

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

1 | INTRODUCTION

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

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

Species dispersal, germination, seedling recruitment and thus, species assembly in plant communities can be understood in terms of a complex filtering scheme including both stochastic processes and trait-based habitat and biotic filtering (Kraft and Ackerley, 2014; Török *et al.*, 2018a). Colonisation of new habitats during primary succession or species migration between similar habitat patches embedded in the landscape matrix is achieved by dispersal in space (Figure 1). Dispersal in space occurs either by abiotic media (most frequently wind and/or water) or by biotic vectors. In heavily altered landscapes with fragmented natural habitats, propagule limitation is not only caused by resource limitation; frequent anthropogenic disturbances also alter the type and availability of dispersal vectors (Figure 1), ultimately changing the size and composition of the

propagule bank. At the local scale, dispersal in space can also be considered as a diaspore flow from the standing vegetation into the propagule banks. The effectiveness of dispersal in space depends heavily on a set of plant traits (Vittoz and Egler, 2007; Tamme *et al.*, 2014), many of them concerning the diaspore (e.g. size, shape and other morphological features; von der Lippe and Kowarik, 2012; Sonkoly *et al.*, 2017). The fate of diaspores settling in a specific community (either from local community rain or over longer distances) is strongly influenced by the composition and structure of the resident vegetation, propagule predation and the availability of regeneration niches for germination and establishment (Larson and Funk, 2016). The dispersing propagules are then trapped in the litter or incorporated into the soil propagule bank and either regenerate into new individuals or are preserved via dormancy over unsuitable periods by retaining their viability for a long time (dispersal in time via persistent seed bank).

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

This Special Feature of the *Journal of Vegetation Science* was initiated at the thematic session on “Dispersal and plant reproduction in disturbance-driven vegetation dynamics” of the 61st Annual Symposium of the International Association for Vegetation Science (Bozeman, Montana, USA, 22–27 July 2018). The session had a relatively broad thematic and geographical coverage and demonstrated interest in the processes of propagule dispersal and plant

establishment to understand vegetation dynamics and resilience. The collection of contributions that we present here deal with many different topics with a focus on regeneration and its role in responses to disturbance and/or resilience of natural and semi-natural vegetation. We have organized the papers into three major regeneration processes (dispersal in space and time, germination and recruitment) to contextualize their importance for understanding the response of plant communities to natural and anthropogenic disturbance (Figure 1). After reviewing the contribution of this Special Feature to state of the art in the topic, we outline a series of conclusions and research gaps that should be addressed in the future.

2 | DISPERSAL IN SPACE

It has long been acknowledged that dispersal is a critical process determining the floristic composition (Zobel, 1997) and responses to perturbations (Noy-Meir and van der Maarel, 1987) of vegetation. But this awareness is only slowly translating into research which enhances our understanding of the precise ways by which dispersal governs vegetation dynamics. One way of dealing with dispersal is to consider it as a stochastic process (HillerisLambers et al., 2012; Ulrich et al., 2016), often in terms of “random draw” from the species in the community or in the wider landscape. This may be convenient, but in line with the concept of environmental filters governing which species the local abiotic and biotic environments allow to establish and persist (Weiher and Keddy, 1995), it is important to consider dispersal as a filter by which species’ dispersal traits, landscape structure, and environmental conditions determine which species, and in what abundance, are in the seed rain for an area of vegetation and so which can contribute to regeneration (Bullock and Pufal, 2020, this issue).

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

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

If we are to understand better the role of dispersal in vegetation dynamics and resilience, we also need to characterize species differences in dispersal processes and abilities. A long-standing method has been to assign species to different dispersal syndromes such as by wind, animals, water or unaided (autochory). These syndromes do capture species differences in dispersal distance and can be used to explain vegetation patterns (Jara-Guerrero et al., 2020, this issue; Korablev et al., 2020, this issue). But there is a great deal of interspecific variation in dispersal abilities within syndromes, due to the exact vector and its behaviour, plant characteristics such as height, and seed traits such as mass (Tamme et al., 2014; Bullock et al., 2017). Using information on these properties derived from global databases, it is possible to calculate a maximum dispersal distance for a species (Tamme et al., 2014), which Peyre et al. (2020, this issue) use to good effect. But many species have multiple dispersal vectors and even exhibit different dispersal modes (Bullock et al., 2006). Improving information on dispersal requires a better understanding of how these different processes play out to determine the Total Dispersal Kernel for a species, taking account of the fact that different propagules may be dispersed by different means, and some propagules may be dispersed by a sequence of vectors (Rogers et al., 2019). To this must be added the under-explored role of humans, their vehicles and livestock in dispersing propagules (Bullock and Pufal, 2020, this issue).

It is common to consider dispersal separately from other processes governing the establishment, but these processes are intrinsically linked, as Korablev et al. (2020, this issue) and Anadon-Rosell et al., (2020, this issue) showed. Jara-Guerrero et al. (2020, this issue) demonstrated a functional link between dispersal syndrome,

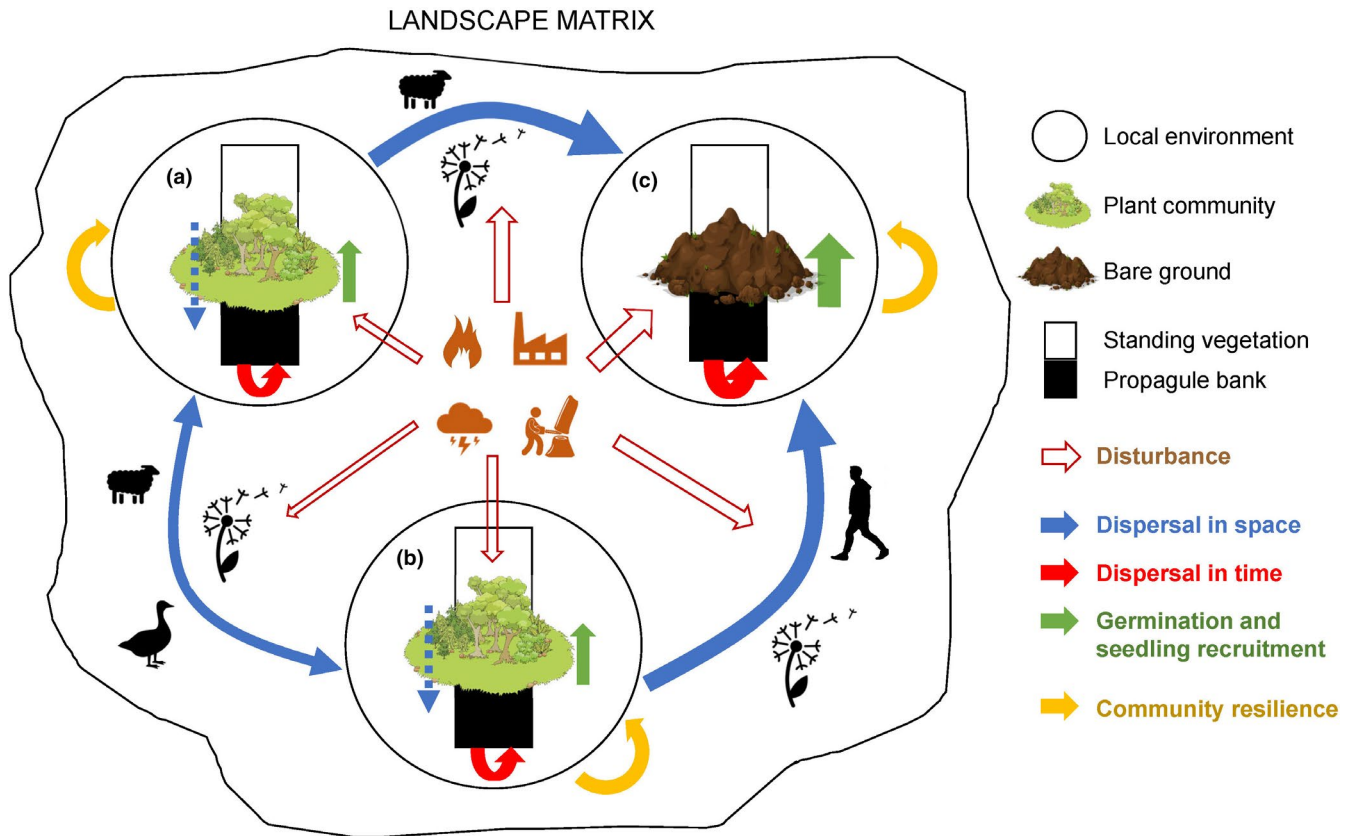


FIGURE 1 Links between disturbance and regeneration processes in relation to community resilience. Disturbance is a crucial driver of community composition. While low intensity/frequency disturbance (e.g. weather extremes and minor spontaneous fires) facilitates species coexistence by creating suitable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

establishment and seed banking in Ecuadorian dry forest. Animal-dispersed species are dispersed in the rainy season and likely germinate immediately, whereas wind-dispersed species do so in the dry season and become incorporated into the seed bank. This meant that the seed rain for animal-dispersed species more resembled the standing vegetation, whereas that of wind-dispersed species more resembled the seed bank. Such findings support the idea that dispersal syndromes are linked to other life-history traits, and may mean we can derive plant functional groups that reflect how dispersal and establishment are linked (Aslan et al., 2019). Such a consolidation would allow us to link dispersal and environmental filters explicitly in assessing the controls on vegetation dynamics.

3 | DISPERSAL IN TIME

Propagule banks (including seeds and buds) are one of the key components of community regeneration and resilience, improving the stability of communities against future disturbances and degradation. They are considered as a successional memory of past

communities and indicators of past disturbances and vegetation changes, and they can also predict future changes or dispersal processes. Propagule banks contribute to the local maintenance of species richness by dispersal in time. In most communities, however, a high dissimilarity is apparent between standing vegetation and seed/propagule banks; at a certain period of time several species are present in the propagule bank but missing from above-ground vegetation and vice versa (Sletvold and Rydgren, 2007; Maren and Vandvik, 2009; Plue and Cousins, 2013).

The importance of propagule banks is considered to be stronger in communities: (a) characterized by a high proportion of short-lived species (Peco et al., 1998); (b) representing the early stages of vegetation development during secondary succession (Török et al., 2009; Kalamees et al., 2011); or (c) in environments with high levels/frequencies of disturbance and/or stress (so-called temporarily unpredictable habitats, Grime, 1979). So far, most research on propagule banks has focused on describing the seed bank composition (usually seeds, rather than other propagules), density and diversity, and also its similarity to the standing vegetation (Frieswyk and Zedler, 2006; Hopfensperger, 2007; Bossuyt and Honnay, 2008). The role of

propagule banks in the temporal dynamics and resilience of vegetation has become an important topic more recently, especially in the light of predicted vegetation change scenarios induced by climate change (Kiss et al., 2018; Perkins et al., 2019).

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

Propagule bank composition is also regulated by the abiotic and biotic processes occurring at the soil surface and in deeper soil layers. Not only the established vegetation, but the accumulated litter at the soil surface can strongly influence species composition and the regeneration potential of the soil propagule bank. Litter can act as a trap for propagules, explaining the high quantities of propagules and large numbers of species that can accumulate in the litter (Ruprecht and Szabó, 2012). At the same time, in some ecosystems litter can act as a propagule source for regeneration. Lipoma et al. (2020, this issue) found that the litter layer and juvenile banks, but not the soil seed banks, can act as sources for regeneration in Neotropical forests. A novel finding of this study is that even the seeds of different species can compete with each other in the soil – while Fenesi et al. (2020, this issue) argue that competition of species occurring at high densities in seed banks may suppress the germination of subordinate ones regardless of their taxonomic relatedness. These effects are more pronounced if moisture availability is limited, i.e., under conditions of drought stress.

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

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

4 | GERMINATION AND RECRUITMENT

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

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

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

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

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

We highlight the need to distinguish between the adult niche and the regeneration niche to understand better how the abiotic filter works (Del Vecchio et al., 2020, this issue; Löhmus et al., 2020, this issue). The difference between the adult niche and the regeneration niche (Grubb, 1977) determines whether under certain environmental conditions, a species is capable of generative reproduction or only of surviving and possibly of vegetative

reproduction. Thus, if we only consider the adult niche of species, we cannot properly assess the resilience of a community and how it would react to disturbance events. When considering disturbance-driven community dynamics, we therefore need to focus on regeneration of seeds and buds to forecast or even understand vegetation changes.

5 | 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 it would be advantageous to address in the future:


1. 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.
2. 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).
3. 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. Metacommunity 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.
4. 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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