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PERSPECTIVE

Title: Ecological mechanisms underlying aridity thresholds in global drylands

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11   PERSPECTIVE

Ecological mechanisms underlying aridity thresholds in global drylands

SUMMARY

15   1. With ongoing climate change, the probability of crossing environmental thresholds promoting
16   abrupt changes in ecosystem structure and functioning is higher than ever. In drylands (areas
17   where it rains less than 65% of what could be potentially evaporated), recent research has
18   shown how the crossing of three aridity thresholds (at aridity [1-Aridity Index] values of 0.54,
19   0.70 and 0.80) leads to abrupt changes on ecosystem structural and functional attributes.
20   Despite the importance of these findings and their implications to develop effective
21   monitoring and adaptation actions to combat climate change and desertification, we lack a
22   proper understanding of the mechanisms unleashing these abrupt shifts.
23   2. Here we review multiple mechanisms that may explain the existence of aridity thresholds
24   observed across global drylands, and discuss the potential amplification mechanisms that may
25   underpin hypothetical abrupt temporal shifts with climate change.
26   3. We propose that each aridity threshold is caused by different and specific mechanisms. The
27   first threshold is mainly caused by physiological mechanisms of plant adaptation to water
28   shortages. The second threshold is unleashed by different mechanisms involving soil
29   processes and plant-soil interactions such as soil erosion, plant community shifts and nutrient

cycling and circulation. The collapse of vegetation observed once the third aridity threshold (0.8) is crossed is caused by mechanisms related to the survival limits of plants that may cause sudden cover and diversity losses and plant-atmospheric feedbacks that link vegetation collapse with further climate aridification.

4. By identifying, revising, and linking relevant mechanisms to each aridity threshold observed, we provide a set of specific hypotheses and identify knowledge gaps concerning the study of threshold emergence in drylands. We also were able to establish plausible factors that are context dependent and may influence the occurrence of abrupt ecosystem changes in time. Our review may help to focus future research efforts on aridity thresholds and to develop strategies to monitor, adapt to or even revert abrupt ecosystem changes across global drylands.

INTRODUCTION

43 Ongoing climate change is producing widespread changes in key ecosystem attributes and functions

44 with far-reaching impacts on life on Earth (Stocker *et al.* 2013). Of particular concern is the fact that

45 climate-change induced impacts on ecosystems may occur abruptly rather than gradually after

46 crossing certain levels of environmental conditions (e.g., temperature, precipitation, soil properties)

47 called thresholds (Groffman *et al.* 2006). Thresholds have two main characteristics that make them

48 important. First, changes in ecosystems when surpassing a threshold are abrupt (i.e., involve a drastic

49 discontinuous shift in the value of an ecosystem attribute or a sudden discontinuous change in the way

50 ecosystem attributes relate to each other), ultimately producing large transformations and

51 reorganizations of biota and ecosystem processes (Suding & Hobbs 2009; Botta *et al.* 2019). Second,

52 abrupt changes resulting from crossing thresholds may involve the change into an alternative stable

53 state of the system, making this change hardly reversible once it happens (Scheffer *et al.* 2001; Morris

54 2011; van Nes *et al.* 2016). This second facet of thresholds is associated to a particular phenomenon

55 called *catastrophic shift* (May 1976; Scheffer *et al.* 2001) in which surpassing a threshold is

56 associated with changes in the resilience of the system (its ability to absorb changes while maintaining

57 its structure and functioning, Gunderson 2000). Importantly, abrupt transformations do not necessarily

58 entail the existence of stable states, and thus these two facets of thresholds are not always connected.

59 Nevertheless, the existence of thresholds has relevant consequences for management, thus this

60 concept is commonly used in policy and management frameworks related to the threats imposed by

61 climate change (Rockström *et al.* 2009; Steffen *et al.* 2015).

62 Although thresholds were previously studied almost exclusively by mathematical models

63 (Filatova *et al.* 2016), studies conducted along spatial gradients in the last decade have provided

64 empirical evidence of environmental thresholds in arctic (Scheffer *et al.* 2012), tropical (Hirota *et al.*

65 2011; Verbesselt *et al.* 2016; Xu *et al.* 2016) and dryland (Wang *et al.* 2014; Luo *et al.* 2016; Berdugo

66 *et al.* 2017, 2020) ecosystems. Here we focus on drylands, areas where it rains less than 65% of

67 potential evapotranspiration (Middleton and Thomas 1992) that collectively account for ~41% of

68 Earth´s surface (Cherlet *et al.* 2018) and host nearly 2 billion people whose livelihood depends on the

69 services these ecosystems provide (Middleton *et al.* 2011; Cherlet *et al.* 2018). Aridity -referred

70 throughout this review as 1 – Aridity Index (the ratio between annual rainfall and potential

71 evapotranspiration)- is a major driver of ecosystem structure and functioning in drylands (Noy-Meir

72 1973; Maestre *et al.* 2016; Berdugo *et al.* 2020).

73 Recent research evaluating how drylands change along aridity gradients shows three major

74 abrupt shifts in multiple ecosystem attributes associated to three aridity thresholds (Wang *et al.* 2014;

75 Hou *et al.* 2019; Berdugo *et al.* 2020). These shifts or phases are named (Berdugo *et al.* 2020):

76 *vegetation decline phase* (aridity ~ 0.54, associated to subsequent vegetation productivity declines),

77 *soil disruption phase* (aridity ~0.7, associated to abrupt changes in soils), and *systemic breakdown*
78 *phase* (aridity ~0.82, associated to abrupt losses of vegetation; see Box.1). Each of these phases
79 characterize a set of ecosystem attributes and functions that respond abruptly to changes in aridity
80 around these aridity thresholds (Box 1). However, we still lack a causal narrative that explains the
81 connection between observed abrupt responses within and across phases through plausible and
82 contrastable hypothesis based on known processes and mechanisms. Doing so is fundamental to know
83 why dryland ecosystems overcome abrupt changes as aridity increases.

84   Understanding the specific mechanisms by which a given ecosystem responds abruptly to
85 environmental changes is a key knowledge gap with potential to improve our capacity to prevent or
86 even revert such abrupt responses (Suding *et al.* 2004; Suding & Hobbs 2009; Kreyling *et al.* 2014;
87 Villa Martín *et al.* 2015). Such understanding can also reveal the existence of intrinsic (e.g., existing
88 soil microbial and/or plant communities) or extrinsic (e.g., changes in land use intensity or in CO_2
89 atmospheric concentration) factors that may make the occurrence of thresholds context-dependent.
90 Indeed, understanding the role played by these factors is key to translate our knowledge of threshold
91 occurrence from spatial gradients into temporal changes, and may help to reconcile discrepancies
92 observed between observational studies and manipulative experiments regarding the existence of
93 thresholds (Hillebrand *et al.* 2020). Finally, unveiling these mechanisms may help to better
94 understand whether abrupt ecosystem changes associated to thresholds are likely to affect ecosystem
95 resilience leading to the emergence of alternative states and catastrophic shifts. There are two broad
96 types of mechanisms that may explain the abrupt nature of the change produced by thresholds
97 (Groffman *et al.* 2006; Andersen *et al.* 2009). The first type explains abrupt changes based on the
98 nonlinear behaviour of the ecosystem attribute that is affected (Andersen *et al.* 2009). For instance,
99 physiological thresholds in organisms' surviving or recruiting (Ficetola & Denoël 2009; Choat *et al.*
100 2018) trigger an abrupt natural response (e.g., death or dormancy). This type of mechanism does not
101 involve changes in the resilience of the ecosystem, nor catastrophic shifts (Andersen *et al.* 2009).
102 Abrupt ecosystem shifts may also result from positive feedbacks, defined as "interactions in which a
103 perturbation in one component of the system causes a change in a second and the change in the
104 second ultimately leads to an additional change in the first" (Stocker *et al.* 2013). Soils and plants, but
105 also plants and atmospheric drivers often exhibit positive feedbacks (e.g., soil erosion and vegetation
106 cover, Schlesinger *et al.* 1990; D'Odorico *et al.* 2012). Importantly, systems exhibiting positive
107 feedbacks usually (but not always, Andersen *et al.* 2009) are strong candidates for exhibiting
108 alternative stable states (Holling 1973; May 1976; Scheffer *et al.* 2001).

109   The objective of this paper is to review the plausible mechanisms associated to observed
110 aridity thresholds, as well as their interconnections, in global drylands. By doing so, we introduce a
111 set of hypotheses and a mechanistic conceptual model for the emergence of such aridity thresholds.
112 Finally, we discuss plausible context-dependent factors that may influence the occurrence of abrupt

113   changes in time, and provide recommendations for future studies. The mechanisms discussed are
114   summarized in Figure 1 and Table 1, and are dissected individually phase by phase in the following
115   sections.

MECHANISMS LINKED TO THE *VEGETATION DECLINE PHASE*

117   In the *vegetation decline phase* observed nonlinear changes in the relationship between productivity
118   and aridity suggest a mechanism of adaptation to the lack of water, or a replacement in the drivers of
119   productivity from temperature to rainfall(Figure 1). We hypothesize that the *vegetation decline phase*
120   starts when water becomes the main limiting factor for plant growth, triggering a physiological
121   mechanism that forces plants to adapt their traits and physiological mechanisms to cope with water
122   shortages at the cost of exhibiting slow and discontinuous growth. In support of this hypothesis, some
123   studies already evidenced that dry-subhumid ecosystems (dryland subsystems whose change into
124   semiarid occurs around aridity of 0.6) are less influenced by water and more by temperature than
125   semiarid systems (Nemani *et al.* 2003). Other studies showed also increasing control of soil moisture
126   on chlorophyll fluorescence after aridity values of 0.5 (Liu *et al.* 2020). Water availability is not only
127   reduced as aridity increases, but also becomes more variable and unpredictable (Le Houérou 2001).
128   Thus plants must deal with both seasonal water shortages and more frequent droughts (Schlaepfer *et*
129   *al.* 2017) forcing them to be active only when "pulses" of water become available (Noy-Meir 1973;
130   Feldman *et al.* 2018).

a. Mechanisms

132   From an evolutionary perspective, plants show concurring evolutionary adaptations in drylands that
133   allow them to tolerate water shortages (Schwinning & Ehleringer 2001; Bussotti *et al.* 2014). These
134   include the production of smaller and thicker leaves that prevent water evaporation through stomatal
135   closure in unfavourable conditions (Quiroga *et al.* 2010), ultimately reducing the costs of mechanisms
136   to endure water shortages (Mansfield & Freer-Smith 1984; Reich 2014; Nunes *et al.* 2017). These
137   adaptations either restrict the normal functioning of photosynthesis or allow its functioning at a slower
138   rate under water stress (Mansfield & Freer-Smith 1984) but allows plants to thrive under unfavourable
139   periods (Schwinning & Ehleringer 2001). Together with the shortening of growth periods for plants as
140   aridity increases, slower growth rates typical from stress tolerant species would result in a reduction
141   of both plant and ecosystem level photosynthetic activity compatible with changes observed in the
142   *vegetation decline phase*. These adaptations are achieved at the individual species level at
143   evolutionary scales. Other processes related to water scarcity adaptation at individual, population or
144   community levels may occur at shorter time scales. Those are more interesting in a scenario of climate
145   change because time scales of climate change would probably not allow for evolutionary adaptation.

146   Plants exhibit a remarkable phenotypic plasticity, which plays a fundamental role on their
147 local adaptation to climatic conditions (Richter *et al.* 2012). At the individual level, phenotypic
148 plasticity allows plants to allocate more resources on roots vs leaves as water availability decreases
149 (Zhang *et al.* 2013). It also confers them a wide spectrum of intra-specific variability in the shapes and
150 physiology of their leaves (Nicotra *et al.* 2010). Such variability, grounded in epigenetic changes at
151 individual levels (changes in the expression of genes that are not related to changes in DNA, Nicotra
152 *et al.* 2010), is important when facing sustained climatic changes (Nicotra *et al.* 2010; Bussotti *et al.*
153 2014; Balao *et al.* 2018; Wang *et al.* 2020). Similarly, at population levels, plants also exhibit
154 remarkable phenotypic plasticity achieved by local adaptation to environmental conditions in a
155 process named ecotypic differentiation (Kawecki & Ebert 2004). Such local adaptation, achieved
156 through genetic differentiation of populations of the same species, has been intensively studied in the
157 context of ongoing climate change (Juenger 2013; Barton *et al.* 2020).

158   While phenotypic plasticity will allow populations of some species to adapt locally to
159 increasing environmental constraints (although certain populations will be more vulnerable than
160 others of the same species to increasing dryness, Barton *et al.* 2020), not all species exhibit a strong
161 ability for local adaptations (Gimeno *et al.* 2009). Thus, studying phenotypic plasticity of key traits
162 related to plant recruitment or growth is key to develop management and conservation policies for
163 sites facing the *vegetation decline phase* as aridity increases. Besides, knowing whether phenotypic
164 plasticity at individual or population levels exhibits any pattern with increasing aridity around the
165 *vegetation decline phase* would be an important achievement to evaluate the potential risks of
166 surpassing this threshold in time.

167   At the community scale, drylands are paradigmatic examples exhibiting high richness, both in the
168 number of species and in the functional traits of their communities (Maestre *et al.* 2021). Such
169 richness is a key buffer against climate change because rich communities likely contain species that
170 might be able to adapt better than others to more constraining environmental conditions, enhancing
171 ecosystem resilience (i.e., the insurance hypothesis Walker *et al.* 1999; Yachi & Loreau 1999;
172 Gallagher *et al.* 2013; Mori *et al.* 2013). Thus, ensuring a high diversity (especially promoting
173 phenotypes able to tolerate water shortages) in ecosystems facing the *vegetation decline phase*, would
174 be critical to ensure a smooth transition throughout this threshold into an ecosystem more dominated
175 by water shortages than prior ones.

176   Community assembly processes (e.g., environmental filtering or plant-plant interactions) are also
177 key modulators of community turnovers across environmental gradients (Cornwell & Ackerly 2009;
178 HilleRisLambers *et al.* 2012), and may have significant relevance at both sides of the *vegetation*
179 *decline phase*. For example, positive plant-plant interactions (facilitation), which prevail in semiarid
180 environments (Soliveres *et al.* 2014, 2015), would be key to preserve those plants less adapted to

181 increasing aridity, enhancing diversity (Valiente-Banuet & Verdú 2007; Cavieres & Badano 2009;
182 Navarro-Cano *et al.* 2019). Again, elucidating the relevance of these processes would be achieved by
183 conducting studies at both sides of the aridity threshold defining the *vegetation decline phase*,
184 targeting functional trait variability and the relative importance of community assembly processes.

b. Summary of recommendations

186 We identified mainly plant physiological mechanisms in response to water scarcity as the main trigger
187 of the *vegetation decline phase*. It is important to note that the connection of these water shortage-
188 adaptation mechanisms with thresholds is currently unknown. Major uncertainties rely on how plants
189 will adapt to water scarcity in a context of rapid climate change for which individual, population and
190 community responses of local adaptation are key. Because an important proportion of non-dryland
191 areas are currently being transformed into drylands due to climate change (Prăvălie *et al.* 2019) or will
192 be in the near future (Yao *et al.* 2020) it is key to elucidate how increasing dryness will affect the
193 physiology of communities maladapted to water scarcity.

MECHANISMS LINKED TO *SOIL DISRUPTION PHASE*

195 The *soil disruption phase* is characterized by the sudden disruption of soil structure and
196 biogeochemical cycles and the replacement of forests or grasslands by shrublands at aridity values
197 ~0.7 (Figure 1). We hypothesize that these abrupt changes are the result of actioning some triggers
198 related with nutrient recycling and productivity losses with aridity increases that are amplified via
199 plant-soil feedbacks. Plant-soil feedbacks include direct and indirect interactions between soils and
200 plants affecting a myriad of ecosystem processes, including nutrient, water and carbon cycling,
201 ecosystem productivity and erosion regulation (Figure 2). Plants are the main contributor of organic
202 matter to the soil (Paul 2016), where litter is decomposed by soil biota turning it into nutrients (which
203 go back to plants, Throop & Archer 2009) and into soil organic carbon (SOC; which affects soil
204 properties and functioning Martínez-Fernández *et al.* 2021; Witzgall *et al.* 2021). Plants also regulate
205 the effect of other abiotic factors on soils by protecting them from erosion (Schlesinger *et al.* 1990)
206 and by regulating infiltration and run-off processes (Laio *et al.* 2001; D'Odorico *et al.* 2007; Amenu
207 & Kumar 2008). This also happens the other way around, with soil texture and organic matter being
208 key regulators of soil water availability for plants (Martínez-Fernández *et al.* 2021). Besides, direct
209 symbiosis exist between certain components of microbial communities (such as mycorrhiza) and
210 plants that are mutually beneficial for both (Bahram *et al.* 2020). Finally, in drylands, where the main
211 limiting factors are water and nutrients, soil is a major driver of plant-plant interactions (Ochoa-Hueso
212 *et al.* 2018; Maestre *et al.* 2021). The degree of interconnection between all these processes makes
213 that a sudden change in any of them propagates easily to the others, amplifying the changes in a
214 feedback loop. These complex interactions and feedbacks make very challenging to disentangle the
215 mechanisms underlying the *soil disruption phase*. However, we can better understand them by

216　identifying some ecosystem processes that propagate from soil to plants (or from plants to soil) and
217　that can be triggered in an abrupt manner by aridity increases.

a.　*From soils to plants*

219　*Changes in soil erosion with increases in aridity*
220　As soil water becomes more limited with aridity increases, soil erosion may increase because soil
221　aggregates are more stable when they are wet than when they are dry (Breshears *et al.* 2003; Xu *et al.*
222　2015). In parallel, it has been hypothesized that aeolian erosion would increase with respect to water-
223　driven erosion as water becomes more limiting (Ravi *et al.* 2007). This implies that there is an aridity
224　level in which aeolian erosion becomes more prevalent than water erosion, although such level is
225　currently unknown (Ravi *et al.* 2007, 2010). Importantly, the identity of erosive drivers determines the
226　spectrum of particle sizes that are eroded (Gillette *et al.* 1974; Zamani & Mahmoodabadi 2013),
227　meaning that wind erosion erodes smaller soil particles than water erosion (Stout 2007). The
228　dependence on particle size in wind erosion produces a bias towards fine particles that, with time,
229　may change soil textural properties (Li *et al.* 2009; Colazo & Buschiazzo 2015). This change in
230　erosive processes may impact other ecosystem features. For instance, fine soil particles are key for
231　soil moisture retention (Martínez-Fernández *et al.* 2021). Besides, soil texture affects directly (Bach *et*
232　*al.* 2010) and indirectly (by affecting soil carbon contents Xiaojun *et al.* 2013; Fierer 2017) both the
233　soil microbiome and the establishment of plant seedlings and plant growth (Gaines & Gaines 1994).
234　Finally, wind erosion is an important, but usually overlooked, driver of soil carbon losses in drylands
235　(Chappell *et al.* 2019).

236　Because this replacement of erosive drivers is still a hypothesis to be tested, this line of reasoning still
237　relies on assumptions such as whether net soil erosion increases with aridity, or whether bias of wind
238　erosion towards fine particles may change textural properties at large scales and, if so, which temporal
239　scales are necessary to do so.

240　*Nutrient cycles are less controlled by soil biota as aridity increases*
241　Nutrient decomposition and cycling rates are substantially modulated by water availability (and thus
242　by aridity; Delgado-Baquerizo *et al.* 2013b; Wang *et al.* 2014; Feng *et al.* 2019; Steidinger *et al.*
243　2019). Some groups of soil biota that take an active role in these processes, such as nematodes, are
244　especially sensitive to aridity increases and find a physiological limit in aridity levels around 0.7
245　(Xiong *et al.* 2019). Likewise, the abundance and diversity of soil fungi and bacteria decrease with
246　increases in aridity across global drylands (Maestre *et al.* 2015). These decreases, however, is uneven
247　across microbial groups (Delgado-Baquerizo *et al.* 2020). For example, ectomycorrhizal fungi (whose
248　relative abundance respect to other mycorrhizal microorganisms is thought to be indicative of very
249　contrasting nutrient economy typologies Phillips *et al.* 2013; Lu & Hedin 2019) exhibit abrupt decays
250　in the *soil disruption phase* (Berdugo *et al.* 2020). These findings highlight that aridity increases may

251 promote shifts in the composition of microbial communities driven by uneven physiological limits of
252 soil biota. In parallel, increasing aridity may enhance the importance of abiotic factors involved in
253 litter decomposition, such as photodegradation, that are particularly important in drylands (Austin &
254 Vivanco 2006; Throop & Archer 2009) and usually disregarded despite their clear connections with
255 aridity and plant functional types (Austin 2011). As a result, nutrient and carbon cycling processes
256 would be more dependent on abiotic factors than on biotic ones, changing their dynamics as some
257 studies are evidencing through manipulative experiments (Almagro *et al.* 2015). This line of evidence
258 is well supported by experiments, yet it has not been linked yet to abrupt responses in ecosystems.
259 Besides, the complexity of soil communities makes it very difficult to study them across large
260 climatic gradients, something that would be necessary to better link soil communities with aridity
261 thresholds in the *soil disruption phase*.

262 *Soil hydrology is affected by soil organic carbon depletion*
263 A common feature of both changes in erosion and changes in nutrient cycles is that they will diminish
264 SOC, a key regulator of soil moisture dynamics (Berdugo *et al.* 2014; Martínez-Fernández *et al.*
265 2021). In particular, soil moisture memory (ability of soils to retain water between rainfall events
266 McColl *et al.* 2017) is increased when SOC increases, as it enhances infiltration rates and prevents
267 evaporation, maintaining water in the soil for longer periods (Berdugo *et al.* 2014; Martínez-
268 Fernández *et al.* 2021). Thus, depleting SOC will likely decrease soil moisture memory. This waning
269 of soil organic carbon control on water dynamics, together with more infrequent rainfall events and
270 higher temperatures, would make the first centimetres of the soil more vulnerable to desiccation as
271 aridity increases, particularly in coarse-textured soils (Martínez-Fernández *et al.* 2021), reducing
272 topsoil water availability (Mavimbela and van Rensburg 2017). The desiccation of the first
273 centimetres of the soil would exert negative effects on soil functioning (Manzoni *et al.* 2012; García-
274 Palacios *et al.* 2016), increase vulnerability of soils to erosion (Breshears *et al.* 2003; Xu *et al.* 2015)
275 and decrease the growth and survival of plants (Feldman *et al.* 2018; Stocker *et al.* 2018).

276 We currently lack evidence regarding the relationships between soil moisture dynamics and its
277 relationship with SOC along global aridity gradients. Finding a critical SOC value necessary to
278 enhance soil moisture dynamics (as has been found for soil fertility around SOC values ~2%; Patrick
279 *et al.* 2013) may highlight SOC depletions as a key driver of abrupt changes.

280 ### b. From plants to soils

281 *Plant cover does not suffice to protect soils from erosion*
282 Plants protect efficiently soils from erosion, thus, when plant cover is reduced soils become
283 vulnerable to erosion, which further promotes reductions in plant cover (Schlesinger *et al.* 1990).
284 Although an abrupt change in plant cover in this phase is not observed (a monotic decrease as aridity
285 increases occurs), it is important to highlight that small cover reductions may trigger abrupt soil

286　losses. For instance, at cover values of less than 60% clumps of vegetation are less likely to occur by
287　chance, exposing more soil surface to erosive drivers (Abades *et al.* 2014). Certain critical plant cover
288　values have been linked with the existence of thresholds on the erodibility of soils (Mora & Lázaro
289　2013). Some studies spot this critical plant cover value to be around 30% (Elwell & Stocking 1976;
290　Francis & Thornes 1990). Importantly, plant-soil erosion feedbacks are often adopted in theoretical
291　studies (Kéfi *et al.* 2007), and are highlighted as a possible way towards desertification producing
292　alternative stable states (Schlesinger *et al.* 1990; Wendling *et al.* 2019). However, the uncertainty on
293　the existence of a threshold in plant cover related to sudden increases in erosion and the fact that
294　drastic reductions in plant cover are not evidenced through environmental gradients in the *soil*
295　*disruption phase* introduce some doubts regarding whether this mechanism might be the most relevant
296　trigger of the *soil disruption phase*.

Plant photosynthesis is insufficient to contribute to soil organic carbon

298　Soil organic carbon is directly related to total carbon assimilation which, in the end, depends on
299　photosynthesis (Patrick *et al.* 2013). Thus, decreasing photosynthesis activity inherited from the
300　*vegetation decline phase*, even if not implying a reduction in plant cover, would affect total SOC
301　pools, easily unleashing sudden changes in soil moisture dynamics if a critical SOC value is achieved
302　(as has been proposed in the previous subsection). Again, models simulating this positive effect of
303　plants on soil hydrology (although usually not simulating explicitly SOC), highlight the possibility of
304　catastrophic shifts triggered by this feedback and leading to desertification (Rietkerk *et al.* 2002,
305　2004; Kéfi *et al.* 2007).

Changes in plant communities triggered by less soil surface water availability

307　As water becomes more limiting, especially in the first centimetres of the soil, a filter that favours
308　plants able to reach deep soil water layers is created. This may unleash large and irreversible
309　community compositional shifts as aridity increases (Viglizzo *et al.* 2015). Because water in deep soil
310　layers is more stable (Noy-Meir 1973), increases in shrubs vs. grasses reported in the *soil disruption*
311　*phase* may be an adaptation to increasing inter-annual fluctuations in rainfall patterns. These
312　fluctuations increase with aridity (Le Houérou 2001; Feldman *et al.* 2018) and, at aridity levels ~0.7
313　reach a coefficient of variation of 30% (Berdugo *et al.* 2020). This coefficient of variation value has
314　been suggested as a limit for triggering vegetation instabilities (von Wehrden *et al.* 2012). Thus, a
315　strong force selecting for plants with water uptake strategies able to uncouple productivity from
316　immediate climatic conditions is suggested; this hypothesis is evidenced by a decay of the vegetation
317　sensitivity to climatic fluctuations in the *soil disruption phase* (Berdugo *et al.* 2020). Here it is worth
318　noting that shrub development in drylands is a known process occurring in several parts of the world
319　and studied in the framework of shrub encroachment (Knapp *et al.* 2008). Several feedbacks act to
320　promote shrub encroachment in drylands, including contrasting responses of grasses cf. shrubs to fire
321　regimes and grazing and increases in soil erosion and temperature (thoroughly revised in D'Odorico

322   *et al.* 2012; Archer *et al.* 2017). Some of these mechanisms might be related with aridity at least
323   indirectly (e.g., through changes in fire regimes or by increasing soil aeolian erosion). However, shrub
324   encroachment is usually studied in relation to grazing activities or land use changes (Roques *et al.*
325   2001; Eldridge *et al.* 2013) and a connection between feedbacks explaining shrub encroachment and
326   aridity is still speculative.

327   Nevertheless, it is less relevant whether this change in the plant community relates to shrub
328   encroachment than the fact that plant communities after the *soil disruption phase* seem to exhibit
329   lower leaf N content (Berdugo *et al.* 2020). This is important because community changes associate to
330   leaf traits means that litter quality would be diminished, strongly impacting nutrient cycling (Prieto *et*
331   *al.* 2019). Indeed, soil microorganisms are very sensitive to nutrient stoichiometry in the litter, and
332   need a given C:N ratio to mineralize nitrogen in the decomposition process (Manzoni *et al.* 2008).
333   Thus, decoupling of nutrient stoichiometry due to impoverishment of litter quality may lead to less
334   efficient nutrient cycling, propagating plant community changes to the soils (Prieto *et al.* 2019).
335   Impoverishment of litter quality is probably not caused by development of shrubs *per se* because, as
336   seen in several studies, shrub encroachment does not necessarily entail lower soil fertility (Maestre *et*
337   *al.* 2009). Instead, new lines of evidence point that lower litter quality may be a consequence of plants
338   root development into deeper soil layers, were nutrients are scarcer than in the first centimetres of the
339   soil (Querejeta *et al.* 2021). Examining the coordination between relevant plant traits along aridity
340   gradients may help to unveil trade-offs between nutrient uptake strategies, the photosynthetic
341   economic spectrum of leaves and plant development (Gleason *et al.* 2013), thus helping to nuance the
342   functional structural changes that accompany shrub development during the *soil disruption phase*.
343   Also important is that plant-plant interactions that vertebrate assembly rules for plant communities
344   may present higher dominance of competitive interactions (cf. facilitation) in this phase (Berdugo *et*
345   *al.* 2019), being a relevant factor transforming plant communities. Finally, changes in plant
346   community structure would probably associate with changes in soil microbial communities because
347   both are tightly connected. An example of this tight connection with key implications on nutrient
348   cycling (Terrer *et al.* 2016) is the well-known specificity of mycorrhizal and plant species (Davison *et*
349   *al.* 2020).

350   ### *c. Summary of recommendations*

351   The main gap of knowledge regarding the mechanisms underlying the *soil disruption phase* (soil
352   erosion, soil microbial community changes, soil hydrology, vegetation community changes and plant
353   cover/carbon assimilation declines) is that we do not know their relative importance or the
354   relationships among them. Future studies should be able to disentangle these relationships and find
355   which mechanism is triggered more easily by aridity increases (i.e., is more sensible to aridification),
356   which one involves a higher number of ecosystem attributes (i.e., is most prone to propagate across

357 ecosystem attributes) and which one unleashes the most abrupt responses. This can be done using
358 experimental approaches taking into account responses of soil microbial communities as a potential
359 trigger of abrupt ecosystem responses. Models should also simulate both vegetation and soil changes
360 along aridity gradients, something not done before because of the high complexity underpinning the
361 functioning of plant-soil-microbiome feedbacks. We think that models about the *soil disruption phase*
362 should explicitly incorporate erosion processes, soil biogeochemical and hydrological feedbacks
363 (including modelling water uptake at deep soil layers) and shrub-grass transitions.

364 MECHANISMS LINKED TO THE *SYSTEMIC BREAKDOWN PHASE*

365 Mechanisms linked to the *systemic breakdown phase* should explain the collapse of vegetation
366 evidenced by abrupt declines in the richness and cover of perennial plants beyond aridity levels
367 ~0.82, turning ecosystems into desert states (Figure 1). This aridity value matches those found in
368 other studies showing a drastic turnover in dryland flora (Ulrich *et al.* 2014) and a shift in leaf
369 strategies to cope with aridity stress (from stress tolerance to stress avoidance; Carvajal *et al.* 2018;
370 Berdugo *et al.* 2020). Our hypothesis is that there are physiological limits imposing drastic declines in
371 vegetation cover at this aridity level, which are also accelerated through plant-plant and plant-
372 atmospheric feedbacks. We discuss three different mechanisms that can explain vegetation responses
373 observed once this aridity threshold is crossed (Figure 3).

374 a. Plant physiological limits

375 The observed 0.82 aridity threshold is likely related to the physiological limits of plants acting on
376 survival rate, as soil water potential is below wilting point of vascular plants at this aridity level most
377 of the year (Feldman *et al.* 2018; Bassiouni *et al.* 2020). Observed losses in plant species richness also
378 suggest that there is a strong convergence of these physiological limits across species, likely driven by
379 the narrowing of the niche to a single limiting factor: water. Indeed, some studies highlight the
380 nonlinear nature of species extinction due to convergent niche limits (Trisos *et al.* 2020), which may
381 explain the abrupt loss of species observed beyond this threshold. Also, at aridity values ~0.8, the
382 precipitation inter-annual variability increases exponentially (Berdugo *et al.* 2020) and this
383 uncertainty in precipitation may be even more detrimental for plant survival than the total amount of
384 rainfall received. Yet, it should be noted that deserts are not equivalent to ecosystems with total lack
385 of vegetation (Brandt *et al.* 2020) and some plants may exhibit remarkably high wilting points (Larter
386 *et al.* 2015). Indeed, the potential mechanisms underlying plant responses observed in this phase are
387 very similar to those of the *vegetation decline phase* (plant epigenetic adaptations, plant acclimation
388 and community changes selecting for plants with very high wilting points) but should be investigated
389 on survival rates rather than on productivity or growth. Besides, some plants may be able to cope with
390 strong water shortages by escaping water stress in a dormant stage (e.g., exhibiting avoidance
391 strategies Carvajal *et al.* 2018). Such strategy has provided some examples of astonishing blooming

392   for very short periods in the Atacama Desert, the driest place on Earth (Holtum *et al.* 2021). Given
393   this plasticity of plants for local adaptation, probably the generalized species loss observed in this
394   phase cannot be explained only by mechanisms of physiological plant limits, but rather are
395   accompanied by others.

396   Importantly, even when (almost) no plant can survive at very high aridity values, some organisms are
397   able to thrive. For instance, biocrusts (communities dominated by lichens, algae, mosses and
398   cyanobacteria living on the soil surface), can be found in deserts worldwide (Belnap and Lange 2013).
399   Biocrusts have large impacts on the hydrological cycle of drylands (Chamizo *et al.* 2013; Berdugo *et*
400   *al.* 2014), can facilitate plant recruitment (Bowker 2007) and ameliorate the loss of soil functioning by
401   improving soil fertility underneath them (Maestre *et al.* 2011; Delgado-Baquerizo *et al.* 2016). Thus,
402   future research should pay particular attention to biocrusts as key organisms for preserving ecosystem
403   functioning in drylands facing the *systemic breakdown phase*.

404   ### *b. Biodiversity feedbacks*
405   Part of the plant diversity loss found in this phase can be attributed to feedbacks occurring at the
406   community level. Two mechanisms are important in this regard.

407   First, plant-plant interactions such as facilitation and competition, which shape the abundance and
408   occurrence of plant species in dryland ecosystems (McCluney *et al.* 2012; Soliveres & Maestre 2014;
409   Berdugo *et al.* 2019), are particularly relevant in the *systemic breakdown phase*. This is so because the
410   structure of interactions may be highly organized in complex networks (Saiz & Alados 2011; Saiz *et*
411   *al.* 2018), making the responses of a given plant species strongly dependent on the responses of
412   accompanying species. On one hand, the strong filtering force imposed by water scarcity may lead to
413   a niche convergence that is usually associated to increasing frequency of competitive interactions
414   between plants (the limiting similarity principle, MacArthur & Levins 1967) and this may boost
415   diversity losses due to competitive exclusion (Suding *et al.* 2003; Adler *et al.* 2010). This may occur
416   both at the community level, as suggested by increases in competition cf. facilitation as aridity
417   increases in some studies (Berdugo *et al.* 2018, 2020), and at the individual level, as suggested by
418   some experiments in which imposed water shortages increases competitive exclusion (Alba *et al.*
419   2019). On the other hand, facilitative interactions are key for survival of the less adapted plants even
420   in extreme environments (Berdugo *et al.* 2018), making plant-plant interaction networks nested on
421   key species whose loss may produce cascading extinctions (Thébault *et al.* 2007; Dunne & Williams
422   2009; Rocha *et al.* 2018). However, studies assessing plant-plant interactions in extreme environments
423   using network analysis are still rare (see Losapio *et al.*, 2019, for a review), and usually do not assess
424   the physiological limits of plants (something key in these very high aridity levels).

425 Second, plant diversity has been found to enhance ecosystem productivity and stability (Isbell *et al.*
426 2015; García-Palacios *et al.* 2018). Thus, the reductions in diversity found in the *systemic breakdown*
427 *phase* may induce instabilities at the ecosystem level that accelerate the collapse of vegetation.
428 Although this biodiversity-ecosystem functioning (BEF) relationship is relevant in all phases, it is key
429 to investigate whether there is a critical diversity point in which functioning decays beyond critical
430 values at this aridity level. These limits are still a conjecture because BEF relationships have never
431 been linked to abrupt ecosystem shifts. However, some studies have uncovered an increase in the
432 importance of BEF relationships as aridity increases (García-Palacios *et al.* 2018), pointing in this
433 direction.

434 ### c. *Plant-atmosphere feedbacks*

435 Previous studies have suggested that a strong feedback between plants and atmospheric processes may
436 promote the formation of desert-like conditions (Texier *et al.* 1997, 2000). These feedbacks build on
437 the rationale that plants have an important effect on climate at regional scales, usually increasing
438 rainfall. Thus, reductions of plant cover, especially if abrupt, induce changes in the atmosphere that
439 may prevent rainfall formation. This effect can be direct and indirect. Among direct effects,
440 vegetation contributes to water recycling at local scales through evapotranspiration, increasing air
441 humidity and enhancing rainfall (Savenije 1995; Trenberth 1999). This mechanism is particularly
442 important in continental semi-deserts (Eltahir & Bras 1996; Yosef *et al.* 2018; Branch & Wulfmeyer
443 2019). Among indirect effects, this modulation may occur via vegetation-induced increases in land
444 roughness (Sud *et al.* 1988) and soil water infiltration and availability (Shukla & Mintz 1982; Alfieri
445 *et al.* 2008) and reductions in dust emissions (Ravi *et al.* 2011) and albedo (indeed, exponential
446 increases in albedo are found in this aridity level Berdugo *et al.* 2020). Climate models that take into
447 account these factors have shown that decreasing vegetation ultimately leads to a reduction of
448 precipitation at regional scales (Xue 2006), and some models have shown that these feedbacks may be
449 strong enough as to create alternative states associated with desertification (Wang & Eltahir 2000a,
450 2000b; Zeng & Neelin 2000). All these feedbacks point to a strong control of vegetation on
451 atmosphere, thus suggesting that a transformation towards deserts is achieved rapidly at very high
452 aridity levels and, most importantly, spanning large spatial scales (Wang & Eltahir 2000b; Yoshioka
453 *et al.* 2005). On the other hand, preserving ecosystems at the brink of *systemic breakdown phase*, or
454 even increasing their biomass through afforestation, may counteract aridity increases (Yosef *et al.*
455 2018; Branch & Wulfmeyer 2019). Yet, the use of afforestation in deserts has a number of caveats,
456 including risk of introducing invading species, risk of displacing non-tree natural ecosystems and the
457 need of expensive and continuous management (e.g., irrigation) to be sustainable (Keller *et al.* 2014).

458   *d.   Summary of recommendations*

459   In the *systemic breakdown phase*, major knowledge gaps exist regarding the interaction between the

460   convergence of plant niche limits for survival and the structure of plant-plant interactions, which

461   should be studied together. Also, limits on the BEF relationships should be investigated to assess

462   whether they can explain part of the abrupt vegetation collapse observed. Vegetation-atmosphere

463   feedbacks are also key, and the research done in this regard still lacks global assessments focused on

464   this aridity threshold. Afforestation efforts carried out/ongoing in deserts provide a promising starting

465   point for studying them. Finally, we still do not know how other organisms that colonize extreme

466   environments, such as biocrusts, may respond to this threshold. This may provide a promising

467   restoration tool that is currently being thoroughly investigated at the theoretical (Conde-Pueyo *et al.*

468   2020) and practical (Antoninka *et al.* 2020) level, but that lacks sufficient background from field and

469   experimental approaches under very high aridity conditions.

470   **GENERAL INTERCONNECTIONS AND CONSIDERATIONS**

471   Although investigating the mechanisms underlying each threshold separately serves as a first

472   approximation, more attention should be paid on how the phases are consecutively affected. For

473   instance, the reduction in the photosynthetic activity of plants at the *vegetation decline phase* may be

474   determinant on initializing smooth cover reductions or lower carbon inputs into the soil, unleashing

475   responses in the *soil disruption phase* if vegetation cover decreases below a given point or SOC

476   contents are insufficient to regulate soil moisture. Thus, if the *vegetation decline phase* is smoothed or

477   stabilized, the *soil disruption phase* may never happen even if aridity exceeds the 0.7 threshold. The

478   opposite is also true: lack of viable populations of drought-adapted plants may unleash more drastic

479   changes than depicted through spatial gradients in the *vegetation decline phase*, and derive in

480   modifications of the aridity levels at which the next phase occurs. As another example, erosive

481   feedbacks discussed in the *soil disruption phase* have been highlighted as a manifestation of

482   desertification (Schlesinger *et al.* 1990; D'Odorico *et al.* 2013). However, the fact that vegetation is

483   not reduced to zero in the *soil disruption phase*, might be related with the existence of shrubs (and

484   some trees, Brandt *et al.* 2020), able to survive soil depletions by reaching water from deep soil

485   layers. In other words, the presence of shrubs and trees can prevent desertification. If so, it might well

486   be that ecosystems surpassing the *soil disruption phase* at aridity levels of 0.7 undergo massive

487   vegetation mortality and show the responses expected for the *systemic breakdown phase* if vegetation

488   with access to deep water sources is not present.

489   At the same time, and while we revised the mechanisms that we think are most relevant in each phase

490   based on existing theoretical frameworks, some of them can be important in all phases or may play a

491   previously unnoticed role on unleashing abrupt shifts or on modulating their occurrence. The main

492   knowledge gap on these mechanisms is that we know virtually nothing about their connection with

493   thresholds. For example, biodiversity can mitigate negative effects of aridity on ecosystem
494   functioning in drylands (Maestre *et al.* 2012; Valencia *et al.* 2015), although its ability to counteract
495   abrupt shifts has not been investigated. Likewise, soil-plant relationships are fundamental because the
496   performance of dryland plants depends on both available nutrients (very limited in drylands Delgado-
497   Baquerizo *et al.* 2013a) and soil physical properties (Gaines & Gaines 1994). Finally, legacy effects
498   (impacts of a species on abiotic or biotic features of ecosystems that persist for a long time after the
499   species has been extirpated or ceased activity Cuddington 2011) provide ecosystems with a certain
500   memory and inertia that is a relevant factor influencing changes through time for all the aridity
501   thresholds reviewed here. Indeed, soils may sustain effects of plants up to 50 years after their
502   extinction (Facelli & Brock 2000), supporting carbon and its role on driving erosion and water
503   redistribution and affecting directly dynamical rates of biogeochemical processes (e.g., soil respiration
504   Hawkes *et al.* 2017; Dacal *et al.* 2019). Both the soil carbon content (Delgado-Baquerizo *et al.* 2017b)
505   and soil microbial communities (Delgado-Baquerizo *et al.* 2017a) have been related to past climatic
506   conditions extending soil legacy effects for millennia. Plants also show dependence on previous
507   community assemblages which determine in part their resistance to climate changes (Cuddington
508   2011), even at evolutionary scales (Valiente-Banuet *et al.* 2006). Plus, plant productivity strongly
509   depends on the productivity of previous years (Seddon *et al.* 2016) and past droughts may affect
510   ecosystem structure and functioning for years (Kannenberg *et al.* 2020). Understanding the strength
511   and drivers of these legacy effects is key for assessing the potential risk of experiencing abrupt
512   ecosystem shifts in all phases.

513   Similarly, human influence may confound the effects of aridity increases. For instance, land use
514   intensification may increase erosion rates and SOC depletion in drylands (Bestelmeyer *et al.* 2015).
515   Land use changes may thus be particularly relevant for the *soil disruption phase*, where vulnerability
516   to erosion has been highlighted as a possible trigger of the abrupt changes. Another example is
517   grazing, which has been shown to produce changes in plant community composition and ecosystem
518   functioning very similar to those expected by aridity increases (Milchunas *et al.* 1988; Quiroga *et al.*
519   2010; Gaitán *et al.* 2017) and thus may confound the effects of aridity increases in all phases.
520   Moreover, the importance of grazing on triggering shrub encroachment (Roques *et al.* 2001) together
521   with its capacity to modulate how plants influence soils (Eldridge *et al.* 2013) makes it very relevant
522   for the *soil disruption phase* (i.e., grazed areas might experience the *soil disruption phase* at lower
523   aridity levels). Finally, some studies have related increases in atmospheric CO_2 with increasing water
524   use efficiency for photosynthesis in drylands (Lu *et al.* 2016a). This "CO_2 fertilization effect" is
525   relevant at all aridity levels because it produces a mismatch between aridity increases and how plants
526   experience such aridity (Lu *et al.* 2016b). Notably, CO_2 fertilization may offset responses expected for
527   the *vegetation decline phase* and the *systemic breakdown phase*, given the prevalence of physiological
528   mechanisms of plants in these phases. On the other hand, CO_2 fertilization may not suffice to relief

529 the effect of increasing dryness conditions (Bussotti *et al.* 2014; Brookshire and Weaver 2015;
530 Peñuelas *et al.* 2017; He *et al.* 2019). In addition, it has been recently shown how increasing
531 evaporative demand by plants is linked to temperature regulation in extremely hot environments
532 (Aparecido *et al.* 2020). Therefore, it is likely that climate warming itself will exacerbate water use in
533 plants. Indeed, whether there is a critical aridity value where CO_2 fertilization effects on
534 photosynthesis lessen respect to water shortages is yet to be elucidated.

535 Other confounding site-specific factors can also affect ecosystem responses to aridity at local and
536 regional scales influencing the incidence of thresholds. For example, soil parental material determines
537 soil physical structure, and affects processes such as erosion or soil hydrology at local scales by
538 determining soil textural properties and the resistance of mineral materials to erosion (Jorgensen &
539 Gardner 1987). Likewise, soil depth influences soil moisture dynamics and the depth in which water
540 can be storage for plant use (Fu *et al.* 2011). Topographic variables such as slope also modulate soil
541 erosion (Xu *et al.* 2015; Zhao *et al.* 2015), with steeper slopes being more vulnerable to erosion (Zhao
542 *et al.* 2015) and having a lower water retention capacity. Moreover, slope orientation induce important
543 meso- and microclimatic heterogeneity in drylands, with slopes facing the equator being drier than
544 those facing the opposite direction (Kutiel & Lavee 1999). Despite all these effects are especially
545 relevant in the *soil disruption phase* (where soil plays a predominant role), they are important in all
546 phases because they are related to ecosystem hydrology and, thus, to how the system experiences
547 existing aridity. Indeed, it should be noted that in the most extreme environments (facing *systemic*
548 *breakdown phase*), meso- and microclimatic conditions (existence of rocks, orientation of slopes, and
549 deep water reservoirs) turn of very high relevance, providing key refuges for plants (e.g., oasis),
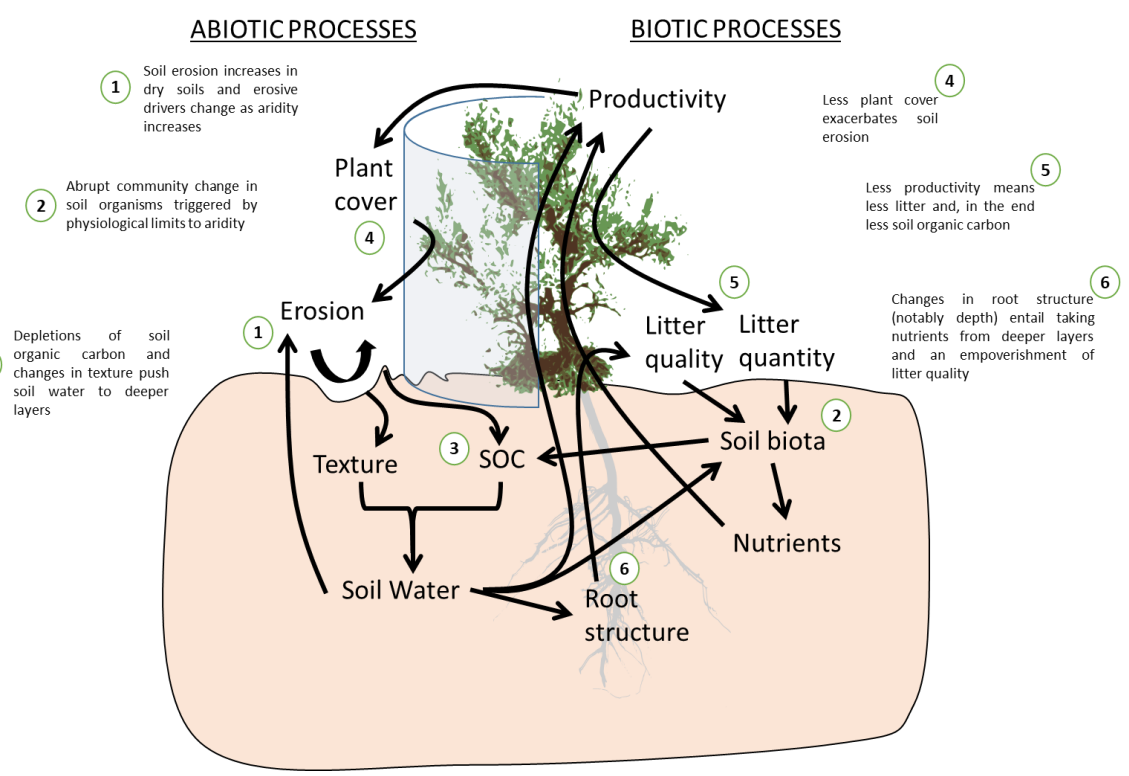550 biocrusts and their associated fauna (Wierzchos *et al.* 2015).

551 ## CONCLUSIONS

552 Here, we reviewed the potential mechanisms behind observed aridity thresholds in global drylands
553 (Figure 1), discuss knowledge gaps that preclude a complete understanding of how these thresholds
554 emerge (Table 1), shed light on the most important confounding factors that may make the occurrence
555 of aridity thresholds context-dependent and provide specific recommendation for future studies (Table
556 2). Given the current forecasts concerning the pace of global warming, addressing the knowledge gaps
557 identified in our review may contribute to save the capacity of drylands to provide essential ecosystem
558 services to millions of people in a more arid and unpredictable world.

559

FIGURES AND TABLES
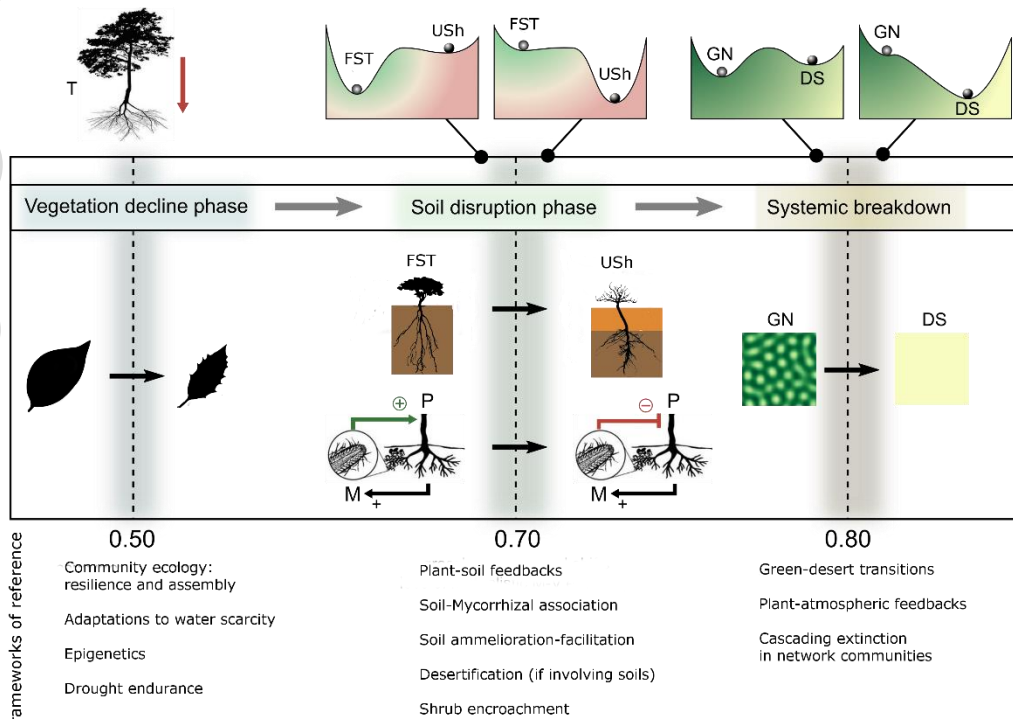
Figure 1. Conceptual diagram on the main shifts found for aridity thresholds and the major mechanisms that may play a role for each. In the vegetation decline phase several concurrent changes related with physiological adaptation to water stress seem to take place close to 0.5 aridity. In the soil disruption phase a change from fertile stress-tolerant communities (FST) into unfertile shrublands (USh) is paralleled with a weakening of plant-soil interactions pointing to plant-soil feedbacks as key drivers of the changes depicted. In the systemic breakdown phase a transitions towards plant-devoid states is probably related with physiological limits of plants but previously discussed in relationship with plant-plant and plant-atmosphere feedbacks. Each transition and their associated concurrent abrupt changes (summarized in Box 1) are thus linked with particular major mechanisms which are related with frameworks of reference in existing literature to be used in this review (at bottom). Whenever the frameworks of reference discuss the existence of alternative states of the ecosystem, we pictured them using a landscape diagram depicted in the upper part. In those the filled marbles are stable states (FST/USh or GN/DS) whereas open circles indicate unstable values separating two different   alternatives.

ABIOTIC PROCESSES

1. Soil erosion increases in dry soils and erosive drivers change as aridity increases

2. Abrupt community change in soil organisms triggered by physiological limits to aridity

3. Depletions of soil organic carbon and changes in texture push soil water to deeper layers

BIOTIC PROCESSES

4. Less plant cover exacerbates soil erosion

5. Less productivity means less litter and, in the end less soil organic carbon

6. Changes in root structure (notably depth) entail taking nutrients from deeper layers and an empoverishment of litter quality

Plant cover · Productivity · Erosion · Texture · SOC · Soil Water · Root structure · Litter quality · Litter quantity · Soil biota · Nutrients

576

Figure 2. Summary of plant-soil feedbacks between different attributes of dryland ecosystems and the processes that they involve. Inset numbers (1-6) exemplify six different mechanisms of initializing abrupt changes when aridity increases in the soil disruption phase. These numbers follow the same order in which they are described in the text. On the left, processes described are mostly abiotic related with soil erosion and soil hydrology. On the right, processes are mostly biotic related to nutrient cycling and changes in plant attributes.
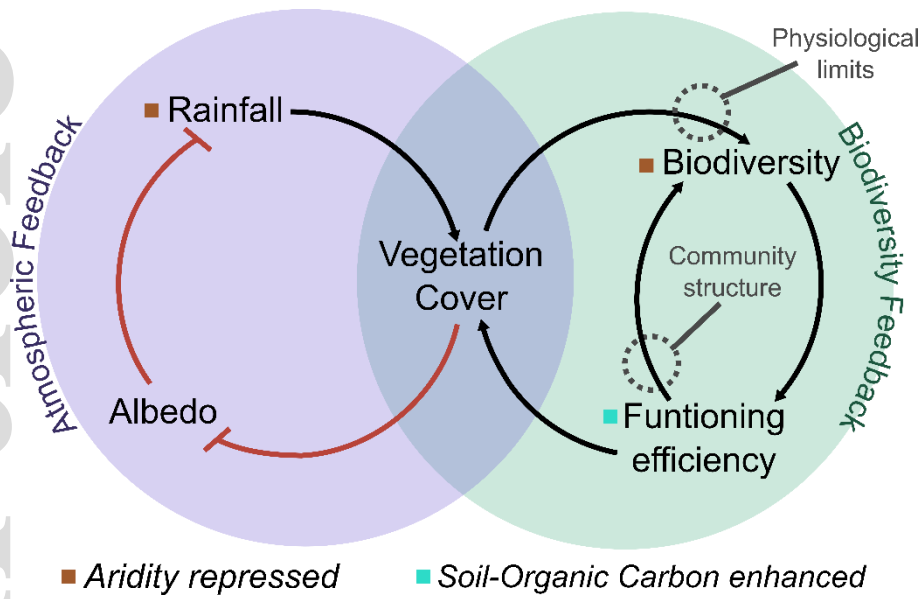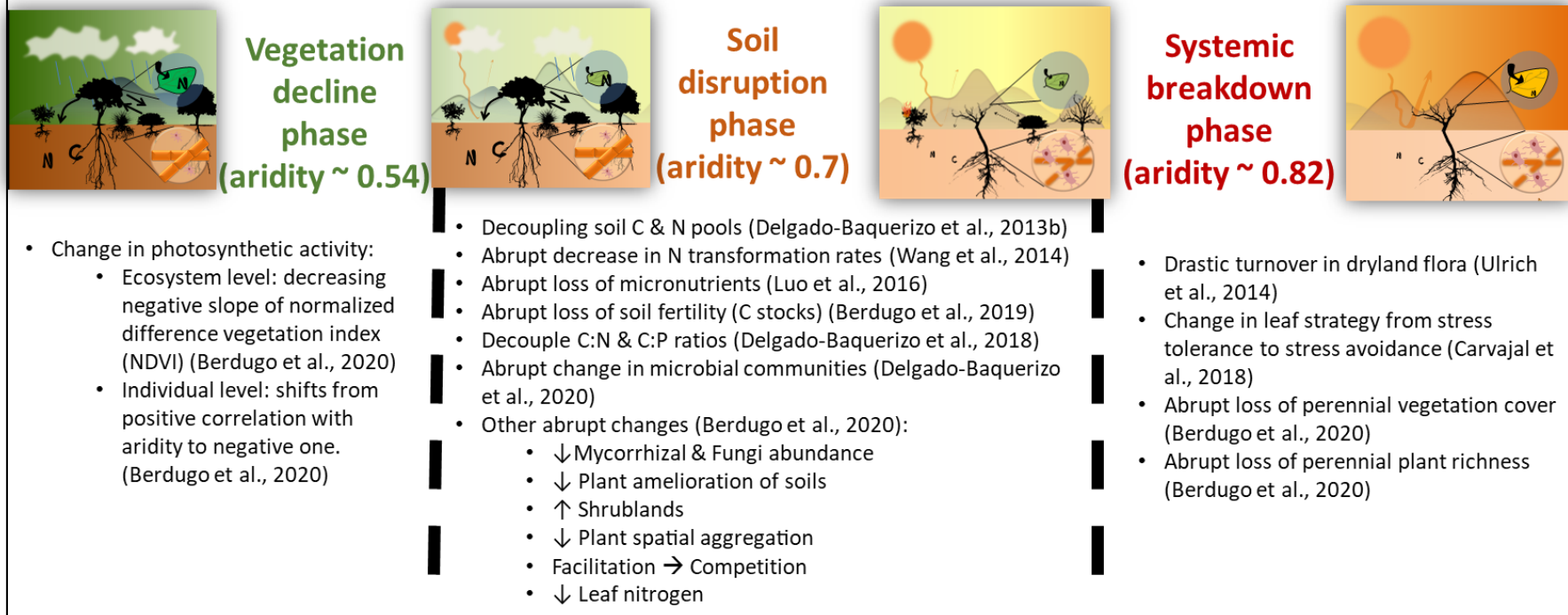
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585 **Figure 3.** Feedbacks hypothetically involved in the *systemic breakdown phase*. These feedbacks are
586 grouped in two potential pathways involving biodiversity-ecosystem functioning (green) and
587 atmospheric (purple) feedbacks. Red and black arrows indicate negative (e.g., increases in aridity
588 induce reduction of rainfall) and positive (e.g., increase in rainfall increases the vegetation cover)
589 correlations between processes. The relationship between aridity and biodiversity is mediated by
590 physiological properties from the organisms (i.e. stress avoidance strategies).

Box 1. Dryland aridity thresholds. Pieces of a puzzle to be assembled.

Concurring evidence from independent studies highlights the existence of systemic (i.e., attaining several ecosystem compartments), sequential (as aridity increases) and global ecosystem thresholds associated with increases in aridity across drylands worldwide. According to aridity forecasts, up to 22% of emerged lands may cross one or several of these aridity thresholds by the end of this century.

These changes initialize with a nonlinear decrease of photosynthetic activity at aridity values of 0.54, followed by different and abrupt changes in the soil system and abrupt increases in shrublands at aridity 0.7. Finally, an abrupt decline of plant cover matches abrupt declines of richness and changes in leaf strategies to stress avoidant at aridity values of 0.82.

Aridity thresholds spotted generally match previous divisions of drylands separating dry-subhumid from semiarid (aridity ~ 0.5) and semiarid from arid (aridity ~ 0.8). Indeed, soil disruption phase matches with the idea that transitioning from semiarid to arid systems involves a lack of suitable soil fertility to perform agriculture. Similarly, definition of semiarid areas as those in which vegetation indices are linearly correlated with aridity coincides with the vegetation decline phase. What aridity thresholds add to previous classification frameworks is matching the exact value of aridity with key ecosystem attributes that are affected by aridity in abrupt manners. This provides us the pieces of a puzzle to be assembled through mechanistic knowledge to understand abrupt changes in drylands.

Vegetation decline phase (aridity ~ 0.54)

Soil disruption phase (aridity ~ 0.7)

Systemic breakdown phase (aridity ~ 0.82)

- Change in photosynthetic activity:
  - Ecosystem level: decreasing negative slope of normalized difference vegetation index (NDVI) (Berdugo et al., 2020)
  - Individual level: shifts from positive correlation with aridity to negative one. (Berdugo et al., 2020)

- Decoupling soil C & N pools (Delgado-Baquerizo et al., 2013b)
- Abrupt decrease in N transformation rates (Wang et al., 2014)
- Abrupt loss of micronutrients (Luo et al., 2016)
- Abrupt loss of soil fertility (C stocks) (Berdugo et al., 2019)
- Decouple C:N & C:P ratios (Delgado-Baquerizo et al., 2018)
- Abrupt change in microbial communities (Delgado-Baquerizo et al., 2020)
- Other abrupt changes (Berdugo et al., 2020):
  - ↓Mycorrhizal & Fungi abundance
  - ↓ Plant amelioration of soils
  - ↑ Shrublands
  - ↓ Plant spatial aggregation
  - Facilitation → Competition
  - ↓ Leaf nitrogen

- Drastic turnover in dryland flora (Ulrich et al., 2014)
- Change in leaf strategy from stress tolerance to stress avoidance (Carvajal et al., 2018)
- Abrupt loss of perennial vegetation cover (Berdugo et al., 2020)
- Abrupt loss of perennial plant richness (Berdugo et al., 2020)

Table 1. Summary of the mechanisms, triggers and key process related to the three aridity thresholds discussed in this review. The possibility of exhibiting alternative states with a given mechanism, and thus catastrophic shifts, is documented based on whether the mechanism is a feedback or not and on whether previous studies have investigated theoretically with this possibility. Finally, plausible secondary factors identified per mechanism that may affect the incidence of thresholds and that are site-specific are highlighted in the last column.

Threshold	Mechanism	Triggers	Key process	Alternative states emerging	Secondary factors
Vegetation decline phase	Photosynthetic physiological	- Water becomes limiting in photosynthesis	Plant drought adaptation	Unlikely	- CO_2 fertilization - Vegetation legacy
Soil disruption phase	Plant-Soil feedbacks: FROM SOILS TO PLANTS	- Wind-water erosion importance	Soil physical erosion	Likely	- Topography - Lithology - Soil legacy - Land use changes
		- Shift in belowground community	Nutrient cycling	Unexplored	
		- Lessen of soil moisture dynamics due to insufficient SOC	Soil moisture dynamics	Likely	
	Plant-Soil feedbacks: FROM PLANTS TO SOILS	- Reduction in carbon assimilation implying SOC shortages	Photosynthesis	Unexplored	- Vegetation legacy - CO_2 fertilization - Grazing
		- Reduction in vegetation cover implying more erosion	Photosynthesis	Likely	
		- Change in aboveground community	Root morphology-soil hydrology	Unexplored	
Systemic breakdown phase	Physiological collapse	- Soil water potential below wilting point	Plant physiological limits	Unlikely	- Vegetation adaptation. - Biocrusts
	BEF feedback	- Cascading collapse through interaction networks	Plant-plant interactions BEF	Unexplored	- Vegetation legacy

		- Species richness below a critical value			
	Plant-atmosphere	- Reductions in plant cover	Rainfall formation	Likely	-Albedo/topology of soil surface

Table 2. Key knowledge gaps and recommendations for future research in relation with the three aridity thresholds discussed in this review.

Threshold	Mechanisms affected	Knowledge gap	Reccommendation
Vegetation decline phase	Plant physiology	- How communities of plants not adapted to water scarcity may respond to increasing dryness	Investigate interactions between CO_2 increases and drying on photosynthesis Investigate migration processes and turnover change of the community in response to increasing dryness
Soil disruption phase	Plant-Soil feedbacks	- Disentangle relative importance of the key drivers of the soil disruption, aiming at identifying the most sensible, the most propagating and the most deep mechanisms - Are there abrupt responses between: soil organic carbon and soil moisture dynamics; vegetation cover and erosion or aridity and relative importance of erosive drivers?	Manipulative experiments on litter decomposition, soil microbial communities and plant community changes to assess its impact on the soil carbon cycling Models explicitly simulating soil, with special emphasis on soil loss (erosion), plant-soil feedbacks (biogeochemical pathway) and plant morphological changes (encroachment) and their relationships Investigate global patterns of these features aiming at finding nonlinear relationships with aridity.
Systemic breakdown phase	Physiological limits + Biodiversity feedbacks	- Do niche convergence scale through plant-plant interaction networks to drive massive extinction of species?	Investigating physiological niche convergence limits in conjunction with plant-plant interaction matrix
	Biodiversity feedbacks	- Is there a limit on diversity loss unleashing instabilities in ecosystem functioning a relevant driver of abrupt vegetation collapse?	Investigating the nonlinear nature of BEF at the brink of systemic breakdown phase, especially aiming at measuring productivity and temporal stability as ecosystem functions.
	Plant-Atmospheric feedbacks	- Are vegetation-atmosphere feedbacks globally important?	Investigate rainfall patterns at regional scales across the globe in relation with afforestation practices.
	Physiological limits	- How do biocrusts respond to systemic breakdown phase?	Asses the response of biocrust across aridity gradients spanning he systemic breakdown phase at global scales.

All	Legacy effects	- What is the relative importance of vegetation and soil legacy effects for dampening abrupt responses in time?	Field experiments and manipulative experiments of climate change aiming at crossing these thresholds should be summarized globally to assess legacy effects across different environments
			Models simulating transition phases on different initialization conditions

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