Dormancy in metacommunities

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Keywords: metacommunity, dormancy, dispersal, coexistence, community monopolization

Date: 15 February 2019

ABSTRACT

Although metacommunity ecology has improved our understanding of how dispersal affects community structure and dynamics across spatial scales, it has yet to adequately account for dormancy. Dormancy is a reversible state of reduced metabolic activity that enables temporal dispersal within the metacommunity. Dormancy is also a metacommunity-level process because it can covary with spatial dispersal and affect diversity across spatial scales. We develop a framework to integrate dispersal and dormancy, focusing on the covariation they exhibit, to predict how dormancy modifies the importance of species interactions, dispersal, and historical contingencies in metacommunities. We examine case studies of microcrustaceans in ephemeral ponds, where dormancy is integral to metacommunity dynamics. We analyze traits of bromeliad-dwelling invertebrates and identify constraints on dispersal and dormancy strategies. Using simulations, we demonstrate that dormancy can alter classic metacommunity patterns of diversity in ways that depend on dispersal–dormancy covariation and spatiotemporal environmental variability. We propose that dormancy may also facilitate evolution-mediated priority effects if locally adapted seed banks prevent colonization by more dispersal-limited species. We present theoretically and empirically testable predictions for other possible ecological and evolutionary implications of dormancy in metacommunities, some of which may fundamentally alter our understanding of metacommunity ecology.

INTRODUCTION

Metacommunity ecology provides a framework for understanding how processes on multiple spatial scales influence the assembly, structure, and dynamics of communities (Leibold et al. 2004; Holyoak et al. 2005; Leibold and Chase 2018). At the local scale, niche selection (due to abiotic constraints and species interactions) and demographic stochasticity regulate community structure (Chesson 2000*a*; Adler et al. 2007; Gravel et al. 2011; Vellend 2016). At the regional scale, spatial heterogeneity and dispersal control the feedbacks that arise among communities, while the diversity of species and their degree of niche differentiation reflect the biogeographical history of the regional species pool (Mittelbach and Schemske 2015; Vellend 2016). Thus far, the primary focus of metacommunity ecology has been on dispersal in relation to local processes, such as niche selection (e.g., "species sorting" and "mass effects" models, Cadotte 2006; Grainger and Gilbert 2016; Soininen 2016), stochasticity (e.g., "neutral" models, Hubbell 2001), or competitive hierarchies (e.g., "patch dynamics" models, Tilman 1994). However, the maturation of metacommunity ecology has demonstrated the need to move beyond idealized models like these and instead focus on a broader metacommunity state space defined by continuous gradients of dispersal, niche selection, stochasticity, and historical biogeography (Vellend 2016; Brown et al. 2017; Leibold and Chase 2018). There is also a growing need to incorporate additional ecological factors to explain discrepancies between theoretical predictions and patterns found in nature.

While metacommunity ecology has overwhelmingly focused on spatial dispersal, many species can also engage in dormancy, a reversible state of reduced metabolic activity that allows individuals to disperse through time via storage in a 'seed bank' of long-lived, inactive propagules (De Stasio 1990; Hairston and Kearns 2002). Dormancy is of particular relevance for metacommunity ecology because (1) it can buffer against temporarily harsh environments that could lead to local extinctions (i.e., dormancy weakens the strength of local niche selection) (Lennon and Jones 2011); (2) it can covary with dispersal (Buoro and Carlson 2014); and (3) it has implications for the eco-evolutionary dynamics that influence species distributions across space and time (De Meester et al. 2016). For example, spatial and temporal patterns of diversity in metacommunities, such as colonization–extinction dynamics in a landscape, are typically explained on the basis of spatial dispersal and niche selection in response to environmental variability (e.g., disturbance and recolonization). However, similar patterns may not only be influenced by dormancy (Mahaut et al. 2018), but may fundamentally depend on it (Box 1).

Despite its potential importance for local- and regional-scale processes, dormancy has yet to be adequately incorporated into metacommunity ecology (Leibold and Norberg 2004; Holt et al. 2005; Alexander et al. 2012). Here, we explore the role of dormancy in metacommunities from both ecological and evolutionary perspectives. We first review the evolutionary ecology of dispersal and dormancy as life-history strategies for coping with variable environments and emphasize that these traits are not necessarily independent (Buoro and Carlson 2014). We then consider the ecological and evolutionary implications of dormancy for community assembly, metacommunity dynamics, and species distributions in metacommunities. We examine case studies where dormancy underlies metacommunity dynamics, we create a simulation model showing that dormancy affects diversity across spatial scales, and we analyze the dispersal and dormancy strategies of a large collection of taxa to show how metacommunity ecologists might incorporate dormancy into their research. We conclude with future directions to further integrate dormancy into metacommunity ecology.

THE EVOLUTIONARY ECOLOGY OF DISPERSAL AND DORMANCY

Dispersal is the net movement of organisms away from their natal habitat. It minimizes the risk of local extinction, reduces kin competition, accommodates foraging strategies, and allows populations to track environmental conditions across the landscape (for recent reviews, see Ronce 2007; Cheptou et al. 2017; Cote et al. 2017). Dispersal also promotes species coexistence at the regional scale if it increases intraspecific competition relative to interspecific competition (Amarasekare 2003). For example, competition–colonization trade-offs allow inferior resource competitors to coexist in the metacommunity if they are better at colonizing recently disturbed habitats (Tilman 1994). Dispersal–mediated coexistence can be further enhanced by spatial heterogeneity. Spatial heterogeneity allows different species to be favored in different patches of the metacommunity, a crucial element of the spatial storage effect (Chesson 2000*b*; Shoemaker and Melbourne 2016). Spatial heterogeneity also provides the environmental context that determines whether dispersal is limiting, sufficient, or too high relative to the strength of local niche selection, which regulates the degree to which species distributions can be explained by environmental variation alone (Leibold and Chase 2018). Although it offers many benefits, dispersal is costly; it requires time, energy, and risk, which suggests possible trade-offs with other life-history traits (Bonte et al. 2012; Stevens et al. 2012), such as dormancy.

Dormancy is a reversible state of reduced metabolic activity that has independently evolved many times across the tree of life (Guppy and Withers 1999; Evans and Dennehy 2005; Lennon and Jones 2011; Rafferty and Reina 2012). We focus on forms of dormancy that result in the production of metabolically inactive propagules that accumulate into a ‘seed bank’. The seed bank buffers against harsh environmental conditions and may contribute to the long-term maintenance of taxonomic, phylogenetic, and functional diversity (Warner and Chesson 1985; Hairston and Kearns 2002; Lennon and Jones 2011). If the environment favors different species at different times, dormancy can promote species coexistence via the temporal storage effect (Warner and Chesson 1985), such that species partition temporal niches due to the preservation of overlapping generations in the seed bank (Chesson 2000*a*). Dormancy may also affect the relative strength of deterministic versus stochastic eco-evolutionary processes by altering population sizes (Ellstrand and Elam 1993; Orrock and Watling 2010; Gilbert and Levine 2017; Shoemaker and Lennon 2018). In unpredictable environments, a fraction of the population could remain dormant even when environmental conditions are favorable (i.e., bet hedging; Evans and Dennehy 2005; Childs et al. 2010; Starrfelt and Kokko 2012). As with dispersal, dormancy has costs, including delayed reproduction, losses due to burial (Hairston et al. 1995) or predation (Janzen 1971; Horst and Venable 2018), and the energetic costs of producing and maintaining dormant life stages (Finkelstein et al. 2008; Lennon and Jones 2011).

As two of the most common strategies for coping with environmental variability, dispersal and dormancy are similar in many ways (Den Boer 1968; Bohonak and Jenkins 2003). Successful spatial and temporal dispersal consists of three phases: (1) emigration, or initiation of dormancy, (2) movement, or survival through unfavorable environments, and (3) colonization, or reactivation from dormancy (Buoro and Carlson 2014). We operationally define the dispersal and dormancy capacities of a species based on their ability to successfully complete these three phases of spatial or temporal dispersal. Species with greater capacities for dormancy may accumulate into a persistent seed bank that spans greater temporal scales (i.e., a large temporal species pool), while species that engage in short-term dormancy could occupy a transient seed bank. The collection of dispersal and dormancy traits among species in the metacommunity can then influence the types of metacommunity dynamics that arise (Fig. 1). Thus, relative to the spatiotemporal scales of environmental variability, some species can disperse further in time, while other species can disperse further in space, enabling assessment in a metacommunity context.

Despite their similarities, dispersal and dormancy can have different implications for metacommunity ecology depending on environmental variability (Levin et al. 1984; Venable and Brown 1988; Cohen and Levin 1991). For example, neither dispersal nor dormancy will be successful in environmentally static landscapes. Species with better dispersal capabilities should be favored in spatiotemporally variable landscapes with lower spatial synchrony, such that populations can track favorable habitats over time in the metacommunity (McPeek and Holt 1992). In contrast, dormancy should be favored in temporally fluctuating landscapes with high spatial synchrony (i.e., many patches experience similar conditions, reducing the effectiveness of dispersal) or when favorable habitats are spatially isolated (for review, see Buoro and Carlson 2014). Dispersal and dormancy may also differ in their ability to maintain diversity in disturbed landscapes (McPeek and Kalisz 1998). Temporal dispersers in the seed bank may be better protected against short-term, regional-scale disturbances that eliminate spatial refuges (e.g., hurricanes). Alternatively, spatial dispersers may be better protected against local-scale disturbances that outlast the range of temporal dispersal, allowing species to persist in other patches of the metacommunity. Currently, dispersal and spatial heterogeneity dominate contemporary understanding of metacommunity dynamics, but dormancy and temporal variability are analogous factors that can interactively influence diversity across space and time (Fig. 1).

Dispersal–Dormancy Covariation

The relationship between dispersal and dormancy is a key component of the life history of a species (Buoro and Carlson 2014; Rubio de Casas et al. 2015). It is often assumed that dispersal and dormancy negatively covary, consistent with the view that there is a trade-off between these life-history strategies, such that species with high capacities for dormancy have low dispersal rates, and vice versa. This trade-off is thought to exist because dormancy reduces local fitness variability, and thus, the need to disperse (Levin et al. 1984; Cohen and Levin 1987, 1991; Venable and Brown 1988). For example, a synthesis of British seed plants indicated that species with better dispersal abilities had lower dormancy capabilities (Rees 1993). Allocation constraints could also prohibit maximal investment in traits that enhance both dormancy and dispersal, setting up the trade-off (Ehrlén and van Groenendael 1998). Additional empirical support for negative dispersal–dormancy covariation exists (Ehrlén and van Groenendael 1998; Bégin and Roff 2002), but it is not universal (Siewert and Tielbörger 2010; Buoro and Carlson 2014), suggesting that other factors may mask this trade-off.

There is also evidence that dispersal and dormancy can exhibit different relationships. Positive dispersal–dormancy covariation, where species with greater capacities for dormancy also disperse greater distances across space, is another possibility. Positive covariation could arise under a number of conditions, such as when environmental favorability changes rapidly or unpredictably in both space and time (Venable and Brown 1988; Cohen and Levin 1991; Snyder 2006; Buoro and Carlson 2014). Positive dispersal–dormancy covariation may also be due to genetic linkage or pleiotropy (Peiman and Robinson 2017), such as when traits that increase capacities for dormancy interact with traits that enhance dispersal abilities, or vice versa. Therefore, positive selection for dispersal or dormancy indirectly selects for the other strategy as well. For example, zooplankton that produce more durable dormant propagules make longer lasting contributions to local seed banks, but they also disperse greater distances by better surviving ingestion by waterfowl, important dispersal vectors of freshwater invertebrates (Figuerola and Green 2002; Viana et al. 2016). Regardless of the mechanism behind dispersal–

dormancy covariation, estimating dispersal and dormancy capabilities is key for predicting how dormancy influences metacommunities (Box 3).

[Insert Box 1 here.]

THE METACOMMUNITY ECOLOGY OF DORMANCY

To demonstrate how covariation between dormancy and dispersal influences metacommunities, we created a simulation model (Box 2, Supplementary Material). Our modeling demonstrates that dormancy affects the distribution of local (α), among-site (β), and regional (γ) diversity along a dispersal gradient (Fig. B2.1). In addition, our models reveal that the effects of dormancy on metacommunity diversity depend on the degree of spatiotemporal variability in the environment, species' capacities for spatial and temporal dispersal, and the type of dispersal–dormancy covariation in the metacommunity. In this section, we expand on our modeling results by discussing the potential mechanisms by which dormancy can affect three important aspects of metacommunity ecology: community assembly, community dynamics, and species distributions.

[Insert Box 2 here.]

Community Assembly

Seed banks can introduce temporal variability in the spatial scale of community assembly. This arises in part because the importance of the seed bank is greatest during the early stages of community assembly (Roxburgh et al. 2004). For example, seed banks allow weeds to rapidly colonize ephemeral crop habitats until niche selection favors more competitive species

(Ryan et al. 2010; Mahaut et al. 2018). Similarly, prior to the arrival of spatial dispersers, microcrustacean seed banks in temporary wetlands can drive rapid community assembly following extended periods of desiccation (Vanschoenwinkel et al. 2010; Kneitel 2018; Box 1). However, even with a local seed bank, dispersal can still play a role in the early stages of assembly. Across a 40-year successional gradient in a subalpine birch forest, dispersal played a consistently strong role in community assembly, but the importance of dormancy declined with increasing time since disturbance (Vandvik and Goldberg 2006). As a result, recently or frequently disturbed plant communities tend to have the highest compositional similarity to the seed bank, but this is not always the case (Hopfensperger 2007; Saatkamp et al. 2014). Thus, transitions from local, dormancy-driven assembly to regional, dispersal-driven assembly appear to be common, but the implications for metacommunity dynamics could depend on the frequency and spatiotemporal pattern of disturbance.

Dispersal–dormancy covariation is important for community assembly because it could determine which species colonize a site from the seed bank versus from elsewhere in the metacommunity. For example, good dispersers may also be abundant in the regional seed bank (positive covariation), and the combination of spatial and temporal dispersal by these species may contribute to the homogenization of diversity among sites (Box 2). Alternatively, local seed banks may contain different species than the active or dormant species found in other patches (as might be expected with negative covariation), so that spatial and temporal dispersal events reflect different species pools. Consequently, the spatial isolation and disturbance frequency of a site may be important controls on community assembly because they determine whether community assembly proceeds primarily from spatial or temporal dispersal. For example, spatial isolation plays a major role in the assembly of benthic macroinvertebrates in intermittent streams in the

U.S. Southwest because sites near perennial headwaters are colonized via spatial dispersal while sites near intermittent headwaters rely on dormancy (Bogan and Lytle 2007; Bogan et al. 2015).

Community Dynamics

Dormancy can interact with local community dynamics in ways that may be decoupled from dispersal rates, depending on dispersal–dormancy covariation. As a result, dormancy could help explain empirical deviations from classical metacommunity predictions based on dispersal rates, niche differences, and spatial heterogeneity alone. For example, sufficient dispersal rates are thought to be necessary for species to persist in disturbance prone landscapes (Hanski and Gilpin 1997), but seed banks can maintain local colonization–extinction dynamics in the absence of dispersal from the metacommunity if environmental conditions fluctuate on time scales that are shorter than the range of temporal dispersal by propagules in the seed bank (Mergeay et al. 2007, 2011; Ventura et al. 2014). The spatial variation in community dynamics generated by temporal dispersal could appear indistinguishable from that generated by spatial dispersal, but it would be due to purely local processes or as a result of combined spatial and temporal dispersal (Mahaut et al. 2018).

Even with strong temporal environmental tracking, reactivation from dormancy does not necessarily lead to successful reestablishment of a population. Reestablishment from the seed bank may fail due to niche preemption by similar species that have already emerged from the seed bank, introducing historical contingencies that may have stochastic elements (Fukami 2015; Schwentner and Richter 2015). Species could also emerge from the seed bank under unfavorable environmental conditions (e.g., due to stochastic reactivation or bet hedging), maintaining sink populations in the community via temporal dispersal (a temporal mass effect, Shmida and Ellner 1984; Rajaniemi et al. 2006; Mahaut et al. 2018). Other species might miss favorable opportunities for growth due to misinterpreted environmental cues or failures during the temporal dispersal process (i.e., they are ‘dormancy limited’) (Donohue et al. 2010), which may allow competitively inferior species to occupy habitats that superior competitors fail to recolonize. Spatial variation in the stochastic or historically contingent outcomes of temporal dispersal would create mismatches between environmental conditions and community composition that current metacommunity theory might attribute to unmeasured spatial heterogeneity or dispersal. It is possible that these mismatches due to temporal dispersal could even occur in the absence of spatial heterogeneity or source–sink relationships.

Species Distributions

Dormancy can also affect the distribution of species across the metacommunity by modifying colonization rates and patch invasibility (Gillespie et al. 2012; Gioria et al. 2012) as illustrated, for example, by the spread of exotic species by the transport of dormant propagules (e.g., in the ballast water of ships, Briski et al. 2011). Dormancy could allow colonizers that arrive during unfavorable environmental conditions to persist until conditions improve, increasing the probability of successful establishment (Gioria et al. 2012). For example, the high dispersal rate and persistent seed bank of *Acacia dealbata* may contribute to its invasiveness and expanding spatial distribution (Gibson et al. 2011). In a recent study, the seed bank density of *A. dealbata* reached more than 60,000 seeds m^{-2} in invaded plots compared to only 9 seeds m^{-2} in uninvaded plots (Passos et al. 2017). Invasion by *Acacia* has also been shown to reduce the density of native seeds in the seed bank, which further reinforces aboveground losses in species diversity (Gioria et al. 2014; Gioria and Pyšek 2016). The large seed banks of invasive species may even buffer the community against subsequent invasion due to rapid colonization. Thus, when coupled with high dispersal ability, dormancy may facilitate spatial homogenization not only by reducing and replacing local diversity within a site, but also by facilitating the rapid spread of species throughout a metacommunity (Box 2).

Dormancy can also affect the spatial distribution of species via temporal mass effects. Even if species have the ability to persist in a seed bank via dormancy, environmental conditions may not always favor establishment. For example, dormancy and dispersal maintain thermophilic bacteria in the cold Arctic Ocean, an environment where they are metabolically disfavored (Hubert et al. 2009). The ability of microorganisms to persist in unfavorable environments via dormancy could also help explain deviations in their spatial and temporal patterns of diversity from those of macro-organisms (Lennon and Jones 2011; Shade et al. 2018). In another example from an alpine lake, local seed banks enabled the recovery of a cladoceran species (*Daphnia middendorffiana*), which can grow asexually, but not a copepod species (*Hesperodiaptomus shoshone*), which relies on sexual reproduction (Sarnelle and Knapp 2004). For the copepod, finding a mate after emerging from the seed bank is rare, causing an Allee effect (Sarnelle and Knapp 2004; Kramer et al. 2008). Although temporal mass effects may explain the occasional presence of a copepod in this lake, their lack of recovery also suggests they could be dispersal limited relative to nearby lakes. Thus, dormancy can influence the spatial distributions of species in a metacommunity, often in unanticipated ways, due to spatial and temporal processes.

EVOLVING METACOMMUNITIES WITH DORMANCY

Dormant seed banks could further influence community assembly and metacommunity dynamics through evolutionary processes by altering the arrival of species and rates of local adaptation (Leibold et al. 2005; Urban and Skelly 2006; Loeuille and Leibold 2008; Urban et al. 2008; De Meester et al. 2016). The community monopolization hypothesis posits that local adaptation by early arriving species can create priority effects that prevent the establishment of later arriving species and alter regional patterns of diversity (Urban et al. 2008; Urban and De Meester 2009; Leibold et al. 2019). Community monopolization is likely to occur when early colonizers can rapidly adapt to local conditions (e.g., due to short generation times) and when colonization events are rare and infrequent (e.g., due to spatial isolation and dispersal limitation) (De Meester et al. 2016; Vanoverbeke et al. 2016). But dormant seed banks provide another mechanism of colonization that could modify the importance of community monopolization for metacommunity dynamics.

Dormancy can regulate community monopolization by shortening or lengthening the time between the arrival of maladapted colonists and the arrival of pre-adapted species that would drive them extinct. For example, because seed banks facilitate recolonization they could lengthen the time for early colonists to locally adapt and monopolize the community, especially when spatial isolation contributes to dispersal limitation. However, even with high immigration seed banks can be locally adapted (De Meester et al. 2002; Falahati-Anbaran et al. 2014; Ventura et al. 2014). Seed banks also store genetic diversity that provides a source of gene flow from the past (Hairston and Kearns 2002; Vitalis et al. 2004; Lundemo et al. 2009; Rubio de Casas et al. 2015). Maladaptive gene flow from the seed bank can inhibit monopolization by slowing the response to directional selection (Templeton and Levin 1979; Hairston and De Stasio 1988; Shoemaker and Lennon 2018; Tellier 2019), a process we call the ‘dormancy load’. Alternatively, under fluctuating selection, seed banks can facilitate local adaptation by allowing different genotypes to be favored at different times (i.e., a genetic storage effect, Ellner and Hairston 1994; Hedrick 1995; Nunney 2002; Vitalis et al. 2004). Thus, high dormancy load can slow local adaptation and allow a preadapted species to interrupt community monopolization. However, if early colonizers build up genetically diverse seed banks in fluctuating patches, they are more likely to monopolize them even when environmental fluctuations occur (Loeuille and Leibold 2008).

Although we have reviewed some of the possibilities above, the role of the seed bank in community monopolization will be highly context dependent. This is because the outcome of community assembly depends on the genetic variation of populations in the seed bank relative to spatial colonizers, the covariation between dormancy and dispersal, colonization order, and environmental variability in relation to the emergence of genotypes and species from the seed bank.

FUTURE DIRECTIONS

We have shown that dormancy can have many consequences for metacommunity ecology and evolution, but there remains much more to learn about how dormancy and seed banks influence the distribution of species through space and time. In this section, we briefly highlight three research needs that would yield greater insight into the possible roles of dormancy in metacommunities.

Modeling Studies

The difficulty of empirically measuring dispersal has led to an increased reliance on models for generating and testing new hypotheses in metacommunity ecology. Likewise, challenges associated with measuring dormancy also pose significant hurdles. Modeling studies (e.g., analytical or simulation-based) can be used explore the vast parameter space of dispersal and dormancy beyond what can be accurately measured in most organisms. A key challenge will be to understand how dormancy might alter the predictions of current metacommunity theory under different collections of species (with varying dispersal–dormancy covariation), under different patterns of environmental variability (e.g., spatial and temporal autocorrelation or disturbance), and under different starting conditions or assembly histories. Even under simplified conditions, our models suggest that dormancy affects a fundamental property of metacommunity ecology: the distribution of diversity across spatial scales (Box 2). However, more complex models would yield much deeper insight into the nuanced roles of dormancy in metacommunities. For example, models could extensively explore how dormancy affects metacommunity structure through local, regional, historical, and evolutionary mechanisms that are difficult or impossible to measure empirically.

Empirical Studies

From the empirical perspective, it is unclear whether different taxonomic groups have characteristic patterns of dispersal–dormancy covariation, and whether dispersal–dormancy covariation is influenced by other traits, such as body size or dispersal mode. We have shown that invertebrate species commonly found in bromeliad plants display a wide range of dispersal and dormancy capacities (Box 3), but generalizations are difficult without extensive trait measurements across diverse taxonomic groups and ecosystems. Accurate measurements of dispersal and dormancy are notoriously difficult to acquire, but estimates of these traits for co-occurring species at the metacommunity scale are invaluable. For example, identifying species differences in dispersal kernels (Sullivan et al. 2018) and dormant propagule survivorship (e.g., Frisch 2002) would be especially informative for predicting how species distributions in metacommunities relate to spatiotemporal variation in the environment. Trait data could then be used to test whether predictions derived from different dispersal and dormancy strategies correspond with patterns of diversity observed in the field. For example, multivariate statistics can quantify the degree to which community dynamics are explained by spatial, temporal, biogeographical, trait, and environmental predictors (e.g., Leibold et al. 2010; Legendre and Legendre 2012; Peres-Neto et al. 2012, 2017; Dray et al. 2014). Furthermore, manipulative experiments in the field or in mesocosms may shed further light on the roles of spatial and temporal dispersal.

[Insert Box 3 here.]

Adding Trophic Complexity

Trophic interactions and consumer movement can influence spatial and temporal patterns of diversity, which may explain discrepancies between empirical studies and competition-based metacommunity theory (Haegeman and Loreau 2014; Grainger and Gilbert 2016; Leibold and Chase 2018; Guzman et al. 2019). Dormant propagules often differ in their vulnerability to predators and pathogens (Hulme 1998; Klobutcher et al. 2006; Waterkeyn et al. 2011; Horst and Venable 2018), which could affect their survival in the seed bank and temporal dispersal capabilities. For example, while high predator dispersal can eliminate spatial refuges for vulnerable prey, predator-resistant dormant stages could introduce temporal refuges that stabilize prey populations in the metacommunity. In some systems, dormancy may even be an adaptation to host–parasite interactions (Verin and Tellier 2018), suggesting dormancy may be a trait of interest in evolving metacommunities that include predation. However, dormant propagules at a high risk of consumption (e.g., Waterkeyn et al. 2011) could increase predator abundances and destabilize prey populations (of several species) at the metacommunity scale via inter-patch apparent competition. In addition, predators might also have the ability to enter a dormant stage. Predator seed banks could prevent prey species from occupying some patches by driving prey extinct upon reactivation (Livingston et al. 2017). These colonization–extinction dynamics resemble, but fundamentally differ from, those driven by dispersal (Huffaker 1958; Hilborn

1975). Our understanding of dormancy in metacommunities would benefit greatly from: (1) manipulative experiments that measure how the presence or absence of predators, seed banks, and environmental heterogeneity contribute to metacommunity dynamics, and (2) modeling approaches that extensively explore how more complex food webs (e.g., including predators, omnivores, mutualists, pathogens, etc.) may regulate the relative importance of dormancy and dispersal for metacommunity structure, diversity, and stability.

CONCLUSIONS

Dormancy is a common life-history trait can influence metacommunity structure, dynamics, and diversity. Our simulations suggest that the effects of dormancy on metacommunity diversity depend on dispersal–dormancy covariation and environmental variability, proposing a tighter integration between spatial and temporal dimensions in metacommunity ecology. Building on our models, we propose that the dispersal and dormancy capacities of species in the metacommunity modify the relative importance of local (e.g., species interactions, abiotic constraints), historical (e.g., priority effects, temporal mass effects) and regional (e.g., dispersal and spatial heterogeneity) factors underlying metacommunity structure. The range of potential metacommunity dynamics expands even further when we incorporate evolution (e.g., via the community monopolization hypothesis), but the outcomes are likely to be highly context dependent. Dormancy can facilitate community monopolization through rapid recolonization from the seed bank and by buffering against maladaptive gene flow, but it may also inhibit monopolization if dormancy load prevents local adaptation. Using case studies from natural metacommunities, simulation models, and an analysis of dispersal–dormancy covariation, we have demonstrated some of the implications of dormancy for metacommunities and have suggested ways to more fully incorporate dormancy into metacommunity research. While the context-dependent role of dispersal in metacommunities is now increasingly clear, our synthesis reveals that dormancy may play a similarly important role that may strongly interact with that of dispersal in ways that remain to be elucidated.

BOXES

Box 1: Evidence from nature: microcrustacean metacommunities

Many species are capable of entering dormant stages that can influence their distributions across time and space. Microcrustaceans, such as cladocerans, copepods, and fairy shrimp, have a broad range of dispersal (Jenkins and Buikema 1998; Cáceres and Soluk 2002; Vanschoenwinkel et al. 2009) and dormancy capabilities (Brendonck et al. 2016; Ellegaard and Ribeiro 2018). For example, the production of dormant ephippia in response to food limitation, crowding, or seasonality (Fig. B1.1A), allows species of *Daphnia* to coexist at the local scale via the temporal storage effect (Cáceres 1997). *Daphnia* have high capacities for temporal dispersal because their ephippia can remain viable for over a century (Cáceres 1998). Dormancy also has direct implications for zooplankton metacommunity dynamics because it enables dispersal between isolated aquatic habitats by wind, water, or animal vectors (Bohonak and Jenkins 2003; Havel and Shurin 2004). Traits related to dormant propagules, such as buoyancy, can influence dispersal–dormancy covariation (Pinceel et al. 2013). For example, floating ephippia are readily dispersed, but sinking propagules remain in the local seed bank (Ślusarczyk and Pietrzak 2008). In contrast to *Daphnia*, cladocera in the genus *Chydorus* attach their ephippia to littoral macrophytes (Fryer 1972; Frey 1986), restricting their dispersal. Thus, we can use species differences in dispersal and dormancy to make predictions for metacommunity dynamics.

The influence of seed banks on metacommunity diversity has been well-documented through the study of crustaceans in temporary aquatic habitats including wetlands and rock pools. In temporary rock pools (Fig. B1.1B), seed banks maintain permanent resident species by allowing them to endure periods of desiccation, but they also facilitate wind-blown dispersal to other pools when the pools are dry (Brendonck and Riddoch 1999; Jocque et al. 2010; Brendonck et al. 2016). The importance of dormancy for among-pool dispersal demonstrates how local cues to enter dormancy can have metacommunity-wide implications. In this system, the early successional niche is available exclusively to dormant organisms, consistent with the prediction that seed banks affect diversity most strongly following disturbances. The seed bank allows early successional species to persist in the metacommunity even though they are often driven locally extinct by competitors and predators that colonize later via aerial dispersal (Vanschoenwinkel et al. 2010). Additional evidence from microcrustaceans in California vernal pools (n = 787) suggests dormancy affects regional patterns of diversity (Kneitel 2016, 2018). Among generalists in this system, passive dispersers with the ability to enter dormancy (ostracods, cladocerans, and copepods) have much higher site occupancy (>50%) than active dispersers that lack dormancy (Kneitel 2018). Together, these examples show how dormancy can influence metacommunity structure and dynamics in spatiotemporally variable landscapes.

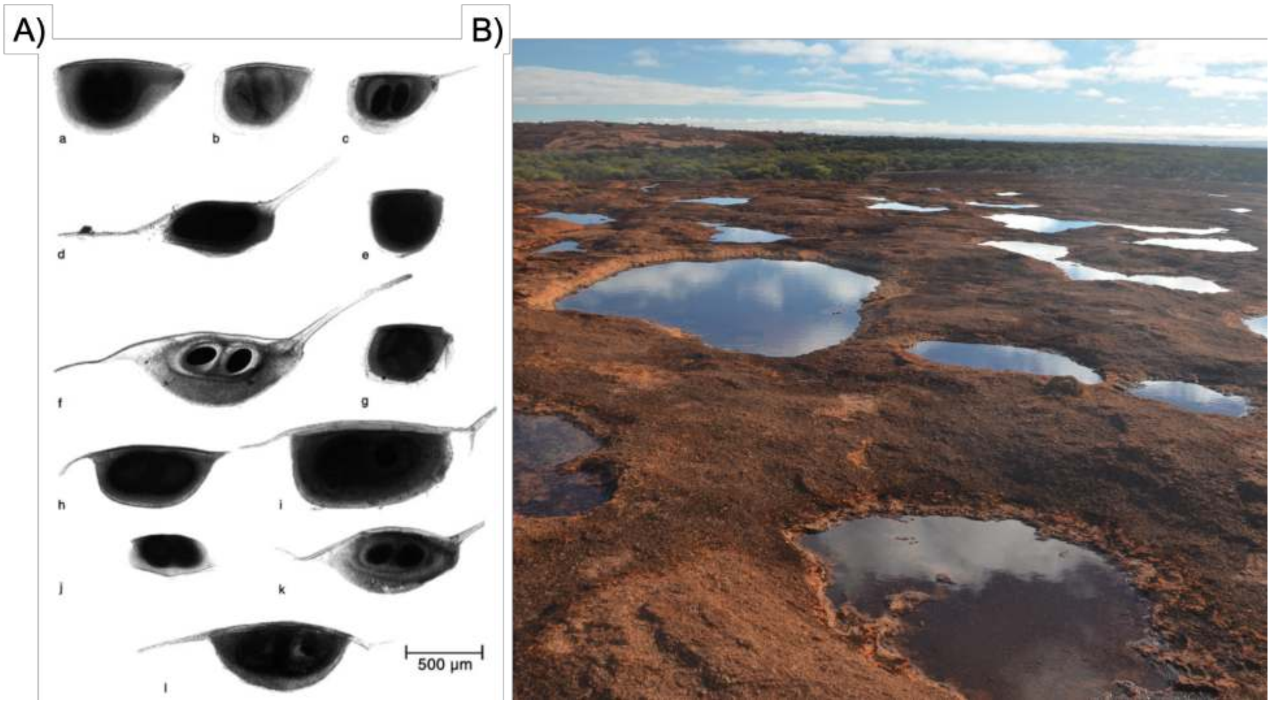

Figure B1.1 — Microcrustacean dormancy is common in variable environments. (A) The diversity of *Daphnia* ephippia from a survey of 41 water bodies in Kenya, where seed bank diversity was more than twice the diversity of active communities (image from Mergeay et al. 2005). The high diversity lurking in the seed bank indicates the potential for dormancy to influence metacommunity trajectories in different ways depending on which species colonize the active community, the order in which they emerge from the seed bank, and the favorability of the environment they experience upon reactivation. (B) Temporary rock pools contain species that typically have some form of dormancy to endure extended periods of desiccation and to facilitate recolonization from the seed bank upon rewetting. Image credit: B. Vanschoenwinkel (source: https://insularecology.files.wordpress.com/2013/09/dsc_06291.jpg).

Box 2: Modeling dormancy in metacommunities

We explored the effects of dormancy in metacommunities using simulation models (see Supplement 1). A fundamental aspect of metacommunity ecology is that species diversity varies across spatial scales and can be partitioned into diversity at the local scale (α-diversity), diversity among sites (β-diversity), and diversity at the regional scale (γ-diversity). The partitioning of diversity across scales is also known to depend on the rate of dispersal in a metacommunity (Mouquet and Loreau 2003; Grainger and Gilbert 2016). Because we propose that dormancy has implications for the maintenance of diversity at the local scale, and because dormancy likely covaries with dispersal, we examined the effects of dormancy on the diversity-dispersal relationship.

We modified a general metacommunity model (Shoemaker and Melbourne 2016) to include transitions in and out of a dormant seed bank. Briefly, population dynamics are modeled in discrete time according to the Beverton-Holt model of population growth, dispersal is global, the metacommunity is spatially heterogeneous, dormancy occurs at a constant rate in and out of the seed bank, and dormant propagules undergo geometric decay. Because dormancy and dispersal are likely to be found in disturbed environments, we modeled random disturbance as the removal of all active individuals in a patch, following a Bernoulli distribution for each patch independently at a specified extinction rate (Shoemaker and Melbourne 2016). More details about the model and its variations can be found in the supplemental information (S1). We partitioned diversity multiplicatively using a Hill numbers approach (order = 1, corresponding to the Shannon index of diversity) and diversity units are species equivalents (Jost 2007).

Our models indicate that dormancy has substantial effects on the partitioning of diversity across scales in ways that depend on the rate of dispersal, dispersal–dormancy covariation, and environmental variability. When dispersal–dormancy covariation is negative (i.e., dormancy comes with a dispersal cost), dormancy maintains diversity when dispersal is limiting relative to disturbance rate because temporal dispersal from the seed bank allows populations to recolonize patches (Fig. B2.1). However, dormancy cannot mitigate the homogenizing effects of high dispersal rates. When there is positive dispersal-dormancy covariation, dormancy and dispersal interactively affect the dispersal rate that maximizes metacommunity diversity: dormancy maintains peak diversity at lower dispersal rates, but magnifies the effects of homogenization; without dormancy, more dispersal is needed for species to keep up with the disturbance regime of the landscape (Fig. B2.1). Even in static landscapes without disturbance, where dormancy is not expected to be evolutionarily favored, seed banks can maintain higher α-diversity at lower dispersal rates and amplify the homogenizing effects of dispersal under positive dispersal–dormancy covariation (Fig. S1.1).

Although by no means comprehensive, our simulations illustrate three important features of biodiversity in metacommunities: 1) dormancy alters the distribution of diversity across spatial scales, 2) these effects can depend strongly on the nature of spatiotemporal environmental variation, and 3) these effects interact with dispersal in ways that depend on the nature of dispersal–dormancy covariation.

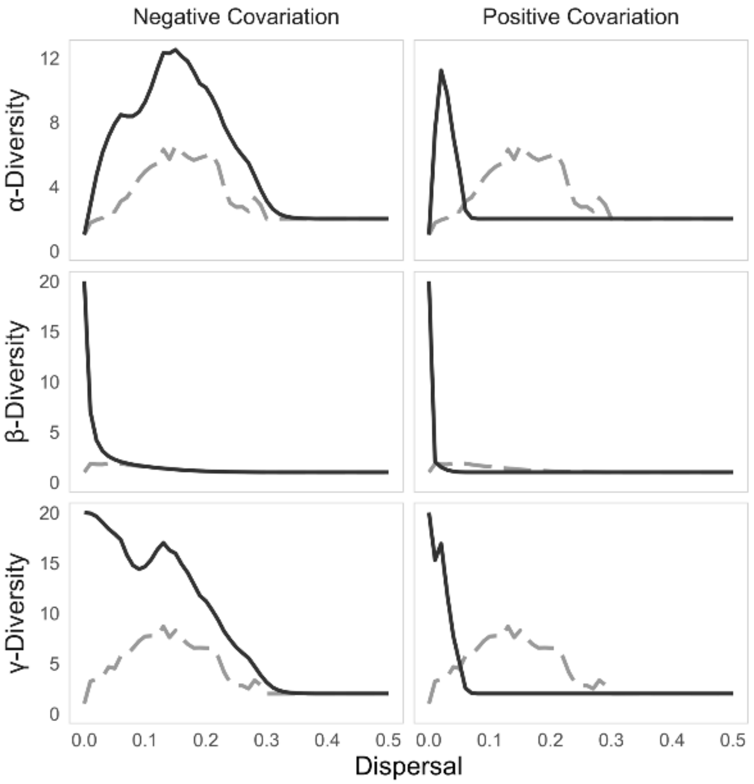

Figure B2.1 — Dispersal–diversity relationships with (dark solid line) and without (dashed light line) dormancy in an environment subject to local disturbance, commonly associated with dispersal and dormancy strategies. Dormancy maintains higher α- and γ-diversity under both negative and positive dispersal–dormancy covariation. With negative covariation (i.e., a trade-off), dormancy maintains higher α- and γ-diversity, especially at lower dispersal rates, and maintains β-diversity under dispersal limitation (i.e., at very low dispersal rates). However, dormancy cannot protect against homogenization (regional diversity decreases with increasing dispersal, regardless of dormancy). With positive dispersal–dormancy covariation, dormancy lowers the dispersal rate that maximizes α-, β-, and γ-diversity, increases maximum α- and γ-diversity, and also increases the homogenizing effects of dispersal. The metacommunity with dormancy is homogenized (e.g., one species dominates) at dispersal rates that were potentially limiting in the absence of dormancy.

Box 3: How to study dispersal–dormancy covariation in metacommunities

Incorporating dispersal–dormancy covariation into empirical and modeling studies is an important next step for fully integrating spatial and temporal dimensions into metacommunity ecology. Recently, a suite of twelve functional traits were measured for 852 invertebrate taxa that represent the species pool of the aquatic inhabitants of tropical tank bromeliads from Mexico to Argentina (Céréghino 2018; Céréghino et al. 2018). A full analysis showed that observed trait variation in the bromeliad invertebrates filled less than 25% of the potential trait space, suggesting trait covariation constrains the niche space of these taxa (Céréghino et al. 2018). Bromeliad invertebrate communities are model systems for studying metacommunities because of their patchy distribution in forests, openness to colonization, and experimental tractability (Lecraw et al. 2014; Petermann et al. 2015).

Using the subset of taxa with trait measurements for both dispersal and dormancy (n = 609 taxa), we sought to identify groups of taxa with similar dispersal and dormancy strategies that may co-occur in a metacommunity. We used a fuzzy clustering algorithm (*c*-means) to group taxa with similar dispersal and dormancy trait values (Kaufman and Rousseeuw 1990; Maechler et al. 2018). We clustered taxa into three groups (k = 3, average silhouette width = 0.68), and used principal components analysis (PCA) on the rank-ordered trait data to visualize the location of these groups in reduced dimensions and to generate continuous descriptions of the dispersal and dormancy strategies among these taxa (Podani 2005; Borcard et al. 2018; Céréghino et al. 2018). We plot vectors showing the PCA loadings to describe the trait differences underlying cluster membership.

We observed wide variation among taxa in their dispersal and dormancy strategies (Fig. B3.1). Notably, the first principal component describes a trade-off between passive and active dispersal ($\rho = -0.76$, $p_{\text{Holm-adjusted}} < 10^{-9}$). The second principal component describes the dormancy capacity of each taxon. As with other trait dimensions (Céréghino et al. 2018), we found that taxa span, but do not fill, the dispersal–dormancy trait space, suggesting that trait covariation partially constrains dispersal and dormancy strategies. Many taxa exhibited patterns consistent with a trade-off between dispersal and dormancy: Cluster 1 (lower-right quadrant) includes strong passive dispersers with low dormancy capacities, Cluster 2 (upper-left) includes weak dispersers with high dormancy capacities, and Cluster 3 (lower-left) includes active dispersers with poor dormancy capacities (Fig B3.1). However, some taxa exhibit high capacities for both dispersal and dormancy (upper-right, upper-left), hence similar membership in the three clusters. More detailed information about the taxa in each cluster is available in the supplemental material.

Our analysis suggests that some species may be better at spatial dispersal and other species are likely better at temporal dispersal, but that dispersal–dormancy covariation could restrict the life-history strategies these taxa could employ. We may be able to predict their distributions in a metacommunity with knowledge of the regional species pool, the dispersal and dormancy traits of those species, and spatiotemporal variation in environmental variables by using the principal components as quantitative predictors in multivariate statistical models (e.g., the fourth-corner approach, Dray and Legendre 2008; Peres-Neto et al. 2017).

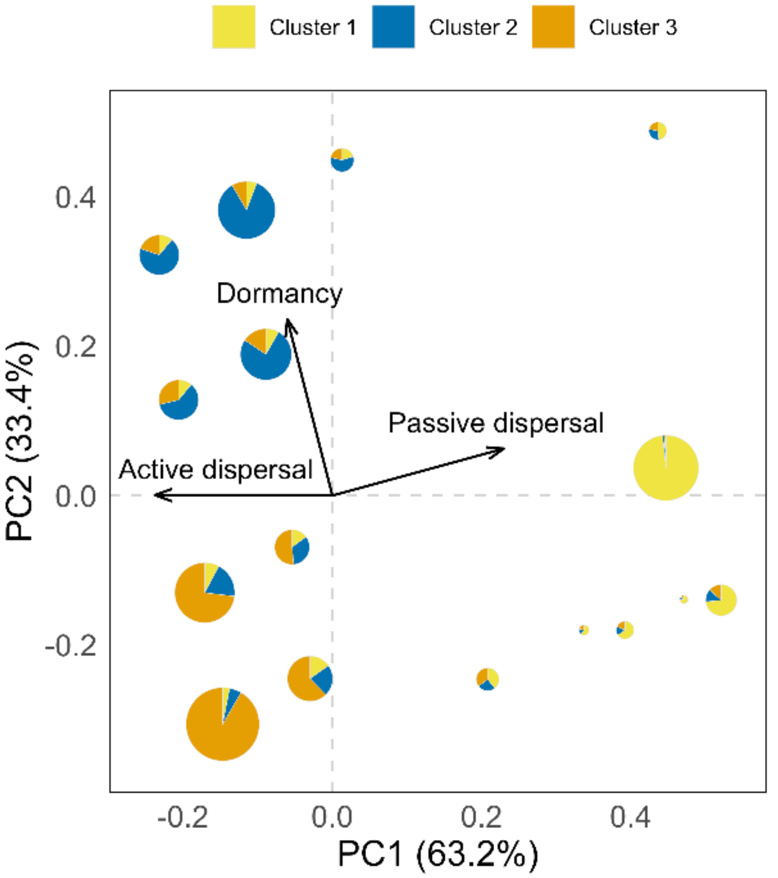

Figure B3.1 — A range of dispersal and dormancy strategies were observed among aquatic invertebrate taxa found in tropical bromeliads across South America (n = 609) (Céréghino 2018). The relative size of each wedge in each pie represents the proportional membership of taxa in each of the three clusters. Vectors describe the location of clusters in dispersal–dormancy trait-space. Total area of the pie is proportional to the number of taxa observed with each trait combination.

TABLES

Table 1 — Modifications to metacommunity theory with the inclusion of dormancy.

Concept	Without dormancy	With dormancy
Colonization–extinction dynamics	Colonization results from spatial dispersal alone.	Colonization can occur from within a patch by propagules from the past.
Turnover in γ-diversity	The loss or gain of a species at the regional scale indicates that a species either went regionally extinct or the metacommunity was invaded.	Species may disappear and reappear in the future as a result of long-term storage in the seed bank.
Diversity–dispersal relationship	Homogenization (i.e., the erosion of β-diversity) results from high rates of contemporary dispersal.	Spatial and temporal dispersal interact to homogenize the metacommunity over space and time, decoupling homogenization from contemporary dispersal rates.
Community monopolization	Following a disturbance, good dispersers are more	Following a disturbance, dormant organisms may

	likely to monopolize a new site because they can locally adapt to new conditions before the arrival of poorer dispersers.	rapidly colonize from the seed bank (despite being poor dispersers), allowing them to monopolize the site before spatial dispersers arrive.
Sink/fugitive populations	Species can be found in suboptimal sites because their superior dispersal abilities	Seed bank emergence could also contribute to the maintenance of populations in unfavorable habitats.
γ-diversity in variable environments	Asynchronous spatiotemporal variability can drive poor dispersers extinct in the metacommunity.	Temporal dispersal can allow environmental tracking within each patch (e.g., temporal storage effect), maintaining regional diversity despite dispersal limitation.
Effects of disturbance on priority effects and β-diversity	Disturbances can eliminate local priority effects, which could generate temporal variability in β-diversity.	Priority effects can persist across disturbance events, which could stabilize patterns of β-diversity over time.

Table 2 — Testable predictions about dormancy in metacommunity ecology

Predictions for dormancy in metacommunities
Large scale, spatially autocorrelated disturbances will decrease β-diversity and increase the abundance of temporal dispersers; small scale, spatially asynchronous disturbances will increase β-diversity and favor spatial and temporal dispersers.
Spatially isolated patches will be more affected by priority effects during community assembly due to a greater role of temporal than spatial dispersal.
Species with high capacities for dormancy and dispersal will occupy more sites in the metacommunity and have larger species ranges than species that exhibit a trade-off between dormancy and dispersal, or lack dormancy altogether.
In directionally changing environments, dormancy will inhibit community monopolization by imposing high dormancy load; in fluctuating environments, dormancy will facilitate monopolization via genetic storage effects.
Species Area Relationships (SARs) will have higher intercepts and steeper slopes (with negative dispersal–dormancy covariation) or shallower slopes (with positive dispersal–dormancy covariation) than SARs without dormancy.
Species with high capacities for dormancy are likely to be dispersal limited under negative dispersal–dormancy covariation, and at risk of spatial mass effects under positive dispersal–dormancy covariation, creating mismatches between species composition and environmental conditions.
In trophic metacommunities, when dormant propagules are vulnerable to predation, dormancy may lead to apparent competition, but when dormant propagules are resistant to predation, dormancy could provide a refuge that maintains prey diversity.

In metacommunities with frequent local disturbances, but high spatial isolation between patches, dormancy may be more important for community dynamics and species distributions than dispersal when species exhibit a trade-off between dispersal and dormancy.

In spatiotemporally fluctuating environments, when local fluctuations occur on longer time scales than the temporal dispersal range of species in the metacommunity, dormancy is less important than dispersal for maintaining diversity under negative dispersal–dormancy covariation (because individuals are lost to the seed bank); under positive dispersal–dormancy covariation, dormancy could help maintain diversity at low spatial dispersal rates.

FIGURES

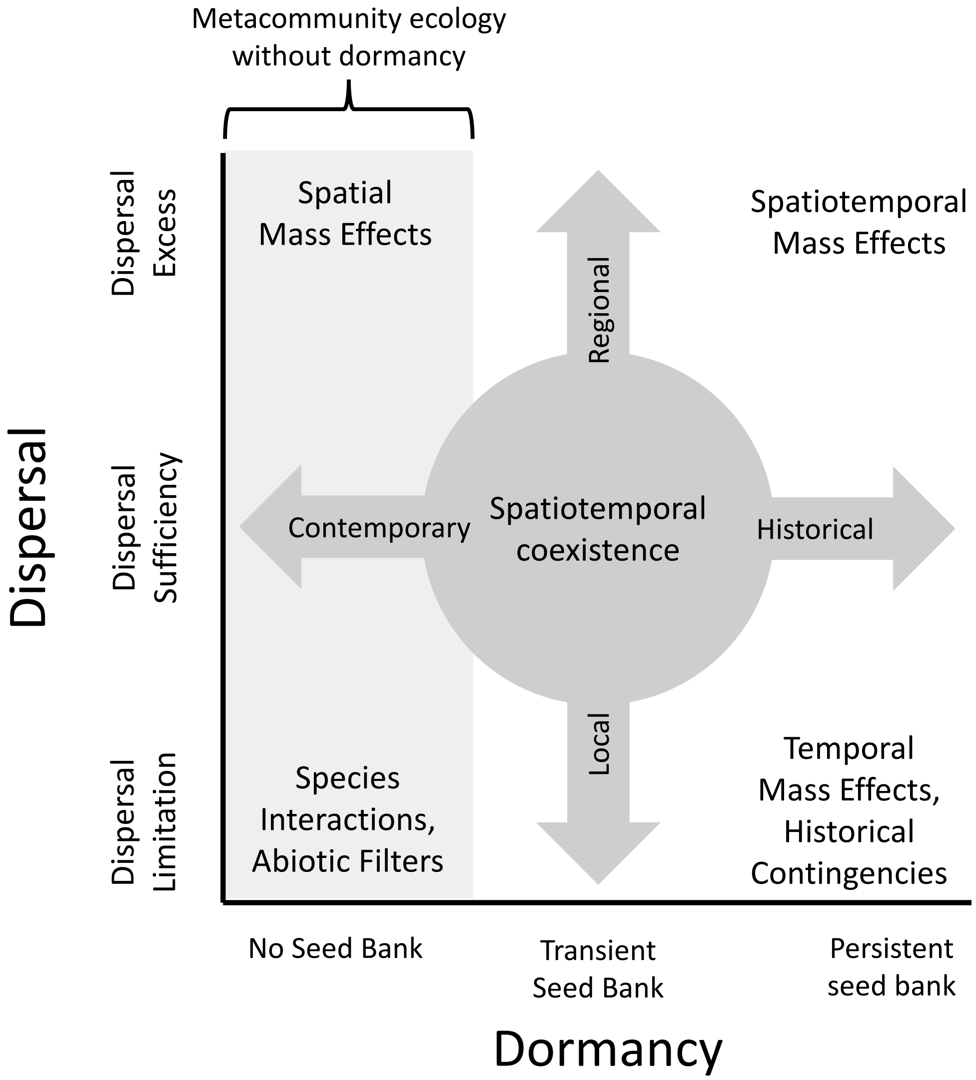

Figure 1 — Dormancy expands the possible metacommunity dynamics to include historical factors due to the presence of a seed bank. As dispersal increases (along the vertical axis), regional factors become increasingly important for local community structure and dynamics. As dormancy increases (along the horizontal axis), propagules in the seed bank have greater temporal dispersal capacities and potential to influence future ecological and evolutionary dynamics. In the absence of a seed bank, traditional metacommunity theory applies, leading to

outcomes predicted when dispersal is limiting, sufficient, or in excess of the strength of local niche selection. Towards the lower right corner (high temporal dispersal, low spatial dispersal), historical contingencies and dispersal limitation may dominate community assembly, causing high spatial turnover relative to what would be expected based on spatial heterogeneity and dispersal alone. Increasing dispersal is likely to mitigate the historical controls from the seed bank, potentially leading to spatial and temporal homogenization, as our models indicate under positive dispersal–dormancy covariation.

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