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Editorial

The importance of dispersal and species establishment in vegetation dynamics and resilience

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Abstract

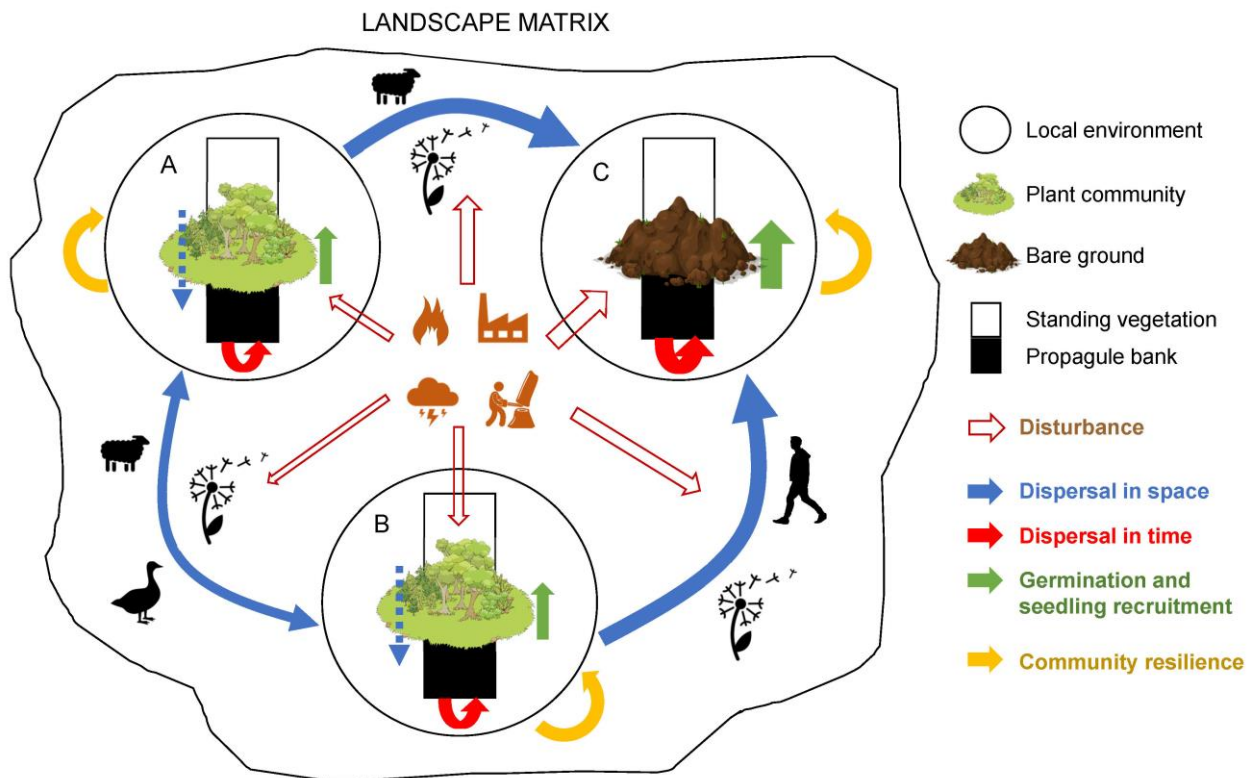
Plant regeneration comprises establishment from seed and other propagules dispersed within and between communities, and from the local propagule bank. Regeneration plays a critical role in vegetation dynamics by underpinning local and landscape-scale processes linked to biodiversity patterns and community resilience to natural and anthropogenic disturbances. The aim of this Special Feature is to discuss the role of regeneration processes related to dispersal and establishment for understanding vegetation dynamics and resilience in disturbance-driven landscapes. The ability of a community to recover from a disturbance based on internal (propagule banks) and external sources (dispersal in space) is key in driving the non-equilibrium dynamics that are now accepted as a central concept for vegetation science. The most important internal source of plant community recruitment is the local persistent vegetative and generative propagule bank, in most cases located in the soil. The main external source of recovery is spatial plant dispersal via metacommunity dynamics. When studying environmental filtering and species assembly processes, plant dispersal is often oversimplified as a general propagule rain, but we need stronger conceptual and empirical links between dispersal and vegetation dynamics. Moreover, the regeneration of plant communities strongly depends on post-dispersal processes affecting propagules and seedlings. Here, we present evidence on the contribution of different regeneration processes to vegetation dynamics, demonstrating how vegetation science can be enhanced by more explicit consideration of dispersal, propagule banks and establishment, and the drivers of variation in these processes.

Keywords: community assembly; disturbance; dormancy; germination; metacommunity dynamics; plant traits; resilience; seed bank; seed dispersal; species establishment; succession; vegetation dynamics

39 **Introduction**

40
 41 One of the challenges for biodiversity research in the next decades will be to understand the
 42 complexity of ecosystem change and resilience at different spatial scales (Díaz et al., 2020). To
 43 address the response of ecosystems to global change, investigating the dynamics of plant
 44 communities that structure natural and semi-natural vegetation (and provide habitat for other trophic
 45 levels) will be a pivotal task. However, we are still far from understanding the balance of processes
 46 that regulate plant community dynamics at local and landscape scales. One major research gap
 47 concerns the role that dispersal and establishment play in the resilience of communities subjected to
 48 natural and anthropogenic disturbances.

49
 50 The stability or the so-called “steady state” of a plant community is sustained by two major
 51 processes: resistance and resilience. While resistance is the ability of the community to withstand
 52 disturbance and retain community composition and functions by persistence; resilience (also called
 53 “recovery”, Oliver et al. 2015) is the ability of the community to recover its pre-disturbance
 54 composition and functions after the changes induced by disturbance (Enright et al., 2014).
 55 Resilience is supported by several regeneration processes including dispersal in space, dispersal in
 56 time, and germination and seedling recruitment in favourable microsites and vegetation gaps. These
 57 processes of plant dispersal and recruitment are summarised in Figure 1.
 58



59
 60 **Fig 1.** Links between disturbance and regeneration processes in relation to community resilience.
 61 Disturbance is a crucial driver of community composition. While low intensity/frequency
 62 disturbance (e.g. weather extremes and minor spontaneous fires) facilitates species coexistence by
 63 creating suitable microsites for germination and establishment (communities A and B), high
 64 intensity/frequency disturbances (mostly anthropogenic) may completely destroy vegetation
 65 (community C). In such extreme cases, vegetation recovery by germination and seedling
 66 recruitment relies exclusively on dispersal in space and/or local propagule banks (dispersal in time).
 67 Humans may also disrupt or supplement dispersal in space, for example, between communities B
 68 and C, where a wild vector (bird) is lost, but humans themselves disperse propagules. These are all
 69 key processes determining community resilience and vegetation dynamics at local and landscape
 70 scales.

71

72 Species dispersal, germination, seedling recruitment and thus, species assembly in plant communi-
73 ties can be understood in terms of a complex filtering scheme including both stochastic processes
74 and trait-based habitat and biotic filtering (Kraft and Ackerley, 2014; Török *et al.*, 2018a). Colonisa-
75 tion of new habitats during primary succession or species migration between similar habitat patches
76 embedded in the landscape matrix is achieved by dispersal in space (Fig. 1). Dispersal in space oc-
77 curs either by abiotic media (most frequently wind and/or water) or by biotic vectors. In heavily al-
78 tered landscapes with fragmented natural habitats, propagule limitation is not only caused by re-
79 source limitation; frequent anthropogenic disturbances also alter the type and availability of disper-
80 sal vectors (Fig. 1), ultimately changing the size and composition of the propagule bank. At the lo-
81 cal scale, dispersal in space can also be considered as a diaspore flow from the standing vegetation
82 into the propagule banks. The effectiveness of dispersal in space depends heavily on a set of plant
83 traits (Vittoz and Egler, 2007; Tamme *et al.*, 2014), many of them concerning the diaspore (e.g.,
84 size, shape and other morphological features, von der Lippe and Kowarik, 2012; Sonkoly *et al.*,
85 2017). The fate of diaspores settling in a specific community (either from local community rain or
86 over longer distances) is strongly influenced by the composition and structure of the resident vege-
87 tation, propagule predation and the availability of regeneration niches for germination and estab-
88 lishment (Larson and Funk, 2016). The dispersing propagules are then trapped in the litter or incor-
89 porated into the soil propagule bank and either regenerate into new individuals or are preserved via
90 dormancy over unsuitable periods by retaining their viability for a long time (dispersal in time via
91 persistent seed bank).

92

93 As a result of internal vegetation dynamics driven by natural or anthropogenic disturbances, the
94 vegetation canopy periodically opens, and several regeneration niches become available for species
95 recruitment (Grubb, 1977; Fenner and Thompson, 2005). These niches are not filled by random sto-
96 chastic processes; vegetation regeneration is thus supported by dispersal in time and space, and spe-
97 cies' abilities to establish new plants (through seed germination or vegetative reproduction). Be-
98 sides the nutrient reserves stored in the propagule, the success of germination and seedling estab-
99 lishment also strongly depends on environmental factors such as soil properties including water and
100 nutrient availability, soil compaction and structure, and light availability at the soil surface (Baskin
101 and Baskin, 1998). All these processes regulate the spatio-temporal dynamics of plant communities
102 at the local and landscape scales (Bullock *et al.*, 2002).

103

104 This Special Feature of the *Journal of Vegetation Science* was initiated at the thematic session on
105 "Dispersal and plant reproduction in disturbance-driven vegetation dynamics" of the 61st Annual
106 Symposium of the International Association for Vegetation Science (Bozeman, Montana, USA, 22–
107 27 July 2018). The session had a relatively broad thematical and geographical coverage and
108 demonstrated interest in the processes of propagule dispersal and plant establishment to understand
109 vegetation dynamics and resilience. The collection of contributions that we present here deal with
110 many different topics with a focus on regeneration and its role in responses to disturbance and/or
111 resilience of natural and semi-natural vegetation. We have organized the papers into three major
112 regeneration processes (dispersal in space and time, germination and recruitment) to contextualize
113 their importance for understanding the response of plant communities to natural and anthropogenic
114 disturbance (Fig. 1). After reviewing the contribution of this Special Feature to state of the art in the
115 topic, we outline a series of conclusions and research gaps that should be addressed in the future.

116

117 **Dispersal in space**

118

119 It has long been acknowledged that dispersal is a critical process determining the floristic composi-
120 tion (Zobel, 1997) and responses to perturbations (Noy-Meir and van der Maarel, 1987) of vegeta-
121 tion. But this awareness is only slowly translating into research which enhances our understanding
122 of the precise ways by which dispersal governs vegetation dynamics. One way of dealing with dis-
123 persal is to consider it as a stochastic process (HillerisLambers *et al.*, 2012; Ulrich *et al.*, 2016), of-

124 ten in terms of “random draw” from the species in the community or in the wider landscape. This
125 may be convenient, but in line with the concept of environmental filters governing which species
126 the local abiotic and biotic environments allow to establish and persist (Weiher and Keddy, 1995), it
127 is important to consider dispersal as a filter by which species’ dispersal traits, landscape structure,
128 and environmental conditions determine which species, and in what abundance, are in the seed rain
129 for an area of vegetation and so which can contribute to regeneration (Bullock and Pufal, 2020, this
130 issue).

131
132 The importance of dispersal in space is most obvious in primary succession, where there is little or
133 no local vegetation and, initially, all propagules must come from some distance away. This process
134 shows how both the landscape composition and species’ diaspore traits drive colonization process-
135 es. It is often concluded that species that can disperse far are the initial colonizers (Makoto and Wil-
136 son, 2019). But Korablev et al. (2020, this issue), working on the Tolbachinsky Dol volcanic Plat-
137 eau in Russia, showed that the most effective dispersal syndrome depends on local conditions and
138 probably an interaction with environmental filters. In the most exposed sites, species having large
139 seeds without appendages predominated, maybe because they can tumble-disperse and good seed
140 reserves allow establishment in inhospitable conditions. Species having seeds with appendages fa-
141 cilitating wind dispersal were likely unable to settle in this terrain but predominated where there
142 was woody debris, which presumably trapped their seeds. These processes are not specific to prima-
143 ry succession. Large anthropogenic disturbances can be seen as analogous, and the interaction be-
144 tween dispersal processes and local conditions are key in determining resilience to these (Bullock
145 and Pufal, 2020, this issue).

146
147 Resilience to these large “pulse” perturbations can be contrasted to the effect of “press” perturba-
148 tions, the most insidious of which is anthropogenic climate change. As the local environment be-
149 comes climatically intolerable for species or assemblages, they must “move, adapt or die” (Corlett
150 and Westcott, 2013). Moving involves dispersal, but, again, many studies of species and vegetation
151 responses to climate change do not consider dispersal, or treat it very simplistically, often con-
152 trasting ubiquitous with no dispersal (Holloway et al., 2016). Peyre et al. (2020, this issue) show
153 how important it is to consider dispersal ability in terms of actual distances different species can
154 disperse. By doing so, they derive more meaningful predictions of how the plant communities of the
155 unique páramo sky islands in Ecuador might be affected by climate change. Treelines are, in some
156 ways, the canaries of climate change; their shifting upwards illustrates how rapidly communities
157 might track climate change (Smith et al., 2009). But, even here, environmental tolerances (to bio-
158 climatic conditions) have predominated in assessing treeline dynamics (Holtmeier and Broll, 2020).
159 Anadon-Rosell et al. (2020, this issue) study a treeline-forming species in the Pyrenees and show
160 the importance of seed production and seed dispersal in limiting the advance of the treeline. Inter-
161 estingly, there was no clear effect of elevation on establishment dynamics, suggesting that dispersal
162 processes are the main constraint on this treeline advancing under climate change.

163
164 If we are to understand better the role of dispersal in vegetation dynamics and resilience, we also
165 need to characterize species differences in dispersal processes and abilities. A long-standing method
166 has been to assign species to different dispersal syndromes such as by wind, animals, water or un-
167 aided (autochory). These syndromes do capture species differences in dispersal distance and can be
168 used to explain vegetation patterns (Jara-Guerrero et al., 2020, this issue, Korablev et al., 2020, this
169 issue). But there is a great deal of interspecific variation in dispersal abilities within syndromes, due
170 to the exact vector and its behaviour, plant characteristics such as height, and seed traits such as
171 mass (Tamme et al., 2014; Bullock et al., 2017). Using information on these properties derived from
172 global databases, it is possible to calculate a maximum dispersal distance for a species (Tamme et
173 al., 2014), which Peyre et al. (2020, this issue) use to good effect. But many species have multiple
174 dispersal vectors and even exhibit different dispersal modes (Bullock et al., 2006). Improving in-
175 formation on dispersal requires a better understanding of how these different processes play out to
176 determine the Total Dispersal Kernel for a species, taking account of the fact that different propa-

177 gules may be dispersed by different means, and some propagules may be dispersed by a sequence of
178 vectors (Rogers et al., 2019). To this must be added the under-explored role of humans, their vehi-
179 cles and livestock in dispersing propagules (Bullock and Pufal, 2020, this issue).

180
181 It is common to consider dispersal separately from other processes governing the establishment, but
182 these processes are intrinsically linked, as Korablev et al. (2020, this issue) and Anadon-Rosell
183 (2020, this issue) showed. Jara-Guerrero et al. (2020, this issue) demonstrated a functional link be-
184 tween dispersal syndrome, establishment and seed banking in Ecuadorian dry forest. Animal-
185 dispersed species are dispersed in the rainy season and likely germinate immediately, whereas wind-
186 dispersed species do so in the dry season and become incorporated into the seed bank. This meant
187 that the seed rain for animal-dispersed species more resembled the standing vegetation, whereas that
188 of wind-dispersed species more resembled the seed bank. Such findings support the idea that dis-
189 persal syndromes are linked to other life-history traits, and may mean we can derive plant functional
190 groups that reflect how dispersal and establishment are linked (Aslan et al., 2019). Such a consoli-
191 dation would allow us to link dispersal and environmental filters explicitly in assessing the controls
192 on vegetation dynamics.

193 194 **Dispersal in time**

195
196 Propagule banks (including seeds and buds) are one of the key components of community regenera-
197 tion and resilience, improving the stability of communities against future disturbances and degrada-
198 tion. They are considered as a successional memory of past communities and indicators of past dis-
199 turbances and vegetation changes, and they can also predict future changes or dispersal processes.
200 Propagule banks contribute to the local maintenance of species richness by dispersal in time. In
201 most communities, however, a high dissimilarity is apparent between standing vegetation and
202 seed/propagule banks; at a certain period of time several species are present in the propagule bank
203 but missing from aboveground vegetation and vice versa (Sletvold and Rydgren, 2007; Maren and
204 Vandvik, 2009; Plue and Cousins, 2013).

205
206 The importance of propagule banks is considered to be stronger in communities i) characterized by
207 a high proportion of short-lived species (Peco et al., 1998), ii) representing the early stages of vege-
208 tation development during secondary succession (Török et al., 2009; Kalamees et al., 2011) or iii) in
209 environments with high levels/frequencies of disturbance and/or stress (so-called temporarily un-
210 predictable habitats, Grime, 1979). So far, most research on propagule banks has focused on de-
211 scribing the seed bank composition (usually seeds, rather than other propagules), density and diver-
212 sity, and also its similarity to the standing vegetation (Frieswyk and Zedler, 2006; Hopfensperger,
213 2007; Bossuyt and Honnay, 2008). The role of propagule banks in the temporal dynamics and resil-
214 ience of vegetation has become an important topic more recently, especially in the light of predicted
215 vegetation change scenarios induced by climate change (Kiss et al., 2018; Perkins et al., 2019).

216
217 The composition and density of soil propagule banks is regulated by complex processes, which are
218 influenced by the interaction of dispersal in space and local propagule production, and the composi-
219 tion of the resident vegetation (Parker et al. 1989). It is also still debated whether the propagule
220 bank drives the composition of the vegetation or the composition of the vegetation drives that of
221 seed banks. As pointed out by Brown and Cahill (2020, this issue), species establishment in vegeta-
222 tion gaps promotes a distinct seed bank composition that differs from both the standing vegetation
223 as well as from seed banks where standing vegetation is kept intact. They also argue that gap crea-
224 tion-induced changes in species regeneration and seed banks are more important drivers of species
225 richness and beta-diversity than compositional changes in standing vegetation.

226
227 Propagule bank composition is also regulated by the abiotic and biotic processes occurring at the
228 soil surface and in deeper soil layers. Not only the established vegetation, but the accumulated litter
229 at the soil surface can strongly influence species composition and the regeneration potential of the

230 soil propagule bank. Litter can act as a trap for propagules, explaining the high quantities of propa-
231 gules and large numbers of species that can accumulate in the litter (Ruprecht and Szabó 2012). At
232 the same time, in some ecosystems litter can act as a propagule source for regeneration. Lipoma et
233 al. (2020, this issue) found that the litter layer and juvenile banks, but not the soil seed banks, can
234 act as sources for regeneration in Neotropical forests. A novel finding of this study is that even the
235 seeds of different species can compete with each other in the soil – while Fenesi et al. (2020, this
236 issue) argue that competition of species occurring at high densities in seed banks may suppress the
237 germination of subordinate ones regardless of their taxonomic relatedness. These effects are more
238 pronounced if moisture availability is limited, i.e. under conditions of drought stress.
239

240 Small-scale to large-scale disturbances created by natural causes (e.g., ecosystem engineer animals,
241 Godó et al., 2018) and/or by habitat management can alter the composition, density and diversity of
242 soil propagule banks in the medium- and long-term. At the local scale, Arruda et al. (2020, this is-
243 sue) found that topsoil disturbances reshape seed interactions with ground-foraging animals in a di-
244 verse grassland; ground-foraging animals strongly influenced seed availability and the arrival of
245 seeds into regeneration safe sites. Indeed, the influence of landscape-scale factors on local vegeta-
246 tion diversity and propagule banks has recently become a hot topic of research (e.g., Török and
247 Helm, 2017, and citation therein). While Lipoma et al. (2020, this issue) found that land-use intensi-
248 fication decreased the role of biodiversity reservoirs (seed and bud-banks) in resilience processes of
249 the resident vegetation; Kapás et al. (2020, this issue) showed that grazing livestock play a key role
250 in facilitating both spatial and temporal dispersal in fragmented grasslands. Functional connectivity
251 provided by grazing management also increases the possibility for species establishment from the
252 propagule bank and the establishment of dispersed propagules from the surrounding landscape.
253

254 The practical importance of propagule banks arises with the need for conservation management and
255 restoration of particular habitat types (Török et al., 2018b). As discussed above, the propagule bank
256 can act as a reservoir of past vegetation, thus it may support the restoration of some habitat types
257 (e.g., in wet hay meadows; Valkó et al., 2011; Metsoja et al., 2014), but can also have a rather lim-
258 ited contribution to the regeneration processes (e.g., grass-dominated moorlands, Mitchell et al.,
259 2008; or dry grasslands, Kiss et al., 2016). Propagule banks can also hamper restoration activities
260 by providing a source of weeds in former temperate cropland areas (Török et al., 2012). They can
261 also form the reservoirs of seeds for the regeneration of restored species in Mediterranean agroeco-
262 systems (Jiménez-Alfaro et al. 2020). Evidence therefore suggests that the study of propagule banks
263 needs to consider the context-dependence for each vegetation type and disturbance process.
264

265 **Germination and recruitment**

266

267 Propagule production and spatio-temporal dispersal will determine the relative abundance of
268 species in the propagule bank. At this point, community dynamics in response to disturbance events
269 are mainly affected by the subsequent fate of the propagules (Larson and Funk, 2016), especially
270 the rate and timing of germination and the establishment success of seedlings (Fig. 1).
271

272 Disturbance can either hamper or promote the recruitment, depending on the exact conditions
273 during and after the disturbance event; thus, there may be considerable differences between the
274 effects of disturbance on seed germination and plant establishment (Stampfli and Zeiter, 2020, this
275 issue). As many species in temperate regions and/or higher altitudes have seasonal dormancy, the
276 timing of disturbance is also of major importance with respect to its effects on vegetation dynamics
277 (Pakeman and Small, 2005; Stampfli and Zeiter, 2008). Stampfli and Zeiter (2020, this issue) tested
278 how seed availability and the timing of disturbance, in this case, serious drought events, determine
279 plant diversity in a semi-natural grassland. They found that spring and late-summer droughts had
280 different effects on seedling recruitment, confirming the importance of disturbance timing, and the
281 need to include this factor in consideration of vegetation dynamics.
282

283 The disturbance regime and how the species in the community react to it can also affect community
284 invasibility. Disturbances can create open microsites in the vegetation that may be occupied by
285 adventive species (Gross et al., 2005). Disturbances such as grazing, mowing or fire may result in
286 the elimination of litter and the perturbation of the soil surface, which may facilitate the germination
287 of invasive plants. Sonkoly et al. (2020, this issue) studied how soil burial depth and litter cover
288 affect the germination of invasive species and whether differences between species' response can be
289 explained by seed size. Their results showed that there are considerable differences in species'
290 responses to being buried by soil or litter, highlighting the need to study further how disturbance
291 events that perturb soil and litter layers shape species' establishment and vegetation dynamics.

292
293 Forest regeneration after land abandonment is also a matter of how ontogenetic shifts in different
294 species are influenced by the changing environmental conditions. Trindade et al. (2020, this issue)
295 studied the functional composition of different ontogenetic stages in regenerating forests along a
296 disturbance and water availability gradient and found that the functional structure of the forest was
297 mostly influenced by water availability. These results also highlight that examining different
298 ontogenetic stages offers additional insights into disturbance-driven vegetation dynamics. During
299 the shift between different ontogenetic stages, the significance of each filter can change
300 considerably; thus, inferring the importance of different filters in vegetation dynamics from
301 studying only the adult individuals might be misleading (Jiménez-Alfaro et al. 2016). As the
302 environmental niche can vary across ontogenetic stages, it is essential to gather information on
303 different ontogenetic stages if we are to have effective models of vegetation dynamics and assembly
304 (Larson and Funk, 2016). Giving more consideration to the regeneration niche could also shed light
305 on alternative recruitment strategies (such as establishing epiphytically on tree fern trunks, Daws
306 and Burns, 2020, this issue), which may have previously unrecognized implications for vegetation
307 dynamics and how disturbances modulate it. Vegetation zonation is also traditionally explained
308 mostly in terms of the adaptations and tolerance of adult plants, although such patterns can also
309 depend on the species regeneration niche. Using the natural zonation of coastal dune habitats as a
310 study system, Del Vecchio et al. (2020, this issue) show how the seed germination niche explains
311 species distributions across disturbance and environmental filters, which may be considerably
312 different from adult plant niches.

313
314 Similarly, vegetation changes due to climate change could not be properly modelled without
315 considering the traits involved in the regeneration niche of species (Jiménez-Alfaro et al., 2016).
316 Under ongoing climate change, the effect of disturbances on vegetation will greatly depend on the
317 ability of its constituent species to germinate and establish under the altered environmental
318 conditions (Svenning and Sandel, 2013). When considering disturbance-driven vegetation
319 dynamics, we need to focus better on the regeneration niche if we are to forecast or even understand
320 vegetation changes. Even if the adult plants are able to tolerate the altered conditions, vegetation
321 regeneration after disturbances can be hampered if the changed climatic conditions of the habitat do
322 not meet the local species' regeneration niche anymore. Under these circumstances, a plant
323 community cannot persist in the long run even if the adult plants can survive the altered conditions,
324 because the community is not able to regenerate after severe disturbance and to return to its
325 previous state.

326
327 We highlight the need to distinguish between the adult niche and the regeneration niche to
328 understand better how the abiotic filter works (Del Vecchio et al., 2020, this issue, Löhmus et al.,
329 2020, this issue). The difference between the adult niche and the regeneration niche (Grubb, 1977)
330 determines whether under certain environmental conditions, a species is capable of generative
331 reproduction or only of surviving and possibly of vegetative reproduction. Thus, if we only consider
332 the adult niche of species, we cannot properly assess the resilience of a community and how it
333 would react to disturbance events. When considering disturbance-driven community dynamics, we
334 therefore need to focus on regeneration of seeds and buds to forecast or even understand vegetation
335 changes.

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Conclusions and research gaps

We conclude that the processes of propagule dispersal and plant establishment play a decisive role in the resilience of plant communities. These processes should not be considered as random or stochastic, although they are frequently considered as such in vegetation science. Disturbance dynamics emphasize the influence of multiple environmental factors on the regeneration process, but we are a long way from understanding the links between disturbance-related drivers and the different aspects of plant regeneration. We identified four research gaps which would be advantageous to address in the future:

(i) Future research should be directed to understanding the relationships between disturbance and the availability of regeneration niches in space and time. Research in this Special Feature clearly indicated that gap creation induces changes in regeneration via the establishment of propagule bank species or dispersal in space that can be more important in species assembly and community change than the composition of the existing vegetation. Despite the regeneration niche being a long-standing concept in vegetation ecology, its role in vegetation dynamics is considered much less than the traits and environmental tolerances of adult plants.

(ii) There is a need to understand how species traits for dispersal, propagule banks and establishment are linked, and processes of dispersal and establishment should be included in the classic filter concept for species assembly. To understand spatial and temporal vegetation dynamics, the importance of seed/propagule traits, not only adult plant traits, should be considered (e.g. a parent plant may have multiple seeds which vary in their traits).

(iii) The influence of spatial processes including the effects of landscape-scale habitat composition or configuration on local diversity is much less considered in vegetation science than the effects of local factors including the resident vegetation composition or abiotic habitat properties. Meta-community concepts need to be considered more centrally in vegetation science to address crucial areas such as biodiversity loss and the effect of global change on ecosystems.

(iv) Last but not least, human impacts need to be considered as a fundamental process in vegetation science, including human-mediated dispersal, landscape degradation, connectivity loss, changed species pools, and altered types and frequency of disturbance. These and other anthropogenic drivers alter interspecific relationships and species assembly processes both in space and time. To reverse negative human impacts through restoration, we will need to understand in detail the influence of disturbance on the diversity of past, current and future plant communities.

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