, cañones o de otros elementos del paisaje que pueden servir como como cortafuegos. Así mismo otros espacios de control son las zonas con mayor carga de combustible fino y sobre todo, como hemos dicho antes, alrededor de los relictos de robledal. Amanera de síntesis de esta sección y como apertura a las conclusiones hemos resumido en la Tabla I las respuestas a las preguntas enunciadas en la introducción de la tesis cuando, presentábamos los capítulos.

Tabla I. Respuestas a las preguntas centrales de la tesis presentadas de acuerdo con el capítulo.

Capítulo	Preguntas	Respuestas
1. *Quercus humboldtii* distribution and wildfire in Northern South America	El régimen actual de incendios es parte de los factores que impulsan la pérdida de hábitat de *Q. humboldtii*, y se suman a los factores históricos de pérdida y transformación de su hábitat.	Si, principalmente en el áreas de distribución potencial. Durante los últimos 30 años, se han producido numerosos incendios dentro de área de distribución potencial de *Q. humboldtii*. *Q. humboldtii* ocupa el 28% de su distribución potencial en Colombia. Los incendios se concentran en la periferia de las áreas de distribución remanente de *Q. humboldtii.*
2. Wildfire dynamics and impacts on a tropical Andean oak forest, the Iguaque mountains	¿Cuál es la frecuencia de incendios reciente en Iguaque?	Entre 1990 y 2017, se registraron 25 incendios de la vegetación, con intervalos de fuego entre 4 y 21 años y una frecuencia de tres a siete incendios.
	¿Existen tendencias interanuales en la frecuencia y extensión de incendios?,	El número y extensión de los incendios presentan variaciones interanuales sustanciales relacionadas con la dinámica climática, especialmente con los ciclos ENSO, y a las actividades humanas.
	¿Es constante la probabilidad de incendios a lo largo del año y en todo el macizo de Iguaque?	En Iguaque, los incendios se concentran en los periodos de sequía estacional, altas temperaturas y mayor afluencia turística. Además principalmente ocurren al sur y sur-oriente del macizo.
	¿Los incendios han afectado a la extensión y distribución espacial del robledal?	Los incendios de la vegetación contribuyeron la reducción del 45% de los bosques de robles junto con la fragmentación de las poblaciones remanentes. Además los incendios afectaron el 28,4% de las montañas de Iguaque y muestran una tendencia creciente en extensión significativa.

Capítulo	Preguntas	Respuestas
3. The current fire regime in northern Andean shrublands hinders tree recruitment and arrest forest succession	¿El aumento de la frecuencia de incendios y la reducción del tiempo transcurrido desde el último incendio están asociados con la riqueza de especies, la densidad de individuos, la cobertura y el área basal de la vegetación?	La composición de la vegetación post-incendio es alta en riqueza y densidad de especies herbáceas y arbustivas. Las especies forestales están ausentes en los matorrales incendiados, al igual que las especies semilleras obligadas. La frecuencia de los incendios no afecta a la composición y estructura del estrato herbáceo. Por el contrario, se reduce sustancialmente la riqueza de especies, cobertura y área basal de las especies leñosas. También con el aumento de la frecuencia de los incendios se disminuye la proporción de rebrotadores arbóreos obligados.
	¿La riqueza de especies y cobertura de gramíneas y especies exóticas depende del régimen de incendios?	Las especies exóticas fueron principalmente herbáceas y estaban dominadas por *Pteridium aquilinum*, *Melinis minutiflora* y *Andropogon lehmannii*. Su cobertura no se vio afectada por la frecuencia de los incendios ni por el tiempo transcurrido desde el último incendio, aunque su composición cambió. Mientras que la cobertura de *P. aquilinum* no se vio afectada por la frecuencia de los incendios, si disminuyó del año 1 al año 6. Nuestros resultados muestran que los actuales regímenes de incendios en las montañas de Iguaque favorecen la persistencia de hierbas y arbustos tolerantes al fuego, comprometen el reclutamiento de árboles y detienen la sucesión forestal.

Capítulo	Hipótesis o preguntas	Respuesta
4. Postfire resprouting and recruitment of *Quercus humboldtii* in the Iguaque mountains	¿Cuál es el impacto del actual régimen de incendios sobre la capacidad de *Quercus humboldtii* de rebrotar post-incendio?	La probabilidad de rebrote fue alta en los árboles quemados dos años después del incendio (alrededor del 80%). La capacidad de rebrote dependió de la severidad del incendio y del tamaño del árbol. La proporción de árboles que rebrotaban desde el tocón estaba relacionada con la gravedad del incendio y el tamaño del árbol. A pesar del fuerte impacto del fuego en las estructuras forestales, los adultos de *Q. humboldtii* pueden resistir el actual régimen de incendios gracias a su fuerte capacidad de regeneración vegetativa y sexual.
	¿Cuál es el impacto del actual régimen de incendios sobre la capacidad de *Quercus humboldtii* de establecerse a partir de bellotas post-incendio	La densidad de bellotas fue mayor en las zonas quemadas que en las no quemadas y dependió de la pendiente, la distancia al borde del bosque y la distancia al roble más cercano. Por el contrario, la densidad de bellotas sanas fue baja en todos los lugares, especialmente en los bosques incendiados. La densidad de plántulas fue relativamente alta en las zonas no incendiadas. La densidad de bellotas y plántulas disminuyó en la periferia de las manchas forestales. El restablecimiento de los robledales post-incendio se debe principalmente a la capacidad de rebrote del reble andino, más que por el reclutamiento de plántulas vía germinación de bellotas.

Capítulo	Preguntas	Respuestas
5. Producción y germinación de bellotas de *Quercus humboldtii* en un robledal andino afectado por incendios recurrentes),	¿Cuál es la cantidad de bellotas viables y abortadas que se cosechan de robles andinos afectados y no afectados por incendios?	En los robles quemados la producción de bellotas con desarrollo incompleto (abortos) fue casi nueve veces mayor que la de bellotas viables. En los árboles no quemados la producción abortos es diez veces inferior que en los árboles quemados.
	¿Existen diferencias en el tamaño, biomasa y tasa de germinación de las bellotas viables provenientes de robles quemados, respecto a las bellotas que provienen de los robles no quemados?	Las bellotas viables provenientes de los árboles quemados presentaron menores tamaños y tasas de germinación en comparación con los árboles no quemados y con la literatura
	Los robles quemados producen una mayor cantidad de bellotas abortadas?	Los robles con mayor área de cicatriz o mayor número de cicatrices fueron propensos a producir abortos. Los robles con mayor copa producen más bellotas. El fuego, el tamaño del árbol y la vecería controlan la producción de bellotas en de Iguaque.
	¿Cuál es la relación entre la temperatura y la precipitación respecto la cantidad de bellotas cosechadas de robles andinos afectados y no afectados por incendios?	La producción de bellotas de *Q. humboldtii* ocurre durante cuatro a seis meses. Inicia finalizando la temporada seca y alcanza la mitad de la temporada lluviosa. No encontramos una relación positiva de la producción de bellotas con la temperatura o la precipitación. Es posible que la producción de bellotas en *Q. humboldtii* esté relacionada con otras variables climáticas, con aspectos biofísicos del ecosistemas o propios de la biología y genética del roble andino. Por ejemplo: la vecería y fertilidad del suelo.

Capítulo	Preguntas	Respuestas
6. *Quercus humboldtii* germination and establishment in Andean forests affected by recurrent wildfires	¿Las condiciones para la germinación de las bellotas y el establecimiento de plántulas difieren en el bosque y en el matorral?	Si, y parece que las condiciones de los matorrales con o sin invasoras son mejores para la supervivencia y crecimiento de *Q. humboldtii* que en el robledal. Principalmente lo atribuimos a que en el interior del bosque la radiación es menor, hay una mayor concentración de hojarasca con alto contenido en taninos y por la predación de las bellotas. El roble andino no parece experimentar limitación de germinación y establecimiento en los matorrales. En su lugar, las limitaciones más fuertes pueden ser la limitación en la fuente y en la dispersión.
	¿La depredación de bellotas es significativa?	Es significativa en el interior del bosque, no en los matorrales.
	¿La germinación de bellotas, y el establecimiento de plántulas y brinzales se ven afectados por la presencia de especies exóticas invasoras?	No, por el contrario si las semillas o plántulas de roble que establecimos en espacios con exóticas invasoras, fueron capaces de germinar, sobrevivir y crecer, incluso mucho mejor que en el interior del bosque de roble. Sin embargo, las especies exóticas invasoras pueden afectar indirectamente el reclutamiento de *Q. humboldtii*. Las altas acumulaciones de necromasa de estas especies actuarán como combustible en un incendio. Aunque los robles hayan sido reclutados en estos matorrales, su supervivencia se verá afectada si no tienen el tamaño suficiente para resistir y rebrotar post-incendio.

Finalmente, al igual que en la introducción, incluimos un ideograma de cierre (Figura II) donde representamos gráficamente los resultados centrales de la tesis en torno a los incendios y la regeneración de los matorrales y robledales andinos post-incendio. Primero, presentamos cartográficamente las regiones de incidencia de incendios en la distribución potencial del roble andino en Colombia y en el macizo de Iguaque. En esta, también representamos la reducción al 28% del área de distribución potencial de *Q. humboldtii* a nivel nacional y en el Macizo de Iguaque, así como los lugares donde los incendios han afectado durante los últimos 30 años. Siguiendo el ideograma en dirección de las flechas que apuntan a la derecha, se representan robledales afectado por incendios, donde *Q. humboldtii* rebrota, incluso después de siete incendios en treinta años y también puede seguir produciendo bellotas. Sin embargo estás en su mayoría son más pequeñas (21mm aprox.) que las cosechadas en robledales no quemados (34 mm aprox.). Además en su mayoría son bellotas con desarrollo incompleto que caen al suelo antes de madurar (abortos). Las pocas semillas de viables de los bosques quemados (40 bellotas/ha) presentan una tasa de germinación en vivero del 15%. También el reclutamiento de plántulas en los bosques quemados es inferior (250 plántulas/ha) que en los bosques no quemados (3110 plántulas/ha). De igual forma, se muestra que al incrementarse la frecuencia o severidad de los incendios, otras especies maderables desaparecen y que los árboles de *Q. humboldtii* se ven afectados en la altura, presentan múltiples cicatrices en el tallo y los rebrotes post-incendio empiezan a ocurrir principalmente en la cepa, cuando los árboles se han visto muy afectados.

Los paneles siguientes muestran que al extraer los robles mediante deforestación o usos agropecuarios, y después, incrementar la frecuencia o severidad de los incendios, la comunidad vegetal resultante post-incendio serían matorrales persistentes, con dominio de especies rebotadoras (obligadas y facultativas) herbáceas y arbustivas. Esta comunidad es resistente al fuego. Las plantas exóticas invasoras son representativas en el estrato herbáceo y se regeneran con facilidad tras los incendios, en un ciclo de retroalimentación positiva. En estas comunidades vegetales no hay reclutamiento de roble ni de otras especies arbóreas. Esto es causado por la limitación en la fuente y en la dispersión de las bellotas. Los incendios afectan la producción de bellotas, la movilidad de los dispersores y quema el banco de plántulas reclutadas en los años sin incendios. En los péneles laterales siguientes y en los inferiores, presentamos algunas acciones como el control de los incendios, la eliminación de las plantas exóticas invasoras para reducir la carga de combustible y la revegetación con bellotas y plántulas de *Q. humboldtii*. Estas acciones buscan el alivio simultáneo de la limitación en la fuente y en la dispersión de *Q. humboldtii*, pero deben complementarse con la gestión integral de los incendios para mejorar las posibles respuestas de los robledales y matorrales afectados por incendios.

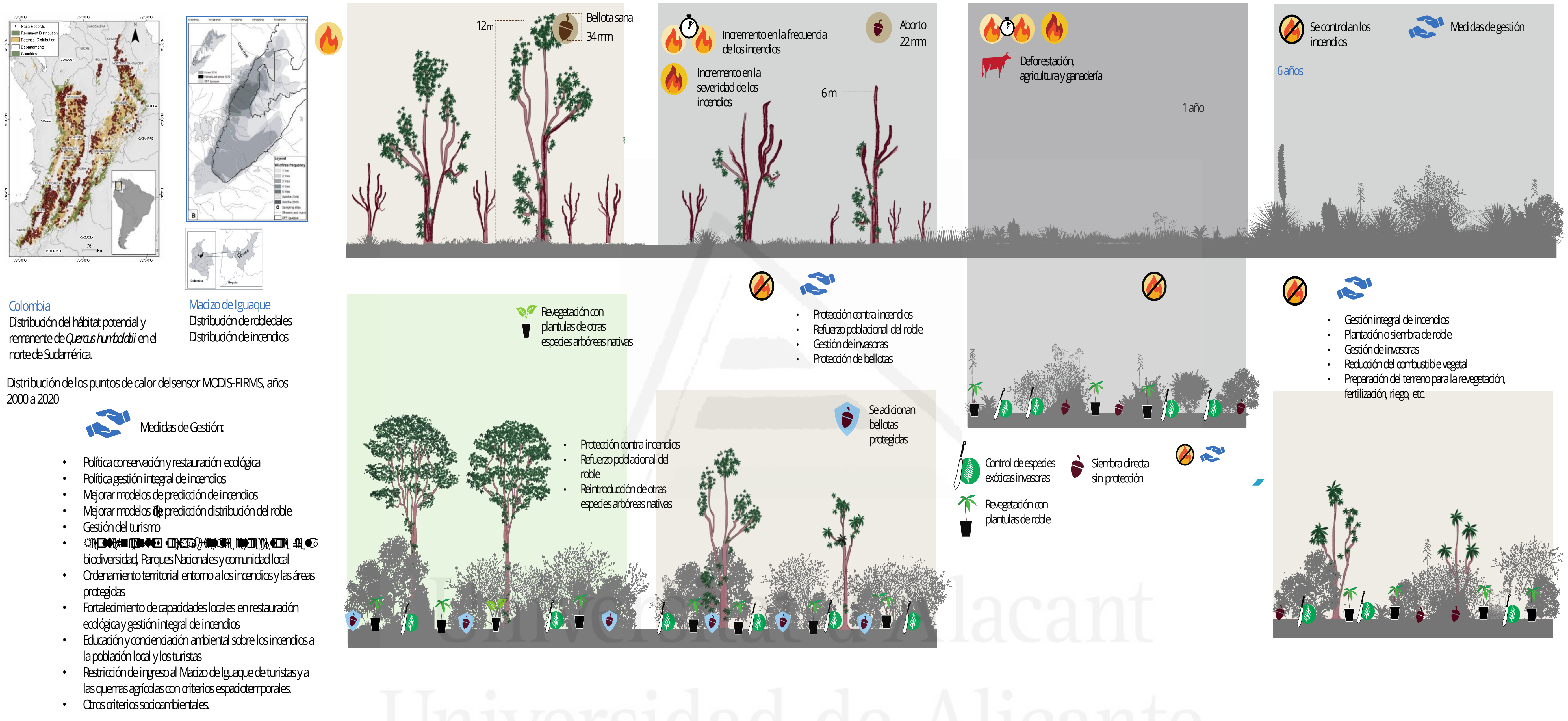

Figura II. Síntesis de los resultados más importantes de la tesis en torno a la regeneración natural de matorrales y robledales andinos post-incendio.

CONCLUSIONES

1. La distribución del hábitat potencial de *Quercus humboldtii* en Colombia ocurre en las tres cordilleras de los Andes colombianos y en los macizos del Caribe, especialmente en elevaciones entre 1.700 y 2.200 m. Sin embargo, su distribución altitudinal puede ir desde los 900 a los 3.200 m. de elevación. *Quercus humboldtii* muestra una amplia adaptación climática, con una particular preferencia por ambientes con una temperatura media de 17°C y una precipitación promedio anual de 2.024 mm/año.

2. Los incendios se han añadido a la serie de impulsores de la transformación que han influido en la pérdida de hábitat de *Q. humboldtii*. Actualmente, el hábitat remanente de esta especie presenta una reducción del 75% respecto a su distribución potencial. Como el uso del fuego ha estado relacionado con la deforestación, la agricultura y la ganadería, podría argumentarse que la pérdida de hábitat de *Q. humboldtii* está relacionada con el esta perturbación. Los incendios están afectando principalmente a las zonas donde se abandonaron los usos productivos, los espacios destinados a conservación y regeneración natural, las periferias de los bosques remanente que entran

en contacto con espacios productivos o las áreas naturales de conservación con conflicto socioambiental.

3. Las hierbas y los pequeños arbustos rebrotadores (obligados y facultativos) dominan las comunidades post-incendio en las montañas de Iguaque y constituyen una comunidad vegetal muy persistente. La riqueza, densidad y cobertura de las especies herbáceas aumenta bajo frecuencias de tres o cinco incendios en treinta años. También, la cobertura de especies exóticas invasoras se incrementa con dicho patrón de incendio. Estas se sustituyeron unas a otras a lo largo de las primeras etapas de la sucesión post-incendio, siendo *P. aquilinum* muy abundante durante el primer año, mientras que *A. lechnianii* y *M. minutiflora* seis años después. Por otra parte, la frecuencia de incendios de la vegetación redujo la riqueza y densidad de los grandes arbustos y árboles, incluyendo a *Q. humboldtii*, que estuvo ausente en todos los matorrales quemados.

4. En los bosques quemados de Iguaque, los robles soportaron aproximadamente tres incendios a lo largo de los últimos 30 años. Dos años después del último incendio, la mayoría de robles rebrotaron (alrededor del 80%), incluso cuando el árbol había recibido daños simultáneos en cepa y copa. La capacidad de rebrote de *Q. humboldtii* se vio afectada negativamente por la altura de carbonización y positivamente por el tamaño del árbol. Además, el tamaño del árbol, el número y el área de las cicatrices, y la densidad de la vegetación leñosa alrededor de la de los relictos de bosque influyeron en la supervivencia y tipo de rebrote de *Q. humboldtii*.

5. Los incendios afectaron a la densidad de bellotas y plántulas de *Q. humboldtii*, al menos durante los tres primeros años después del incendio. Los robledales quemados produjeron

un mayor número de bellotas con desarrollo incompleto (abortos). Por otra parte, las pocas bellotas sanas de estos robledales presentaron menores tamaños y tasas de germinación más bajas que los robledales no quemados. Las bellotas viables y las plántulas aparecieron solamente al interior y bordes de la mancha forestal. Por lo tanto, durante los años posteriores al incendio la regeneración natural de las áreas quemadas dependió más del rebrote que del reclutamiento de plántulas.

6. El bajo reclutamiento de *Q. humboldtii* en las áreas quemadas se debió principalmente a la limitación en la fuente y en la dispersión. Por otra parte, la limitación a la germinación y al establecimiento fueron más severas en el robledal que en los matorrales con o sin herbáceas exóticas invasoras. Los matorrales podrían evolucionar hacia bosque si las bellotas o plántulas de roble tuvieran la capacidad de llegar y si se aumentara el tiempo de retorno de los incendios, para permitir que los brinzales alcancen un tamaño adecuado para rebrotar (3 a 11 m de altura).

7. En el macizo de Iguaque las acciones de gestión tendrían que aliviar simultáneamente la baja disponibilidad y dispersión de las bellotas, así como reducir la frecuencia y severidad de los incendios. Para esto, es necesario un cambio de paradigma en la gestión de los incendios, yendo más allá de la supresión. Como acciones mínimas se deben desarrollar programas de prevención y educación ambiental sobre la gestión incendios, y hacer cumplir la normativa ambiental. Posteriormente, se debe controlar el combustible fino que se empieza a regenerar en las áreas post-incendio, especialmente en las transiciones entre el bosque y otros tipos de cobertura, y finalmente, fomentar la regeneración del roble andino mediante siembra y plantación.

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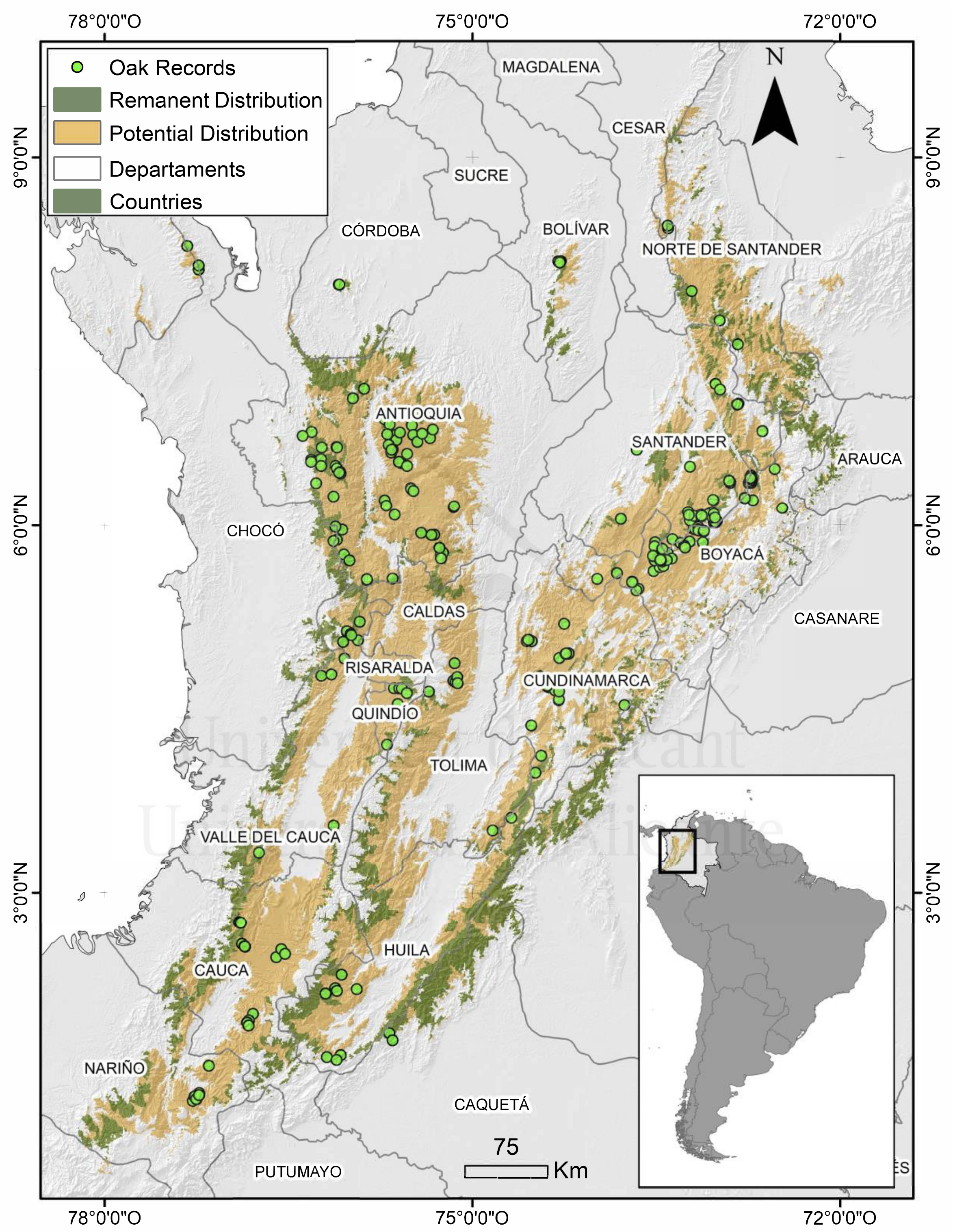
APPENDIX

SUPPLEMENTARY MATERIAL 1.

Quercus humboldtii **(Fagaceae) distribution and wildfire in northern South America.**



Appendix 1.1. Andean oak (*Quercus humboldtii*) records and models of their potential and remnant distributions.

Appendix 1.2. Bioclimatic variables used for modeling the distribution of *Quercus humboldtii.*

Variable	Source
Mean Annual AET	https://cgiarcsi.community/data/global-high-resolution-soil-water-balance/
Monthly Soil Water Stress	https://cgiarcsi.community/data/global-high-resolution-soil-water-balance/
Priestley-Talor Alpha Coefficient	https://cgiarcsi.community/data/global-high-resolution-soil-water-balance/
Minimum Temperature (°C)	https://worldclim.org/version2
Maximum Temperature (°C)	https://worldclim.org/version2
Average temperature (°C)	https://worldclim.org/version2
Precipitation (mm)	https://worldclim.org/version2
Solar Radiation (kJ m-2 day-1)	https://worldclim.org/version2
BIO1 = Annual Mean Temperature	https://www.worldclim.org/bioclim
BIO4 = Temperature Seasonality (standard deviation *100)	https://www.worldclim.org/bioclim
BIO5 = Max Temperature of Warmest Month	https://www.worldclim.org/bioclim
BIO6 = Min Temperature of Coldest Month	https://www.worldclim.org/bioclim
BIO12 = Annual Precipitation	https://www.worldclim.org/bioclim
BIO13 = Precipitation of Wettest Month	https://www.worldclim.org/bioclim
BIO14 = Precipitation of Driest Month	https://www.worldclim.org/bioclim
BIO15 = Precipitation Seasonality (Coefficient of Variation)	https://www.worldclim.org/bioclim
Slope	https://www.ngdc.noaa.gov/mgg/topo/gltiles.html
Directionality DEM	https://www.ngdc.noaa.gov/mgg/topo/gltiles.html

Appendix 1.3. Total potential and remnant habitat area of *Quercus humboldtii* classified by the department and their corresponding habitat loss percentage.

Department	Potential (km^2)	Remnant (km^2)	Loss (%)
Antioquia	28,754	5,265	-82
Cauca	17,345	5,190	-70
Cundinamarca	15,459	2,482	-82
Santander	14,884	3,420	-77
Tolima	13,314	2,674	-80
Boyacá	13,146	2,212	-83
Norte de Santander	11,625	3,817	-67
Huila	11,501	4,374	-62
Valle del Cauca	9,686	1,909	-80
Nariño	8,717	2,954	-66
Caldas	5,757	441	-92
Caquetá	4,631	3,994	-14
Meta	4,254	3,733	-12
Chocó	3,614	2,792	-23
Risaralda	3,506	906	-74
Quindío	1,974	283	-86
Bolívar	1,386	685	-51
Arauca	731	673	-8
Cesar	669	176	-74
Córdoba	568	460	-19
Casanare	215	83	-61
Putumayo	60	60	0
Total	171,796	48,583	-72

Appendix 1.4. Values of 19 bioclimatic variables (BIO from WordClim) for potential habitat distributions of *Quercus humboldtii*.

BIO	**Variable**	**Min**	**Max**	**Range**	**Median**	**Mean**	**SE**	**CI. mean. 0.95**	**Variance**	**Coef. var**
BIO1	Annual Mean Temperature	4	26.6	22.6	17.6	17.1	0	0	14.9	0.2
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp)	6.8	12.4	5.6	9.8	9.7	0	0	0.9	0.1
BIO3	Isothermality (BIO2/BIO7) (×100)	6.8	9.6	2.8	8.7	8.6	0	0	0.2	0.1
BIO4	Temperature Seasonality (standard deviation ×100)	10.4	74.5	64.1	31.7	33.3	0	0	100.8	0.3
BIO5	Max Temperature of Warmest Month	8.7	33.7	25	23.2	22.9	0	0	16.9	0.2
BIO6	Min Temperature of Coldest Month	-1.4	21	22.4	12	11.5	0	0	15	0.3
BIO7	Temperature Annual Range (BIO5-BIO6)	7.6	17	9.4	11.4	11.3	0	0	1.7	0.1
BIO8	Mean Temperature of Wettest Quarter	4.1	26.4	22.3	17.4	17	0	0	14.3	0.2
BIO9	Mean Temperature of Driest Quarter	3.5	27	23.5	17.5	17.1	0	0	15.3	0.2
BIO10	Mean Temperature of Warmest Quarter	4.3	27.3	23	17.9	17.5	0	0	14.9	0.2
BIO11	Mean Temperature of Coldest Quarter	3.5	26	22.5	17.1	16.6	0	0	14.8	0.2
BIO12	Annual Precipitation	623	6,978	6,355	1,934	2,024.1	1.6	3.2	494,046.7	0.3
BIO13	Precipitation of Wettest Month	80	850	770	259	272.2	0.2	0.4	8,614.7	0.3
BIO14	Precipitation of Driest Month	4	410	406	69	72.3	0.1	0.2	1,409.5	0.5
BIO15	Precipitation Seasonality (Coefficient of Variation)	12	81	69	38	38.4	0	0	90.3	0.2
BIO16	Precipitation of Wettest Quarter	215	2,395	2,180	669	707.8	0.6	1.1	61,438.8	0.4
BIO17	Precipitation of Driest Quarter	53	1,310	1,257	264	268.9	0.3	0.6	14,951.7	0.5
BIO18	Precipitation of Warmest Quarter	79	1,748	1,669	475	509	0.5	0.9	38,792.5	0.4
BIO19	Precipitation of Coldest Quarter	53	2,309	2,256	574	576	0.7	1.3	81,132.2	0.5

Appendix 1.5. Values of 19 bioclimatic variables (BIO from WordClim) for remnant habitat distributions of *Quercus humboldtii*

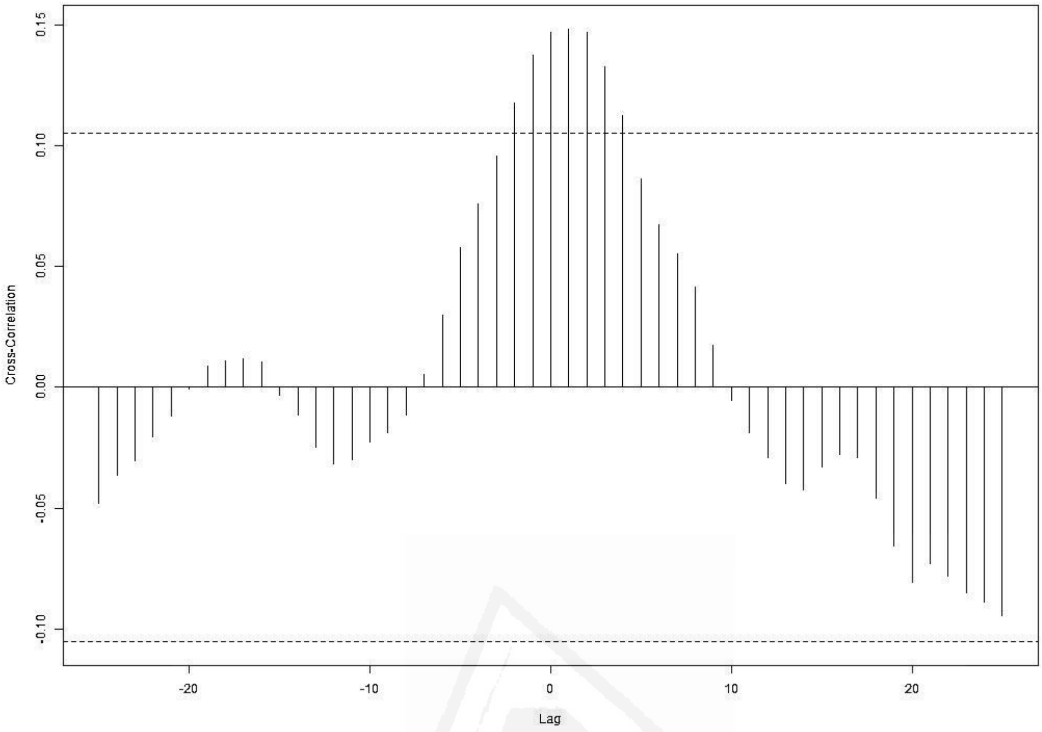
BIO	Variable	Min	Max	Range	Median	Mean	SE	CI.mean. 0.95	Variance	Coef. var
BIO1	Annual Mean Temperature	4.8	26.4	21.6	16	16	0	0	15.4	0.2
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp)	6.9	11.9	5	9.6	9.5	0	0	0.9	0.1
BIO3	Isothermality (BIO2/BIO7) (×100)	7	9.6	2.6	8.6	8.6	0	0	0.2	0.1
BIO4	Temperature Seasonality (standard deviation ×100)	10.4	74.1	63.7	31.7	32.4	0	0.1	88.2	0.3
BIO5	Max Temperature of Warmest Month	10.4	33.6	23.2	21.4	21.6	0	0	17.8	0.2
BIO6	Min Temperature of Coldest Month	-1.4	20.9	22.3	10.6	10.5	0	0	14.9	0.4
BIO7	Temperature Annual Range (BIO5-BIO6)	7.6	16.1	8.5	11.2	11.1	0	0	1.7	0.1
BIO8	Mean Temperature of Wettest Quarter	4.1	25.8	21.7	15.9	15.8	0	0	14.8	0.2
BIO9	Mean Temperature of Driest Quarter	4.8	26.8	22	15.9	16	0	0	15.9	0.2
BIO10	Mean Temperature of Warmest Quarter	5.2	27	21.8	16.3	16.3	0	0	15.5	0.2
BIO11	Mean Temperature of Coldest Quarter	4.1	25.8	21.7	15.5	15.5	0	0	15.4	0.3
BIO12	Annual Precipitation	716	6,978	6,262	1,890	2,051	3	5.9	516,745.7	0.4
BIO13	Precipitation of Wettest Month	99	850	751	243	270.9	0.4	0.8	9,346.7	0.4
BIO14	Precipitation of Driest Month	9	410	401	71	75.8	0.2	0.3	1,705.1	0.5
BIO15	Precipitation Seasonality (Coefficient of Variation)	12	69	57	37	36.8	0	0.1	116.7	0.3
BIO16	Precipitation of Wettest Quarter	253	2,395	2,142	643	717.4	1.1	2.2	69,081	0.4
BIO17	Precipitation of Driest Quarter	57	1,310	1,253	271	278	0.5	1.1	16,872.7	0.5
BIO18	Precipitation of Warmest Quarter	79	1,619	1,540	469	507	0.8	1.5	32,118.7	0.4
BIO19	Precipitation of Coldest Quarter	63	2,309	2,246	542	585.5	1.3	2.5	92,489.3	0.5

SUPPLEMENTARY MATERIAL 2.

Wildfire dynamics and impacts on a tropical Andean oak forest

Appendix 2.1. Correlation analysis to compare the relative surface area burned in the Iguaque mountains (Colombia) with El Niño Ocean Index (ONI).

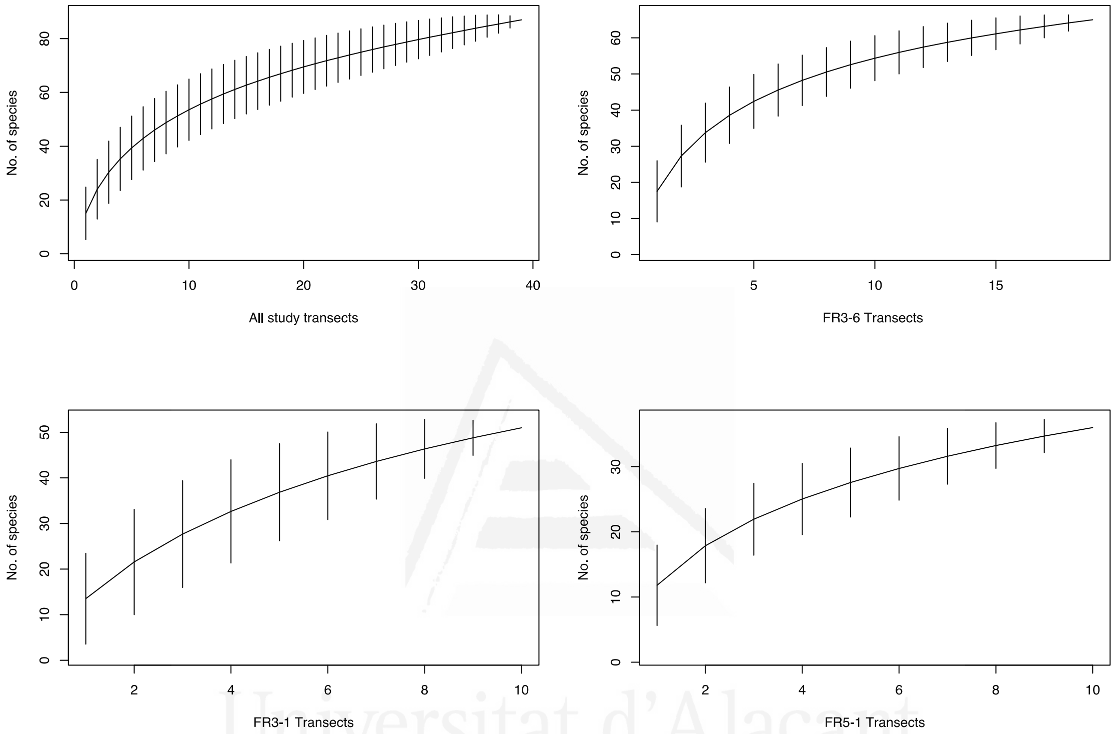
Test name	**Iguaque Surface area burned vs. ONI**				**Iguaque Surface area burned vs. Niño**				**Iguaque surface area burned vs. Niña**			
	Value	**df**	***p***	**Sample estimates**	**Value**	**df**	***p***	**Sample estimates**	**Value**	**df**	***p***	**Sample estimates**
r Pearson	t = 2.8	346	0.006	r = 0.15	t = 2.8	346	0.005	r = 0.15	t = 1.5	346	0.14	r = 0.08
Rho Spearman	S = 6366831		0.08	rho = 0.09	S = 6318989		0.06	rho = 0.1	S = 6469748		0.14	rho = 0.9
Tau Kendall	z = 1.7		0.08	tau = 0.08	z = 1.9		0.06	tau = 0.09	z = 1.5		0.14	tau = 0.07



Appendix 2.2. Cross-Correlation Function (CCF) plot for relative surface area burned in the Iguaque mountains (Colombia) and the El Niño Ocean Index (ONI) series.

SUPPLEMENTARY MATERIAL 3

The current fire regime in northern Andean shrublands hinders tree recruitment and arrests forest succession.



Appendix 3.1. Species accumulation curves for all transects and fire regimes studied**.**

Appendix 3.2. Species, attributes, and number of individuals of the vascular flora of the Iguaque Mountains.

Taxon	Species abbreviation (CCA)	Growth habit	Dispersal mode	Postfire regenerative strategy	Origin	Number of individuals		
						FR3-6	FR3-1	FR5-1
Magnoliidae Novák ex Takht.								
Adoxaceae E. Mey.								
Viburnum tinoides L.f.	Viti	tree	zoochory	resprouter	native	0	0	3
Apiaceae Lindl.								
Eryngium humboldtii F. Delaroche	Erhu	shrub	barochory	facultative	native	1	0	0
Aquifoliaceae Bercht. & J. Presl								
Ilex kunthiana Triana	Ikku	shrub	zoochory	facultative	native	11	3	0
Asteraceae Bercht. & J. Presl								
Achyrocline mollis Benth.	Acmo	herb	anemochory	na	native	4	1	0
Ageratina glyptophlebia (B.L. Rob.) R.M. King & H. Rob	Aggl	shrub	anemochory	facultative	native	32	17	14
Ageratina pichinchensis (Kunth) R.M King & H. Rob.	Agpi	shrub	anemochory	resprouter	native	4	0	0
Ageratina theaefolia (Benth.) R.M King & H. Rob	Agth	shrub	anemochory	resprouter	native	1	0	0
Baccharis bogotensis Kunth	Babo	shrub	anemochory	resprouter	native	9	0	0
Baccharis latifolia (Ruiz & Pav.) Pers.	Bala	shrub	anemochory	facultative	native	30	1	0
Baccharis macrantha Kunth	Bama	shrub	anemochory	resprouter	native	4	0	2
Baccharis tricuneata (L. f.) Pers.	Batr	shrub	anemochory	facultative	native	19	0	0
Calea peruviana (Kunth) Benth. Ex. S.F. Blake	Cape	herb	anemochory	resprouter	native	65	7	8
Chromolaena bullata (Klatt) R. M. King & H. Rob.	Chbu	herb	anemochory	na	native	2	0	0
Chromolaena odorata Kunth	Chod	herb	anemochory	na	native	2	0	0

Continue Appendix 3.2.

Taxon	Species abbreviation (CCA)	Growth habit	Dispersal mode	Postfire regenerative strategy	Origin	Number of individuals		
						FR3-6	**FR3-1**	**FR5-1**
Chromolaena perglabra (B.L. Rob.) R.M. King & H. Rob	Chpe	herb	anemochory	na	native	4	2	0
Conyza bonariensis (L.) Cronquist	Cobo	herb	anemochory	na	native	0	3	0
Diplostephium rosmarinifolium (Benth.) Wedd.	Diro	herb	anemochory	na	native	2	0	0
Espeletiopsis pleiochasia (Cuatrec.) Cuatrec.	Espl	shrub	anemochory	resprouter	native	124	3	1
Gamochaeta coarctata (Willd.) Kerguélen	Gaco	herb	anemochory	resprouter	native	0	3	0
Gnaphalium cheiranthifolium Lam.	Gnch	herb	anemochory	resprouter	native	4	1	0
Gnaphalium elegans Kunth	Gnel	herb	anemochory	resprouter	native	5	4	0
Hyppochaeris radicata L.	Hyra	herb	anemochory	resprouter	exotic	0	0	1
Lepidaploa karstenii (Sch. Bip) H. Rob.	Leka	shrub	anemochory	resprouter	native	34	0	4
Lourteigia microphylla (L. f.) R.M. King & H. Rob	Lomi	herb	anemochory	na	native	7	1	0
Pentacalia corymbosa (Benth.) Cuatrec.	Peco	shrub	anemochory	facultative	native	21	15	15
Pentacalia pulchella (Kunth) Cuatrec.	Pepu	shrub	anemochory	facultative	native	3	1	0
Taraxacum officinale F. H. Wigg.	Taof	herb	anemochory	na	exotic	0	2	1
Verbesina elegans Kunth	Veel	shrub	anemochory	facultative	native	23	0	0
Bromeliaceae Juss.								
Puya bicolor Mez	Pubi	shrub	anemochory	facultative	native	12	20	9
Campanulaceae Juss.								
Diastatea micrantha (Kunth) Mx Vaugh	Dimi	herb	barochory	facultative	native	1	0	0
Siphocampylus columnae (L. f.) G. Don	Sico	herb	barochory	facultative	native	0	3	0

Continue Appendix 3.2.

Taxon	Species abbreviation (CCA)	Growth habit	Dispersal mode	Postfire regenerative strategy	Origin	Number of individuals		
						FR3-6	**FR3-1**	**FR5-1**
Chloranthaceae R. Br. Ex Sims								
Hedyosmum crenatum Occhioni	Hecr	tree	zoochory	na	native	3	0	0
Clethraceae Klotzsch								
Clethra fimbriata Kunth	Clfi	tree	barochory	resprouter	native	13	3	3
Clusiaceae Lindl.								
Clusia multiflora Kunth	Clli	tree	barochory	resprouter	native	5	0	0
Cyperaceae Juss.								
Carex jamesonii Boott	Caja	herb	anemochory	facultative	native	0	1	2
Rhynchospora macrochaeta Steud. ex Boeckeler	Rhma	herb	anemochory	facultative	native	2	0	2
Rhynchospora nervosa (Vahl) Boeckeler subsp. *ciliata* (G. Mey.) Kük.	Rhne	herb	anemochory	facultative	native	9	4	2
Ericaceae Juss.								
Bejaria resinosa Mutis ex L. f.	Bare	shrub	zoochory	facultative	native	157	38	27
Cavendishia bracteata (Ruix & Pav. Ex J. St.-Hil.) Hoerold	Caba	shrub	zoochory	facultative	native	4	9	10
Gaylussacia buxifolia Kunth	Gabu	shrub	zoochory	facultative	native	8	1	1
Macleania rupestris (Kunth) A. C. Sm.	Maru	shrub	zoochory	facultative	native	5	0	0
Vaccinium floribundum Kunth	Vafl	shrub	zoochory	facultative	native	0	2	2
Euphorbiaceae Juss.								
Croton purdiei Müll. Arg	Crpu	tree	barochory	facultative	native	1	0	0
Fagaceae Dumort.								
Quercus humboldtii Bonpl.	Quhu	tree	barochory	resprouter	native	0	0	1

Continue Appendix 3.2.

Taxon	Species abbreviation (CCA)	Growth habit	Dispersal mode	Postfire regenerative strategy	Origin	Number of individuals		
						FR3-6	**FR3-1**	**FR5-1**
Hypericaceae Juss.								
Hypericum juniperinum Kunth	Hyju	shrub	barochory	facultative	native	9	0	0
Hypericum marahuacanum N. Robson	Hyma	shrub	barochory	facultative	native	23	0	0
Iridaceae Juss.								
Orthrosanthus monadelphus Ravenna	Orma	herb	barochory	facultative	native	12	5	6
Loranthaceae Juss.								
Gaiadendron punctatum (Ruiz & Pav.) G. Don	Gapu	shrub	zoochory	resprouter	native	2	0	0
Lythraceae J. St.-Hil.								
Cuphea decandra Aiton	Cude	herb	barochory	facultative	native	1	0	0
Melastomataceae Juss.								
Bucquetia glutinosa (L. f.) DC.	Bugl	shrub	zoochory	facultative	native	0	1	0
Miconia alborosea L. Uribe	Mial	shrub	zoochory	facultative	native	1	0	0
Miconia squamulosa (Sm.) Triana	Misq	shrub	zoochory	facultative	native	37	18	1
Monochaetum myrtoideum (Bonpl.) Naudin	Momy	shrub	barochory	resprouter	native	2	0	2
Myricaceae Rich. Ex Kunth								
Morella parvifolia (Benth.) Parra-Os	Mopa	shrub	zoochory	facultative	native	52	12	11
Myrtaceae Juss.								
Myrcianthes leucoxyla (Ortega) Mc Vaugh	Myle	tree	zoochory	na	native	0	0	1
Myrcianthes rhopaloides (Kunth) Mc Vaugh	Myrh	tree	zoochory	na	native	0	1	1
Orchidaceae Juss.								
Epidendrum secundum Jacq	Epse	herb	anemochory	resprouter	native	4	0	0

Continue Appendix 3.2.

Taxon	Species abbreviation (CCA)	Growth habit	Dispersal mode	Postfire regenerative strategy	Origin	Number of individuals		
						FR3-6	FR3-1	FR5-1
Papaveraceae Juss.								
Bocconia integrifolia Bonpl.	Boin	shrub	zoochory	resprouter	native	0	9	0
Passifloraceae Juss. Ex Roussel								
Passiflora bicuspidata (H. Karst.) Mast.	Pabi	vine	zoochory	na	native	1	0	0
Phytolaccaceae R.Br.								
Phytolacca rugosa A. Bran & C.D. Bouché	Pyru	shrub	zoochory	na	native	0	3	0
Poaceae Barnhart								
Andropogon lehmannii Pilg.	Anle	graminoid	anemochory	facultative	exotic	24	4	4
Aristida adscencionis L.	Arad	graminoid	anemochory	resprouter	exotic	0	1	0
Eragrostis lugens Nees	Erlu	graminoid	anemochory	resprouter	native	1	2	4
Heteropogon contortus (L.) P. Beauv. Ex Roem. & Schult.	Heco	graminoid	anemochory	facultative	native	5	6	10
Melinis minutiflora P.Beauv.	Memi	graminoid	anemochory	facultative	exotic	21	4	9
Polypogon viridis (Gouan) Breistr.	Povi	graminoid	barochory	facultative	native	30	13	13
Polygonaceae Juss.								
Muehlenbeckia tamnifolia (Kunt) Meisn.	Muta	vine	zoochory	resprouter	native	0	1	0
Primulaceae Batsch ex Borkh.								
Myrsine coriacea (Sw.) R.Br. Ex Roem. & Schult.	Myco	tree	zoochory	resprouter	native	12	4	7
Myrsine guianensis (Aubl.) Kuntze	Mygu	tree	zoochory	resprouter	native	1	0	0
Rosaceae Juss.								
Rubus robustus C. Presl	Ruro	shrub	zoochory	resprouter	native	0	1	0

Continue Appendix 3.2.

Taxon	Species abbreviation (CCA)	Growth habit	Dispersal mode	Postfire regenerative strategy	Origin	Number of individuals		
						FR3-6	FR3-1	FR5-1
Rubiaceae Juss.								
Arcytophyllum nitidum (Kunth) Schltdl.	Arni	shrub	barochory	resprouter	native	9	3	1
Galium hypocarpium (L.) Endl. Ex Griseb	Gahy	herb	zoochory	resprouter	native	0	2	1
Palicourea angustifolia Kunth	Paan	shrub	zoochory	resprouter	native	9	5	0
*Palicourea paniculata (*L. f.) P.L.R. Moraes & C.M. Taylor	Papa	shrub	zoochory	resprouter	native	2	5	0
Psychotria boqueronensis Wernham	Psbo	shrub	zoochory	resprouter	native	19	0	0
Spermacoce capitata Ruiz & Pav.	Spca	herb	barochory	na	native	3	2	0
Salicaceae Mirb.								
Xylosma spiculiferum (Tul.) Triana & Planch.	Xysp	tree	zoochory	resprouter	native	3	0	0
Sapindaceae Juss.								
Dodonea viscosa Jacq.	Dovi	shrub	barochory	facultative	native	161	26	6
Smilacaceae Vent.								
Smilax tomentosa Kunth.	Smto	vine	zoochory	resprouter	native	0	2	0
Solanaceae Juss.								
Cestrum buxifolium Kunth	Cebu	shrub	zoochory	facultative	native	20	5	6
Cestrum cuneifolium Francey	Cecu	shrub	zoochory	na	native	2	0	0
Solanum americanum Mill	Soam	herb	zoochory	na	native	0	2	0
Symplocaceae Desf.								
Symplocos theiformis (L. f.) Oken	Syth	shrub	zoochory	resprouter	native	9	1	0
Violaceae Batsch								
Viola odorata L.	Viod	herb	barochory	resprouter	native	1	0	0

Continue Appendix 3.2.

Taxon	Species abbreviation (CCA)	Growth habit	Dispersal mode	Postfire regenerative strategy	Origin	Number of individuals		
						FR3-6	**FR3-1**	**FR5-1**
Pinus patula Schltdl. & Cham.	Pipa	tree	anemochory	facultative	exotic	0	0	2
Dennstaedtiaceae Lotsy								
Pteridium aquilinum (L.) Kuhn	Ptaq	herb	anemochory	facultative	exotic	45	84	26
Lycopodiaceae P. Beauv. Ex Mirb.								
Lycopodium clavatum L.	Lycl	herb	hydrochory	resprouter	native	0	1	0
Sphagnaceae								
Sphagnum sp	Spsp	herb	hydrochory	resprouter	native	8	0	0
Total families						29	24	18
Total species						62	52	36
Total individuals						1158	363	217

Appendix 3.3. Richness, density, and representative species in the different vegetation layers of the Iguaque Mountains under three fire regimes. Averages by layer and standard error (± 1 SE).

Fire regime	**Vegetation layer**	**Species richness**	**Individual density**	**Dominant species**
FR3-6	Herbaceous	5.80 ± 0.40 sps/m^2	5.92 ± 0.40 inds/m^2	*P. aquilinum, P. viridis, A. lehmannii*
	Small shrubs	0.09 ± 0.01 sps/m^2	0.12 ± 0.06 inds/m^2	*E. pleiochasia, D. viscosa, B. resinosa*
	Large shrubs	192 ± 44.30 sps/ha	476 ± 122.91 inds/ha	*B. resinosa, D. viscosa, M. squamulosa*
FR3-1	Herbaceous	5 ± 0.3 sps/m^2	5.14 ± 0.36 inds/m^2	*P. aquilinum, B. resinosa, P. viridis*
	Small shrubs	0.06 ± 0.01 sps/m^2	0.24 ± 0.04 inds/m^2	*B. resinosa, D. viscosa, P. corymbosa*
	Large shrubs	90 ± 42.03 sps/ha	215 ± 103.56 inds/ha	*M. squamulosa, B. integrifolia, D. viscosa*
FR5-1	Herbaceous	5.2 ± 0.4 sps/m^2	5.27 ± 0.37 inds/m^2	*P. aquilinum, P. viridis, H. contortus*
	Small shrubs	0.03 ± 0.010 sps/m^2	0.04 ± 0.01 inds/m^2	*P. corymbosa, B. resinosa, M. parvifolia*
	Large shrubs	10 ± 6.67 sps/ha	10 ± 6.67 inds/ha	*B. resinosa*

Appendix 3.4. Results of PERMANOVA to assess the effects on time after the last fire, one (2015) and six years (2010), and the frequency (three and five fires) on species richness and density in the herbaceous, small shrub, and large shrub layers. Statistical significance was set at $p < 0.05$.

Test series	***df***	***Sum Sq***	***R2***	***f***	***p***
Herbaceous layer richness					
Year	1	36	0.04	5.43	0.001
Frequency	1	16	0.02	2.60	0.061
Residual	114	749	0.93		
Total	116	802	1.00		
Herbaceous layer density					
Year	1	0.02	0.02	4.5	0.001
Frequency	1	0.01	0.02	2.2	0.025
Residual	114	0.42	0.95		
Total	116	0.45	1.00		
Small shrubs layer richness					
Year	1	55	0.08	5.8	0.002
Frequency	1	26	0.04	2.8	0.027
Residual	69	651	0.89		
Total	71	732	1.00		
Small shrubs layer density					
Year	1	0.38	0.09	7.2	0.001
Frequency	1	0.19	0.04	3.5	0.019
Residual	69	3.67	0.87		
Total	71	4.23	1.00		
Large shrubs layer richness					
Year	1	30	0.04	4.1	0.007
Frequency	1	15	0.02	2.0	0.052
Residual	93	677	0.93		
Total	95	721	1.00		
Large shrubs layer density					
Year	1	9.1	0.04	3.9	0.005
Frequency	1	4.6	0.02	2.0	0.068
Residual	93	214	0.94		
Total	95	228	1.00		

Appendix 3.5. Results of Wilcoxon Mann-Whitney tests (U) to assess the effects one and six years after the last fire (FR3-1 and FR3-6) on the cover, basal area, native and exotic species proportions (%), and the significance of cover (%) of native species and invasive species in the herbaceous, small shrub and large shrub layers. Statistical significance was set at $p < 0.05$.

Indices	*U*	*p*
Herbaceous layer		
Cover (%)	13	0.5
Proportion of obligate resprouters (%)	126	4.5^{-4}
Species cover (%) in herbaceous layer		
Pteridium aquilinum	284	8.0^{-2}
Andropogon lehmannii	135	2.0^{-2}
Melinis minutiflora	122	0.6
Heteropogon contortus	101	0.6
Other exotic species	247	5.0^{-2}
Native species	194	0.7
Small shrub layer		
Basal area (cm^2/m^2)	68	0.2
Proportion of obligate resprouters (%)	848	7.0^{-2}
Large shrub layer		
Basal area (m^2/ha)	65	0.2
Proportion of obligate resprouters (%)	125	0.7

Appendix 3.6. Cover, BSD, DBH, and height of plants under different fire regimes in the Iguaque Mountains. The fire regimes are FR3-6 (six years, last fire in 2010, fire frequency = 3), FR3-1 (one-year, previous fire in 2015, fire frequency = 3), and FR5-1 (one-year, last fire in 2015, fire frequency = 5). Averages by layer and standard error (± 1 SE).

Fire regime	**FR3-6**		**FR3-1**		**FR5-1**	
Variable	***Mean***	***SE***	***Mean***	***SE***	***Mean***	***SE***
Cover % (Herbaceous layer)	14.3	0.8	18.8	22.7	10.4	1
BSD (Small shrub layer)	1.4	0.01	1.3	0.03	1.3	0.04
DBH (Large shrub layer)	3.5	0.2	3.6	1.4	0.5	0.33
Height (Large and small shrub layers)	164.8	8.5	242.7	172.4	135	70

Appendix 3.7. The proportion of obligate resprouting species under the fire regimes FR3-6 (six years, last fire in 2010, fire frequency = 3), FR3-1 (one-year, previous fire in 2015, fire frequency = 3), and FR5-1 (one-year, last fire in 2015, fire frequency = 5). Averages by layer and standard error (± 1 SE).

	Resprouters species proportion (%)					
Vegetation layer	**FR3-6**		**FR3-1**		**FR5-1**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
Herbaceous	49	3.1	70	4.8	67	4.47
Small shrubs	56	4.7	68	7.2	50	8.3
Large shrubs	57	8.5	53	13.3	20	13.3

Appendix 3.8. Cover of native species, invasive species, and bare soil (%) under the fire regimes: FR3-6 (six years, last fire in 2010, fire frequency = 3), FR3-1 (one-year, last fire in 2015, fire frequency = 3), and FR5-1 (previous fire in 2015, fire frequency = 5). Averages by layer and standard error (± 1 SE).

	Fire regime					
Species cover %	**FR3-6**		**FR3-1**		**FR5-1**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
Pteridium aquilinum	8.6	2.7	12	3.8	17.2	3.7
Andropogon lehmannii	25	6.2	1.2	0.7	1.1	0.9
Melinis minutiflora	9.3	3.5	2.4	1.4	1.1	0.6
Heteropogon contortus	3.7	1.8	3.1	1.9	2.8	1.2
Other exotic species	0	0	0.5	0.4	0.8	0.8
Native species	48.5	5.9	45.1	7.7	32.2	6.2
Bare soil	4.9	2.2	35.7	2.3	45.6	1.7

Appendix 3.9. Results of Wilcoxon Mann-Whitney tests (U) to assess the effects of fire frequencies on the cover, basal area, native and exotic species proportions (%), and the significance of cover (%) of native species and invasive species under two different fire frequencies (FR3-1 and FR5-1) one year after a fire on the herbaceous, small shrub and large shrub layers. Statistical significance was set at $p < 0.05$.

Indices	***U***	***p***
Small shrub layer		
Cover (%)	17	0.9
Proportion of obligate resprouters (%)	486	0.6
Species cover (%) in herbaceous layer		
Pteridium aquilinum	89	0.3
Andropogon lehmannii	119	0.7
Melinis minutiflora	122	0.6
Heteropogon contortus	101	0.6
Other exotic species	119	0.6
Native species	137	0.3
Small shrub layer		
Basal area (cm^2/m^2)	49	1
Proportion of obligate resprouters (%)	302	0.1
Large shrub layer		
Basal area (m^2/ha)	85	5.0^{-3}*
Proportion of obligate resprouters (%)	71	9.0^{-2}*

A) Wildfire-affected area in the Iguaque mountains.

B) Fire regime FR3 – 6.

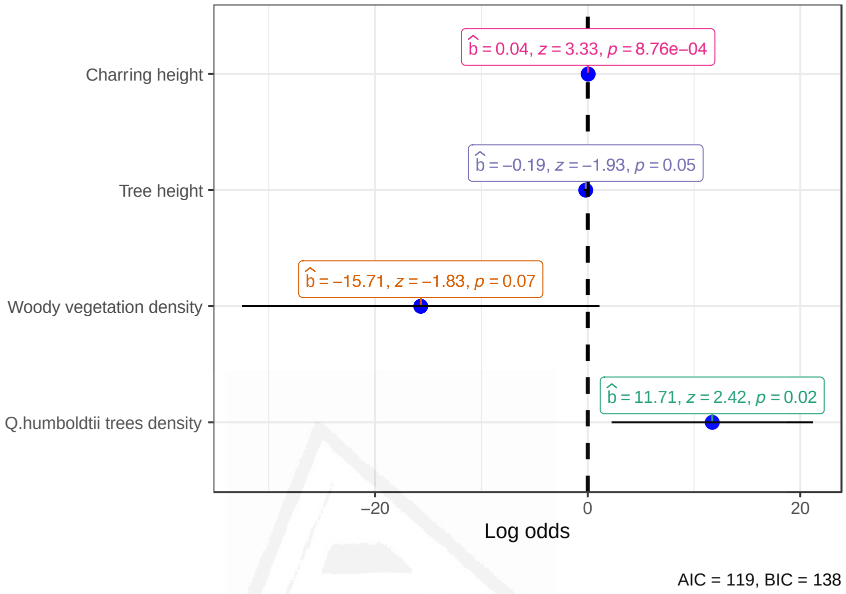
C) Fire regime FR3 – 1.

D) Fire regime FR5 – 1.

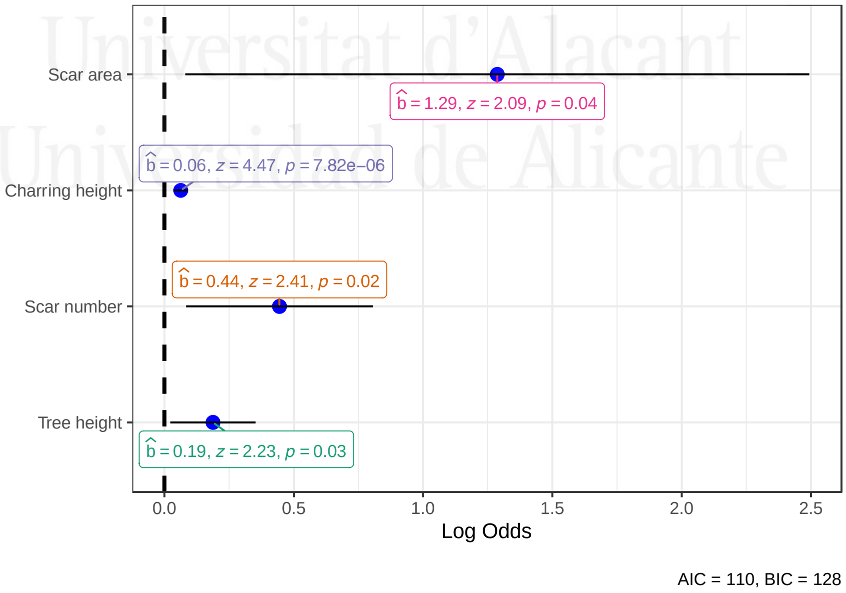
Appendix 3.10. Photographs of the study area. A) Panoramic view of the mountains of the areas affected by the fires to the southwest of the Iguaque mountains. On the right are areas with fire regime FR6-1; in the center are FR5-1; and to the left, the areas FR3-1. B) Fire regime FR3-6, six years since the last wildfire, frequency of 3 fires. C) Fire regime FR3-1, one year since the last wildfire, frequency of 3 fires. D) FR5-1, frequency of five fires one year since the last wildfire.

SUPPLEMENTARY MATERIAL 4

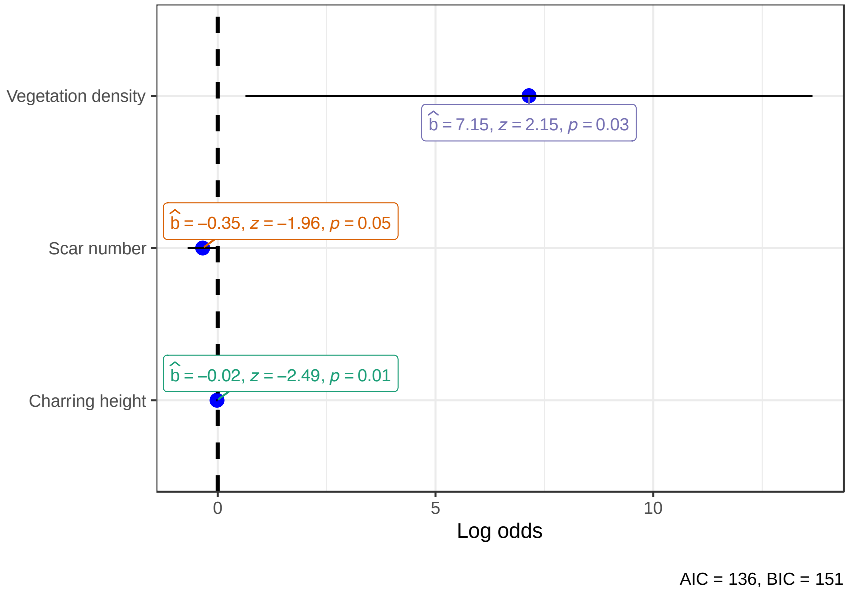
Postfire resprouting and recruitment of *Quercus humboldtii* in the Iguaque Mountains (Colombia)



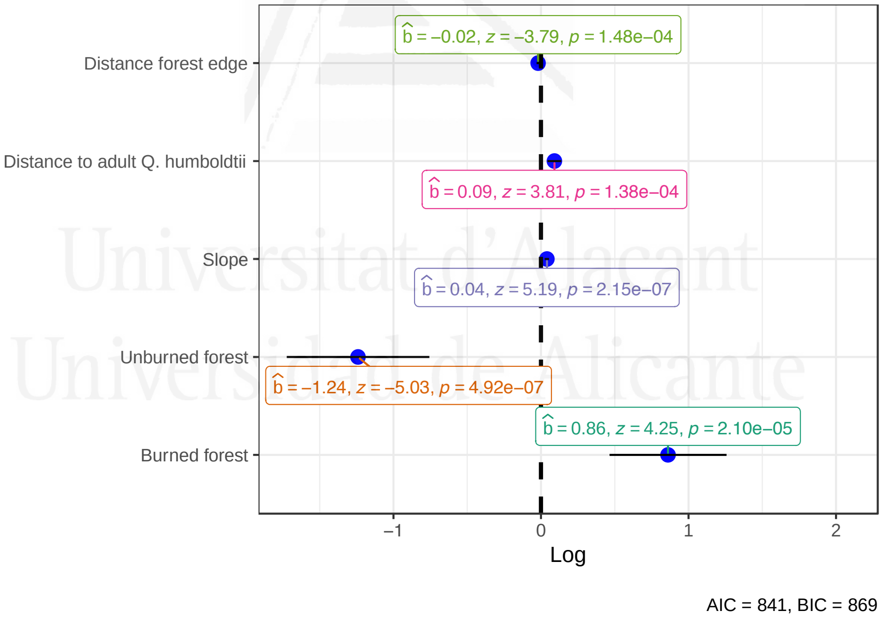
Appendix 4.1. Parsimonious resprouting ability model and odds ratios for *Quercus humboldtii*.



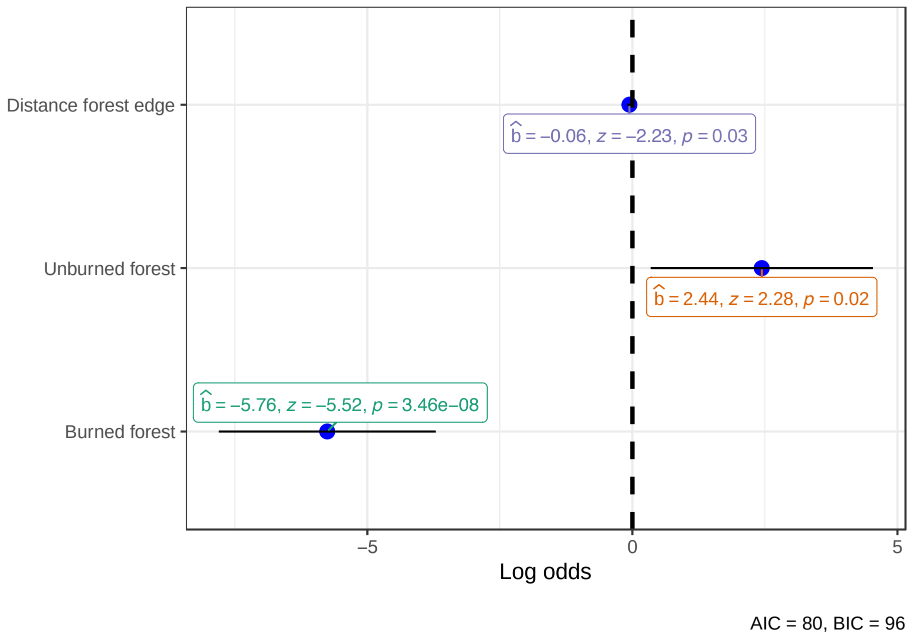
Appendix 4.2. Parsimonious stump resprouting model and odds ratios for *Quercus humboldtii*.



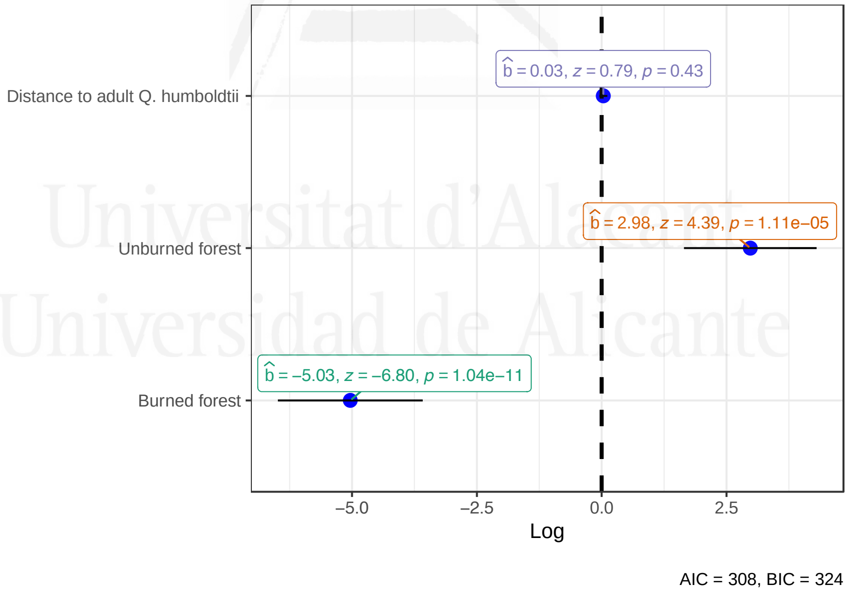
Appendix 4.3. Parsimonious crown resprouting model and odds ratios for *Quercus humboldtii*



Appendix 4.4. Parsimonious acorn density model and odds ratios for *Quercus humboldtii*.



Appendix 4.5. Parsimonious healthy acorn density model and odds ratios for *Quercus humboldtii*

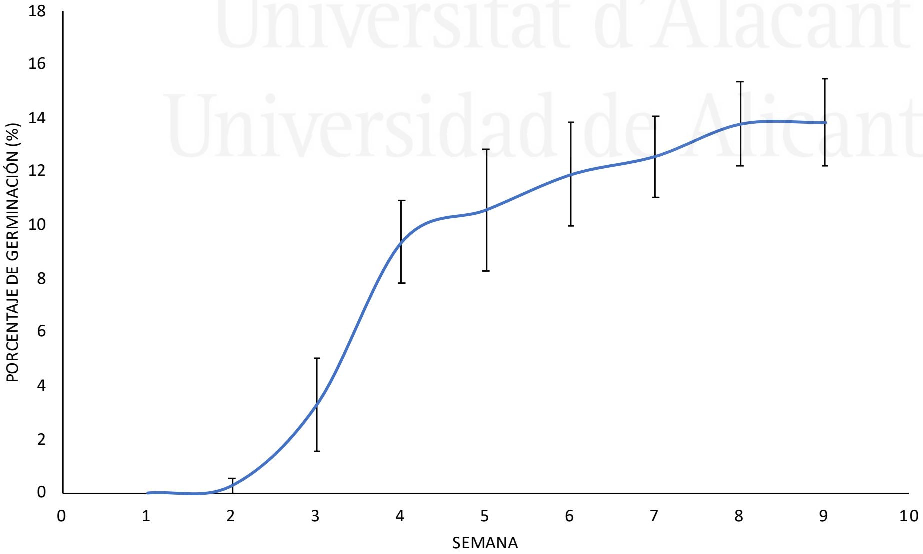


Appendix 4.6. Parsimonious seedling density model and odds ratios for *Quercus humboldtii.*

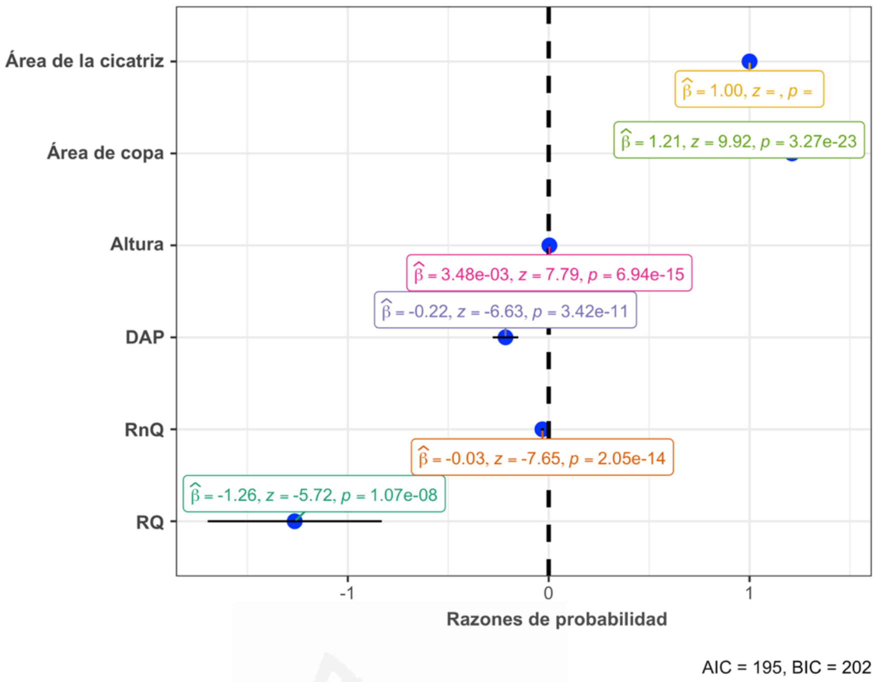
SUPPLEMENTARY MATERIAL 5

Producción y germinación de bellotas de *Quercus humboldtii* en robledales andinos afectados por incendios recurrentes.

Apéndice 5.1. Cicatrices casi triangulares sobre troncos de *Quercus humboldtii*.



Apéndice 5.2. Curva de germinación para las bellotas viables colectadas en el bosque quemado durante nueve semanas.



Apéndice 5.3. Modelo parsimonioso de producción de bellotas abortadas y razones de probabilidad.

SUPPLEMENTARY MATERIAL 6

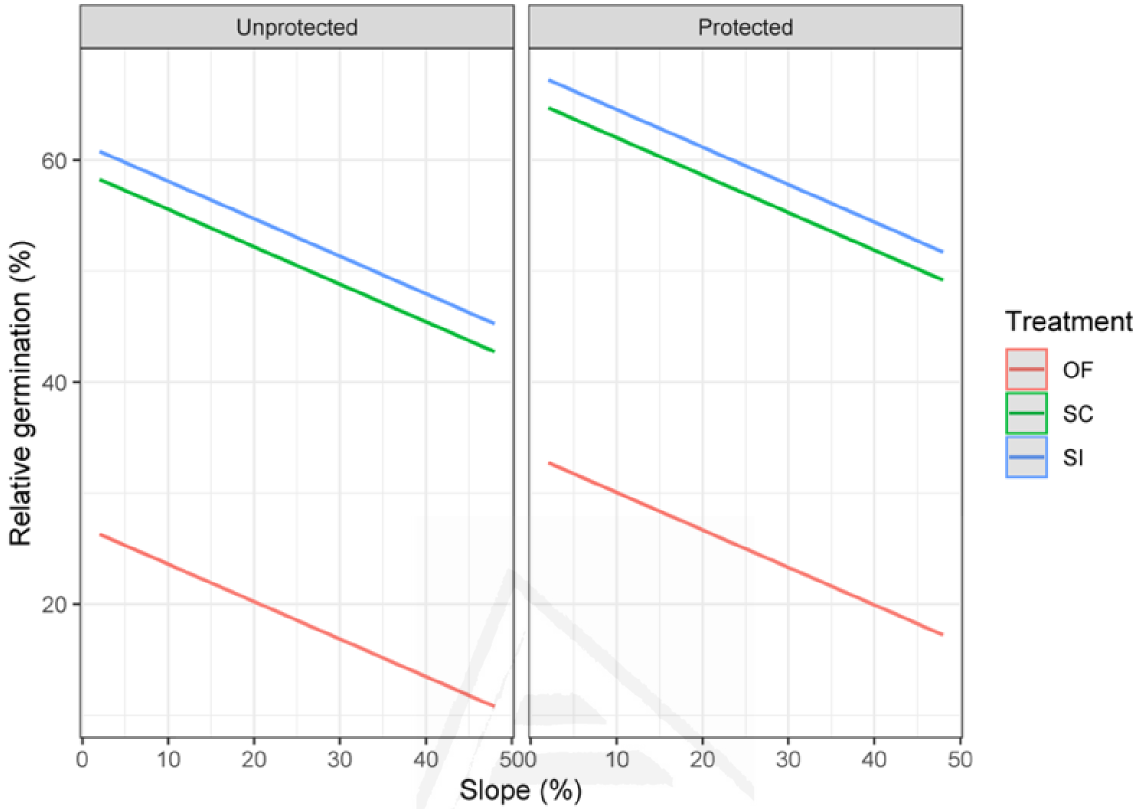
Quercus humboldtii germination and establishment limitations in Andean vegetation affected by wildfires.

Appendix 6.1. Temperature and relative humidity differences between the experimental plots.

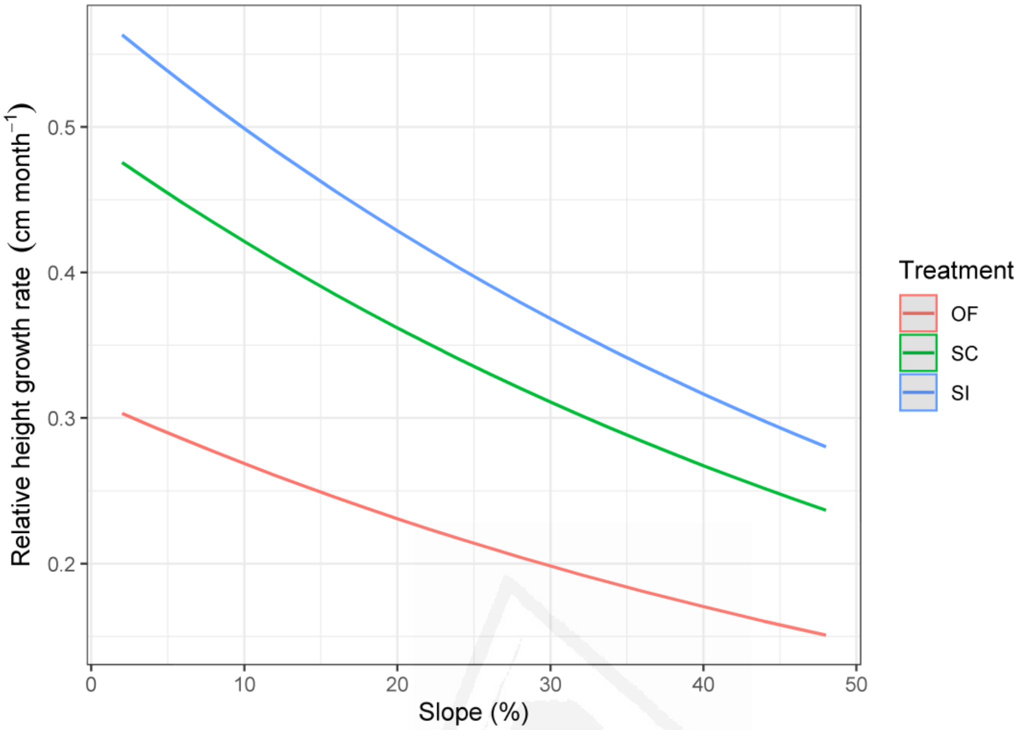
Indices	**Test series**	***df***	***Sum Sq***	***Mean Sq***	***f***	***p***	***Tukey homogeneous groups***
Temperature ºC	Coverage	2	25552	127763	837.8	$<2.0^{-16}$	OF<SI=SC
	Residuals	55872	851992	15			
Humidity %	Cover	2	725348	362674	1598	$<2.0^{-16}$	OF>SI=SC
	Residuals	55872	12677967	227			

Appendix 6.2. Germination, survival, and growth rate for *Quercus humboldtii* acorns sown in Oak Forest (OF), Shrubland with invasive species (SI), and Shrubland without invasive species (SC) in the Iguaque Mountains experimental plots. *Protection level only for acorns.

Variable	**Protection level***	**Year 2018**			**Year 2019**		
		OF	**SC**	**SI**	**OF**	**SC**	**SI**
Germination (%)	Protected	6.0 ± 2	64.0 ± 6	66.0 ± 9	42.0 ± 5	61.0 ± 7	59.0 ± 8
	Unprotected	3.0± 2	47.0 ± 8	59.0 ± 12	31.0 ± 6	42.0 ± 7	46.0 ± 6
Seedling survival (%)		70.3± 2	30.8 ± 1	32.8± 0.6	82.0 ± 1	83.0 ± 1	84.0 ± 0.3
Seedling RGR Height (month-1)		0.13 ± 0.1	0.59± 0.1	0.59 ± 0.1	0.37 ± 0.1	0.51 ± 0.1	0.74 ± 0.1
Seedling RGR Diameter stem (month-1)		0.05 ± 0.1	0.08 ± 0.1	0.12 ± 0.1	0.11 ± 0.1	0.20 ± 0.1	0.21 ± 0.1



Appendix 6.3. Generalized Linear Mixed-Effects Model for the relative germination of protected and unprotected *Quercus humboldtii* acorns from two cohorts sown in three vegetation types: Oak Forest (OF), Shrubland with invasive species (SI) and Shrubland without invasive species (SC), in the Iguaque Mountains experimental plots.



Appendix 6.4. Relative seedlings height growth model on tree different coverages: Oak Forest (OF), Shrublands whiteout exotic species (SC), and Shrublands mixed with exotic species (SI) as a function of slope (%). The colored lines represent the coverage type.

Appendix 6.5. Species, number of individuals, and relative abundance of potential-seed predators' mammals among cover and protection levels of the experimental quadrats where *Quercus humboldtii* acorns were planted. In bold, the most abundant potential seed-predator mammals**.**

Coverage	Protection	Species	Individuals	AR
OF	Protected	*Notosciurus granatensis* (Humboldt 1911)	2	**13.33**
	Unprotected	*Notosciurus granatensis* (Humboldt 1911)	74	**8.55**
		Didephis peregrina (Allen 1900)	39	**4.51**
		Sylvilagus andinus (Thomas 1897)	3	0.35
		Thurdus fuscater (Lafresnaye & D'Orbigny 1837)	3	0.35
		Canis lupus familiaris (Linnaeus 1758)	1	0.12
		Mus musculus (Linnaeus 1758)	1	0.12
		Patagioenas fasciata (Say 1822)	1	0.12
		Caprimulgus longirostris (Bonaparte 1825)	1	0.12
SC	Protected	*Thurdus fuscater* (Lafresnaye & D'Orbigny 1837)	5	0.121
		Anolis auratus (Daudin 1802)	2	0.048
		Notosciurus granatensis (Humboldt 1911)	2	**0.048**
		Troglodytes aedon (Vieillot 1809)	1	0.024
		Didephis peregrina (Allen 1900)	1	0.024
		Sylvilagus andinus (Thomas 1897)	1	0.024
	Unprotected	*Canis lupus familiaris* (Linnaeus 1758)	11	0.074
		Zonithrichia capensis (Statius Müller 1776)	10	0.067
		Notosciurus granatensis (Humboldt 1911)	6	**0.040**
		Thurdus fuscater (Lafresnaye & D'Orbigny 1837)	6	0.040
		Didephis peregrina (Allen 1900)	4	0.027
		Patagioenas fasciata (Say 1822)	2	0.013
		Zenaida auriculata (Des Murs 1847)	1	0.007
		Sylvilagus andinus (Thomas 1897)	1	0.007
SI	Protected	*Thurdus fuscater* (Lafresnaye & D'Orbigny 1837)	6	0.098
		Notosciurus granatensis (Humboldt 1911)	3	**0.049**
		Didephis peregrina (Allen 1900)	2	0.033
		Canis lupus familiaris (Linnaeus 1758)	2	0.033
		Sylvilagus andinus (Thomas 1897)	1	0.016
	Unprotected	*Canis lupus familiaris* (Linnaeus 1758)	8	0.130
		Notosciurus granatensis (Humboldt 1911)	7	**0.114**
		Zonithrichia capensis (Statius Müller 1776)	6	0.098
		Thurdus fuscater (Lafresnaye & D'Orbigny 1837)	5	0.081
		Didephis peregrina (Allen 1900)	4	0.065
		Zenaida auriculata (Des Murs 1847)	1	0.016
		Sylvilagus andinus (Thomas 1897)	1	0.016

A


2019-04-16 1:36:10 PM M 3/3
20°C
HC500 HYPERFIRE
RECONYX

B


2019-07-09 10:25:17 AM M 2/3
16°C
HC500 HYPERFIRE
RECONYX

C


2019-04-28 6:29:24 AM M 1/3
12°C
HC500 HYPERFIRE
RECONYX

D


2019-05-10 5:52:41 AM M 1/3
12°C
HC500 HYPERFIRE
RECONYX

E


2019-05-04 4:31:33 PM M 1/3 22°C
HC500 HYPERFIRE
RECONYX

F


Bushnell
TROPHY CAM
44°F 6°C
05-23-2019 08:44:51

G


2019-04-15 9:02:25 PM M 2/3
15°C
HC500 HYPERFIRE
RECONYX

H


2019-04-17 4:09:26 AM M 2/3
12°C
HC500 HYPERFIRE
RECONYX

I


2019-05-17 6:28:10 PM M 2/3
14°C
HC500 HYPERFIRE
RECONYX

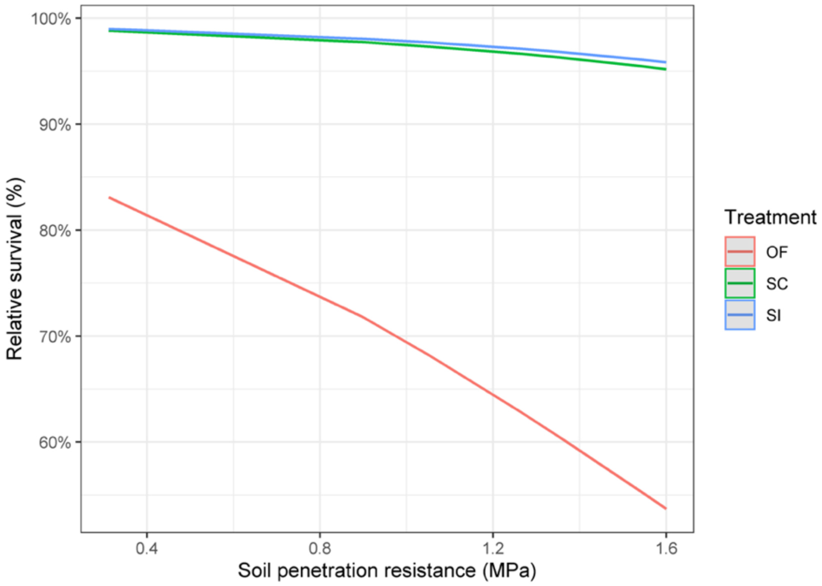
J


2019-06-17 4:14:04 AM M 2/3
12°C
HC500 HYPERFIRE
RECONYX

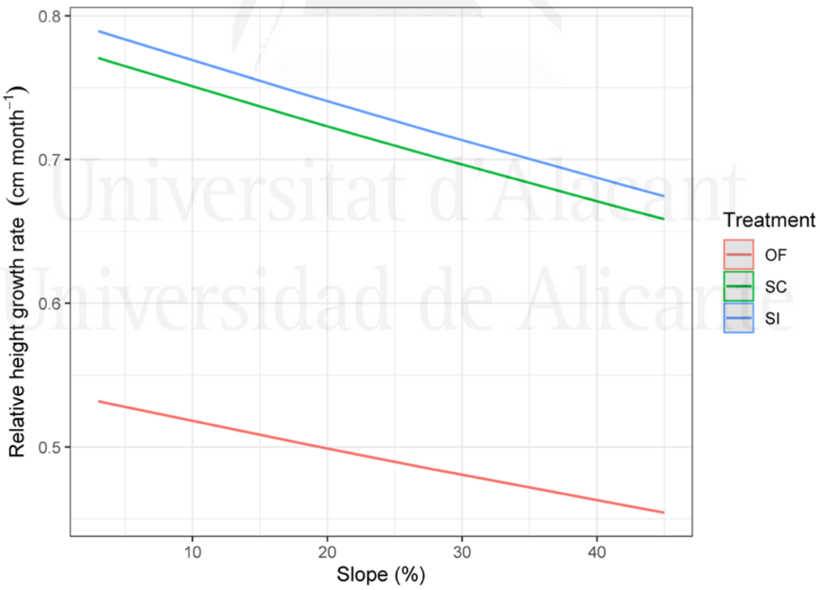
Appendix 6.6. Camera traps in experimental plots detected the most abundant seed dispersers/predatory mammals. Photographs A - D *Notocirius granatensis* (red-tailed squirrel) in the experimental oak forest (OF) plots with an acorn in its mouth and hands. Photo E shows two individuals of *Notocirius granatensis* recurrently visiting the experimental fields in the oak forest (OF). Photograph F *Notocirius granatensis are* attempting to enter an experimental plot with shrubland protection without invasive species (SI). Photograph G. *Didelphis peregrina* (Andean white-eared opossum) was exacerbating *Quercus humboldtii* seeds sown in an experimental field in the oak forest (OF). Photograph H. Two individuals of *Didelphis peregrina* vying for *Quercus humboldtii* seeds sown in an experimental plot in the oak forest (OF). Photograph I. Young *Didelphis peregrina* in an experimental field in the non-invasive shrubland (SC). Photograph J. *Sylvilagus andinus* (Andean rabbit) in an experimental plot in the oak forest (OF).

Appendix 6.7. Survival and growth of saplings in three experimental cover types: oak forest (OF), shrubland without invasive species (SC), and mixed shrubland with invasive species.

Variable	**OF**	**SC**	**SI**
Saplings survival (%)	71± 3.4	96 ± 1.4	97 ± 1.3
Saplings RGR Height (cm month-1)	0.5 ± 0.03	0.7 ± 0.04	0.8 ± 0.04
Saplings RGR Diameter stem (cm month-1)	0.01 ± 0.001	0.03 ± 0.001	0.02 ± 0.01
Saplings RGR Cover (cm month-1)	10.6 ± 0.9	15.4 ± 1.4	12.2 ± 1
Herbivory frequency (%)	0.98 ± 0.06	0.83 ± 0.06	0.48 ± 0.05
Damage frequency (%)	1.1 ± 0.06	0.94 ± 0.05	1 ± 0.05



Appendix 6.8. Relative saplings survival model on tree different coverages: oak forest (OF), Shrublands whiteout exotic species (SC), and Shrublands mixed with exotic species (SI) as a function of soil penetration resistance (MPa). The colored lines represent the coverage type.



Appendix 6.9. Relative height growth rate model on different tree coverages: oak forest (OF), Shrublands whiteout exotic species (SC), and Shrublands mixed with exotic invasive species (SI) as a function of slope (%). The colored lines represent the coverage type.