

Appendix A from N. I. Wisnoski et al., “Dormancy in Metacommunities” (Am. Nat., vol. 194, no. 2, p. 000)

Simulation Modeling: Expanded Methods

To examine the effects of dispersal and dormancy on metacommunity diversity, we created simulation models. In these simulations, we modeled population growth under different types of environmental variability and then analyzed diversity along gradients of dispersal using the parameters listed in table A1. All simulations and analyses were performed in R (R Core Team 2018). All code is provided in a zip file (available online) and is also available on GitHub (<https://github.com/LennonLab/MCdorm>).¹

Population Growth in the Metacommunity

We adapted the metacommunity model of Shoemaker and Melbourne (2016), which models metacommunity dynamics in discrete time, with global dispersal occurring following a round of local population growth. Prior to dispersal, within-patch population growth follows the Beverton-Holt (1957) model, where population growth is the product of the species intrinsic growth rate, the current population size, and a measure of intra- and interspecific competition:

$$N_{t+h,jx} = R_{jx} N_{t,jx} \frac{1}{1 + \sum_k \alpha_k N_{t,kx}},$$

where $N_{t+h,jx}$ is the population density of species j in patch x ; R_{jx} is the intrinsic, density-independent growth rate of species j in patch x ; $N_{t,jx}$ is the current population size; and

$$\frac{1}{1 + \sum_k \alpha_k N_{t,kx}}$$

is a measure of competition as the sum of competition coefficients, α_k , weighted by the abundances, $N_{t,kx}$, of all species k in the patch.

To regulate fitness differences in species across the heterogeneous landscape, we made R_{jx} a Gaussian function:

$$R_{jx} = R_{\max} \exp\left(\frac{(E_{t,x} - E_{j,\text{opt}})^2}{2 \times \sigma_{j,\text{nb}}^2}\right),$$

where $E_{j,\text{opt}}$ is species j 's environmental niche optimum, $\sigma_{j,\text{nb}}^2$ is its niche breadth, and $E_{t,x}$ is the current environmental condition in patch x at time t . Thus, increasing mismatch between species optima and the environment will lead to suboptimal growth during the time step.

Dispersal was global, meaning that all patches received an equal proportion of immigrants at each time step, and it occurred after local population growth. We introduced a simple dormancy transition between the active community and the seed bank that was modeled by a constant rate of entering and exiting dormancy, as might be expected under bet hedging. With dispersal and dormancy included, the full metacommunity model then becomes

$$N_{t+1,jx} = N_{t+h,jx} + d_j \left(\sum_{z \neq x} \frac{N_{t+h,jz}}{p-1} - N_{t+h,jx} \right) + \beta D_{t+h,jx} - \delta N_{t+h,jx},$$

$$D_{t+1,jx} = D_{t+h,jx}(1-m) + \gamma \times d_j \left(\sum_{z \neq x} \frac{D_{t+h,jz}}{p-1} - D_{t+h,jx} \right) - \beta D_{t+h,jx} + \delta N_{t+h,jx},$$

1. Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

where $N_{t+1,jx}$ is the population size of the active population following population growth and $D_{t+1,jx}$ is the population size of the dormant population of species j in patch x . The net effects of dispersal are determined for each species j as the sum across the total number of patches p , where immigrants arrive at a rate d_j from all patches $z \neq x$ where x is the focal patch. The transitions between active $N_{t+1,jx}$ and dormant $D_{t+1,jx}$ populations in the metacommunity depend on the parameters β , which is the activation rate of dormant propagules; δ , which is the rate of entering dormancy; and m , which is the mortality rate of dormant propagules. Dispersal-dormancy covariation is modeled at the extreme case of whether dormant propagules are able to disperse or not, with γ representing the covariation.

Environmental Variability

To analyze how different types of environmental variability influence the importance of dormancy in the metacommunity, we examined three simple cases: static environments, static environments with local disturbances, and perfectly spatiotemporally asynchronous environments. Environmental conditions were modeled as a single environmental variable with a range of $[0, 1]$, which corresponds to species optima in the metacommunity.

Environmentally static landscapes can allow source-sink dynamics and mass effects to arise because the patches where species optima are well matched to the environment are able to serve as source patches. Spatial heterogeneity was created by setting each patch to a value in the range $[0, 1]$. This environmental gradient from 0 to 1 was evenly partitioned among all p patches, ensuring that each species was the best competitor in at least one patch.

When there are local disturbances, some form of recolonization is required for species to persist in the landscape, from either spatial dispersal or temporal dispersal. We implemented a local disturbance in the way of Shoemaker and Melbourne (2016), where disturbance followed a Bernoulli distribution for each patch independently according to an extinction rate, e . We imposed disturbance by removing all individuals present in the active patch but not the dormant patch.

When the optimal environmental conditions fluctuate in both space and time, some degree of spatial or temporal dispersal is necessary for species to coexist. We enforced perfect asynchrony in spatiotemporal environmental fluctuations following Loreau et al. (2003). Here, environmental fluctuations oscillate according to a sine wave where each patch is equally out of phase with all other patches, such that the environmental conditions in patch x , E_x , is determined by

$$E_x = \frac{1}{2} \left[\sin \left(E_{x,0} + \frac{2\pi t}{T} \right) + 1 \right],$$

where $E_{x,0}$ is the starting environmental condition for each patch (partitioned equally, as above in the static landscape), t is the current time step, and T is the period of oscillations, such that longer periods converge on the static model and shorter periods fluctuate rapidly enough to converge on a single average patch of intermediate quality.

Diversity Partitioning Analysis

Our partitioning of diversity across spatial scales into local (α), regional (γ), and among-site (β) diversity follows the multiplicative approach of Whittaker (1972), as modified by Jost (2007) and implemented in the R package `vegetarian` (Charney and Record 2012). Therefore, the relationship among α , β , and γ is

$$\beta = \frac{\gamma}{\alpha},$$

where γ is diversity measured on the scale of the entire metacommunity and $\bar{\alpha}$ is the average diversity at the local scale. In this analysis, diversity is measured in units of species equivalents or Hill numbers at the order ($q = 1$), which corresponds to the number of equally abundant species needed to reach the observed value of diversity measured by the Shannon index.

Table A1: Model parameters for simulations in box 3 and appendix A

Parameter	Symbol	Value(s)
No. sites	p	20
No. species	k	20
Disturbance frequency	e	[0, .001]
Environmental period	T	1,000
Niche breadth	σ^2	.5
Intrinsic growth rate	R_{\max}	1.2
Strength of competition	α_k	4×10^{-4}
Dormant decay rate	m	1×10^{-6}
Dormancy rate	δ	.7
Reactivation rate	β	.1
Dispersal-dormancy covariation	γ	[0, 1]

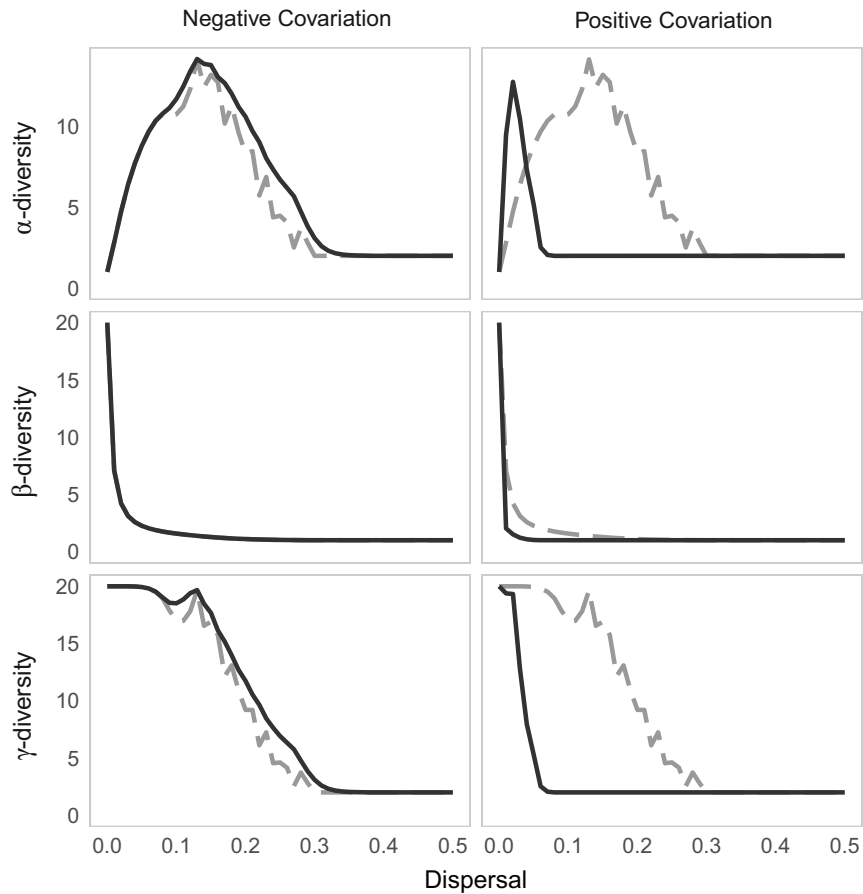


Figure A1: Dispersal-diversity relationships with (dark solid line) and without (dashed light line) dormancy in a spatially heterogeneous but temporally static environment without disturbances. With negative dispersal-dormancy covariation, dormant propagules are simply lost to the seed bank because they do not disperse. As a result, dormancy does not improve persistence under temporally static conditions. With positive dispersal-dormancy covariation, dormancy maintains α -diversity at low dispersal rates but also rapidly increases the onset of homogenization.

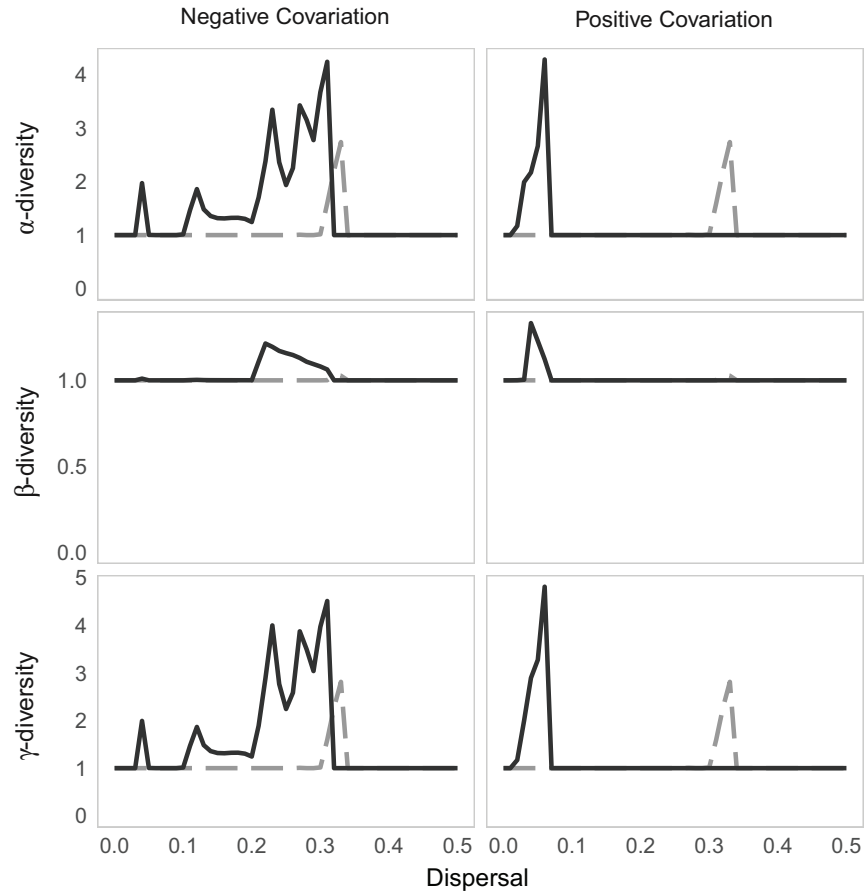


Figure A2: Dispersal-diversity relationships with (dark solid line) and without (dashed light line) dormancy in an environment that exhibits asynchrony in space and time. With negative dispersal-dormancy covariation (i.e., a trade-off), dormancy increases α - and γ -diversity and maintains β -diversity under dispersal limitation (i.e., at low dispersal rates), but it cannot protect against homogenization (diversity plummets at the same rate 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 (i.e., one species dominates) at dispersal rates that were limiting in the absence of dormancy.

Appendix B from N. I. Wisnoski et al., “Dormancy in Metacommunities” (Am. Nat., vol. 194, no. 2, p. 000)

Bromeliad Community Trait Data Analysis: Expanded Methods

To demonstrate a potential approach to assessing dispersal-dormancy covariation in a metacommunity context, we analyzed a large trait data set of taxa commonly operating as a metacommunity. Twelve functional traits were measured for 852 aquatic invertebrate taxa that live in the pools of water that accumulate in bromeliad plants (Céréghino et al. 2018). The data are available for download from the Knowledge Network for Biocomplexity at <https://doi.org/10.5063/F1VD6WMF> (Céréghino 2018). Of these 852 taxa, 609 had measurements for dispersal and dormancy. We used this subset of taxa for the analysis.

The traits were measured categorically as “none,” “low,” “intermediate,” and “high” capacities for three traits: active dispersal, passive dispersal, and dormancy. We independently compared dormancy capacities with capacities for active and passive dispersal, and we computed the fraction of taxa that fit into all possible combinations of none, low, medium, and high for both dispersal and dormancy.

We first standardized the trait measurements by converting the ordinal factors into ranks, assigning ties to average values (Podani 2005; Céréghino et al. 2018), using the decostand function of the R package *vegan* (Oksanen et al. 2019). We used *c*-means fuzzy clustering (with $k = 3$) to cluster the taxa into different dispersal-dormancy strategies (tables B1–B4; Kaufman and Rousseeuw 1990; Borcard et al. 2018), using the R package *cluster* (Maechler et al. 2018). We performed principal component analysis (PCA) on the rank-transformed trait data to reduce the dimensionality of the trait space, and we extracted the PCA loadings to explain the divergence among clusters. Taxa belonging to each cluster are listed in tables B1–B4.

Table B1: Taxa primarily belonging in cluster 1

Taxon	<i>n</i>
Chironomidae	38
Orthoclaadiinae	15
Tanypodinae	14
Platyhelminthes	12
<i>Polypedilum</i>	10
Hirudinea	9
Oligochaeta	8
<i>Tanytarsus</i>	5
Chironominae	4
<i>Larsia</i>	4
<i>Metricnemus</i>	4
<i>Chironomus</i>	3
Elmidae	3
<i>Elpidium</i>	3
<i>Monopelopia</i>	3
Sphaeroceridae	3
Copepoda	2
<i>Corynoneura</i>	2
<i>Dero</i>	2
<i>Dero superterrenus</i>	2
<i>Elpidium bromeliarum</i>	2
<i>Limnophyes</i>	2
Naididae	2
<i>Phytotematocladus delarosai</i>	2
<i>Pristina</i>	2
<i>Tanytarsus bromelicola</i>	2
<i>Aelosoma</i>	1
<i>Alona bromelicola</i>	1

Table B1 (Continued)

Taxon	<i>n</i>
<i>Annelida</i>	1
<i>Apocyclops</i>	1
<i>Aulophorus superterrenus</i>	1
<i>Boreochlus</i>	1
<i>Bryocamptus</i>	1
<i>Callistocypris mckenziei</i>	1
Canacidae	1
<i>Candonopsis kingsleyi</i>	1
<i>Ceriodaphnia</i>	1
<i>Ceriodaphnia laticaudata</i>	1
Chironominae or Tanypodinae	1
Chironomini	1
Daphnidae	1
<i>Elpidium maracaoensis</i>	1
<i>Eukiefferiella</i>	1
<i>Gravatamberus</i>	1
<i>Harnischia</i>	1
Harpacticoida	1
<i>Latinopsis</i>	1
<i>Paratanytarsus</i>	1
Podonominae	1
<i>Polypedilum kaingang</i>	1
<i>Polypedilum marcondesi</i>	1
<i>Pristina osborni</i>	1
<i>Rheocricotopus</i>	1
<i>Smittia</i>	1
<i>Stempellinella</i>	1
<i>Stenochironomus atlanticus</i>	1
Tanytarsini	1

Note: These taxa have high capacities for passive dispersal. Their capacities for dormancy, however, span a range of values. Some are high, others low.

Table B2: Subset of cluster 1 taxa with high capacities for dispersal and passive dispersal

Taxon	<i>n</i>
Copepoda	2
<i>Alona bromelicola</i>	1
<i>Apocyclops</i>	1
<i>Bryocamptus</i>	1
<i>Ceriodaphnia</i>	1
<i>Ceriodaphnia laticaudata</i>	1
Daphnidae	1
Harpacticoida	1

Table B3: Taxa primarily belonging in cluster 2

Taxon	<i>n</i>
Diptera	42
<i>Culex</i>	28
<i>Wyeomyia</i>	24
Ceratopogonidae	22
Psychodidae	19
<i>Toxorhynchites</i>	17
Ephydriidae	15

Table B3 (Continued)

Taxon	<i>n</i>
<i>Bezzia</i>	13
<i>Telmatoscopus</i>	8
Culicidae	7
<i>Forcipomyia</i>	7
<i>Culicoides</i>	3
<i>Pericoma</i>	3
Anophelinae	2
<i>Culex albipes</i>	2
<i>Culex aphyllactus</i>	2
<i>Culex imitator</i>	2
Culicinae	2
<i>Sphaeromias</i>	2
Trichoptera	2
<i>Alepia apexalba</i>	1
<i>Alepia zavortinkii</i>	1
<i>Anopheles bellator</i>	1
<i>Anopheles cruzi</i>	1
<i>Anopheles homunculus</i>	1
<i>Anopheles kompii</i>	1
<i>Anopheles neivai</i>	1
<i>Anopheles</i> , <i>Wyeomia</i> , or <i>Culex</i>	1
<i>Culex antillumagnorum</i>	1
<i>Culex bisulcatus</i>	1
<i>Culex carioca</i>	1
<i>Culex daumastocampa</i>	1
<i>Culex daumastocampa</i> , <i>jenningsi</i> , or <i>rejector</i>	1
<i>Culex daumasturus</i>	1
<i>Culex davisii</i>	1
<i>Culex hedys</i>	1
<i>Culex inimitabilis</i>	1
<i>Culex jenningsi</i>	1
<i>Culex neglectus</i>	1
<i>Culex rejector</i>	1
<i>Culex shopei</i>	1
<i>Culex siphonulatus</i>	1
<i>Culex stonei</i>	1
<i>Culex worontzowi</i>	1
<i>Dasyhelea</i>	1
Dasyheleniae	1
<i>Haemagogus</i>	1
<i>Limatus durhami</i>	1
Nematocera	1
<i>Orthopodomyia</i>	1
<i>Phylloicus bromeliarum</i>	1
<i>Psychoda romeroi</i>	1
<i>Runchomyia frontosa</i>	1
<i>Stilobezzia</i>	1
<i>Toxorhynchites guadeloupensis</i>	1
<i>Toxorhynchites haemorroidalis</i>	1
<i>Toxorhynchites portoricensis</i>	1
<i>Toxorhynchites purpureus</i>	1
<i>Toxorhynchites solstitialis</i>	1
<i>Toxorhynchites theobaldi</i>	1
<i>Toxorhynchites trichopygus</i>	1
<i>Wyeomyia abebela</i>	1
<i>Wyeomyia abebela</i> , <i>circumcincta</i> , or <i>melanopus</i>	1
<i>Wyeomyia aphobema</i>	1
<i>Wyeomyia circumcincta</i>	1

Table B3 (Continued)

Taxon	<i>n</i>
<i>Wyeomyia edwardsi</i>	1
<i>Wyeomyia edwardsi</i> , <i>mulhensi</i> , or <i>theobaldi</i>	1
<i>Wyeomyia forattinii</i>	1
<i>Wyeomyia forcipenis</i>	1
<i>Wyeomyia greyii</i>	1
<i>Wyeomyia melanopus</i>	1
<i>Wyeomyia mitchellii</i>	1
<i>Wyeomyia mulhensi</i>	1
<i>Wyeomyia pallidoventer</i>	1
<i>Wyeomyia palmata</i>	1
<i>Wyeomyia pseudopecten</i>	1
<i>Wyeomyia splendida</i>	1
<i>Wyeomyia theobaldi</i>	1

Note: These taxa have high capacities for dormancy and low capacities for passive dispersal. They typically have some capacity for active dispersal.

Table B4: Taxa primarily belonging in cluster 3

Taxon	<i>n</i>
Cecidomyiidae	22
Forcipomyiinae	18
Syrphidae	18
Brachycera	17
Tipulidae	17
Coleoptera	16
Tabanidae	16
Scirtidae	15
Heteroptera	14
<i>Atrichopogon</i>	13
<i>Corethrella</i>	13
Empididae	11
Dolichopodidae	10
<i>Copestylum</i>	9
<i>Trentepohlia</i>	9
Dytiscidae	8
Hydrophilidae	7
Limoniinae	7
Sciaridae	6
Phoridae	5
Limoniidae	4
Stratiomyidae	4
<i>Aedes</i>	3
Corethrellidae	3
<i>Meromacrus</i>	3
<i>Olbiogaster</i>	3
<i>Scirtes</i>	3
<i>Brachypremna</i>	2
Ceratopogoninae	2
Coenagrionidae	2
Eristalinae	2
<i>Eristalis</i>	2
<i>Hermetia</i>	2
Lampyridae	2
<i>Leptagrion andromache</i>	2
Leptoconopinae	2
<i>Microvelia</i>	2
Polyphaga	2

Table B4 (Continued)

Taxon	<i>n</i>
Ptilodactylidae	2
Scatopsidae	2
Sphaeridiinae larva	2
Thaumaleidae	2
<i>Aedes albopictus</i>	1
aff. Drosophilidae	1
Anisopodidae	1
<i>Aulacigaster</i>	1
Axymyiidae	1
<i>Bromeliagrion</i>	1
<i>Celina</i>	1
<i>Cheilotrichia</i>	1
<i>Contacyphon</i>	1
<i>Copelatus bimaculatus</i>	1
<i>Corethrella belkini</i>	1
<i>Corethrella fulva</i>	1
<i>Corethrella infuscata</i>	1
Ctenophorinae	1
<i>Fidena</i>	1
<i>Fidena rufopilosa</i>	1
Gerridae	1
Hexatominae	1
<i>Lejops barbiellini</i>	1
<i>Leptagrion</i>	1
<i>Leptagrion bocainense</i>	1
<i>Leptagrion bocainense</i> or <i>macrurum</i>	1
<i>Leptagrion elongatum</i>	1
<i>Leptagrion macrurum</i>	1
<i>Leucotabanus</i>	1
<i>Limonia</i>	1
Limoniini	1
<i>Mecistogaster modesta</i>	1
Mesoveliidae	1
<i>Ocyptamus</i>	1
<i>Omicrus ingens</i> adult	1
<i>Omicrus ingens</i> larva	1
<i>Ormosia</i>	1
<i>Palpada</i>	1
<i>Paravelia</i>	1
Perisclididae	1
<i>Pipiza</i>	1
<i>Quichuana</i>	1
<i>Rhabdomatrix</i>	1
Sphaeridiinae adult	1
Sphaerodinae	1
<i>Stibasoma bicolor</i>	1
<i>Stibasoma fulvohirtum</i>	1
<i>Tipula</i>	1
Tipulinae	1
<i>Trentepohlia dominicana</i>	1
Veliidae	1
<i>Xilota</i>	1
Zigoptera	1

Note: These taxa have low capacities for dormancy and relatively low capacities for active dispersal.