

# Species sorting and patch dynamics in harlequin metacommunities affect the relative importance of environment and space

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**Abstract.** Metacommunity theory indicates that variation in local community structure can be partitioned into components including those related to local environmental conditions vs. spatial effects and that these can be quantified using statistical methods based on variation partitioning. It has been hypothesized that joint associations of community composition with environment and space could be due to patch dynamics involving colonization–extinction processes in environmentally heterogeneous landscapes but this has yet to be theoretically shown. We develop a two-patch, type-two, species competition model in such a “harlequin” landscape (where different patches have different environments) to evaluate how composition is related to environmental and spatial effects as a function of background extinction rate. Using spatially implicit analytical models, we find that the environmental association of community composition declines with extinction rate as expected. Using spatially explicit simulation models, we further find that there is an increase in the spatial structure with extinction due to spatial patterning into clusters that are not related to environmental conditions but that this increase is limited. Natural metacommunities often show both environment and spatial determination even under conditions of relatively high isolation and these could be more easily explained by our model than alternative metacommunity models.

**Key words:** *metacommunity; patch dynamics; spatial effects; species sorting; stochastic effects; variation partitioning.*

## INTRODUCTION

A metacommunity is a set of local communities that are connected by the dispersal of at least one of the component species (Hanski and Michael 1991, Leibold et al. 2004, Holyoak et al. 2005). Although theories of species interactions at local scales are well understood (see Chase and Leibold 2003), metacommunity ecology considers ecological dynamics at larger spatial scales by considering how dispersal among local communities affects these dynamics. The concept is a useful way to integrate what we know about spatial dynamics in community ecology by expanding the field of community ecology to include larger spatial scales.

The array of processes and patterns involved is complex but theory on this topic can be crudely categorized into four different “perspectives” (Leibold et al. 2004, Holyoak et al. 2005, Leibold 2011, Logue et al. 2011) that differ in the assumptions they make about dispersal, random extinctions, and the relevance of environmental heterogeneity among patches. These perspectives are the “species-sorting” view, in which community assembly in local communities always goes to an endpoint that depends only on local environmental

conditions; “neutral theory,” in which community assembly depends only on stochastic demography and dispersal and has no such environmental dependence; “mass effects,” in which strong source–sink relations exist between patches that vary in local environmental conditions and result in communities that contain species that are not always optimally suited for the local conditions; and “patch dynamics,” in which regular stochastic extinctions due either to demographic stochasticity or local environmental disturbances (Lande 1993) disrupt the process of community assembly to a final endpoint.

Cottenie (2005) suggested that the prevalence of different types of metacommunity dynamics could be evaluated by the degree to which community composition is related to environmental factors vs. purely spatial effects by using a method of variation partitioning on community composition in the metacommunity (Borcard et al. 1992, Peres-Neto et al. 2006, Dray et al. 2012). Species sorting predicts that only environmental variation among patches should determine variation in community composition, whereas the neutral models predict that there should be no such environmental regulation and that spatial effects should predominate. Mass effects predict that both environmental and spatial effects should be present assuming that source sink relations occur among nearby patches. Patch dynamics models are more complex: if they ignore environmental variation (assume all patches are environmentally

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identical), they of course predict only spatial effects (Cottenie 2005). However, if they allow patches to vary in environmental conditions (Horn and MacArthur [1972] called these “harlequin landscapes”), it seems likely that they would also predict that both spatial and environmental effects should be present (Ng et al. 2009, Pinto and MacDougall 2010, Leibold 2011) because recolonization after extinctions would be biased by immigration from nearby patches.

Cottenie (2005) used variation partitioning methods (Borcard et al. 1992, Peres-Neto et al. 2006, Dray et al. 2012) on empirical datasets to quantify how local variation in community composition was related to environmental factors, spatial patterning or random effects (unexplained residual variation). Variation partitioning is a statistical method that partitions variation in community composition to four distinct groups of predictor variables. These include purely environmental effects ( $[E|S]$ ) that quantify associations between composition and environment (correcting for any spatial patterning), purely spatial effects ( $[S|E]$ ) that quantify spatial patterns (that could not be explained by variation in local environmental conditions), an effect due to the confounded effects of space and environment ( $[EW|S]$ ) that could be explained by either or both environment and spatial patterning (but that could not easily be further resolved due to correlations between the two), and a residual effect ( $[R]$ ) that was unrelated to either local environment or to spatial patterning (and is thus “random” or unexplained). He conducted a meta-analysis of 158 such data sets and found a perhaps surprising degree of support for environmental regulation of community composition compared to spatial effects, therefore suggesting the dominance of species-sorting processes. This is surprising because species sorting seems to require that dispersal be neither too high (otherwise leading to spatial effects due to mass effects; Mouquet and Loreau 2003) nor too low (otherwise leading to spatial effects due to proximity effects in recolonization of patches following local extinctions in patch dynamics perspectives) as well as having little demographic drift (as assumed by the neutral perspective). Nevertheless, despite a much stronger effect of environment than of space on composition, most data sets also had relatively high amounts of unexplained variation, indicating either that environmental descriptors were insufficient, that spatial effects were inadequately modeled, or that there were substantial effects of either demographic stochasticity or movement. There is now a substantial literature refining the statistical methodology of variation partitioning (reviewed in Dray et al. [2012]) and using it to infer metacommunity dynamics in a wide array of ecosystems (reviewed by Logue et al. [2011] and by Soininen [2014]). Soininen's (2014) meta-analysis of over 300 analyses confirms Cottenie's (2005) general conclusions but highlights that their connections with theory are still very weak.

A broadly synthetic theory of metacommunities would encompass all four perspectives but has yet to be developed. Previous publications have addressed how

species sorting and mass effects interact (e.g., Amarasekare and Nisbet 2001, Mouquet and Loreau 2002, 2003, Abrams and Wilson 2004) and how patch dynamics and neutral theory interact (Hubbell 2001, Hanski 2008). Horn and MacArthur (1972) also did some pioneering work on the maintenance of diversity in what they called harlequin communities (in which patch dynamics and species sorting interact) but much less is known about how the interaction of species sorting and patch dynamics may influence patterns of distributions of species in landscapes.

Species sorting and patch dynamics are likely to interact because both are assumed to occur for similar ranges of (intermediate) dispersal. In theoretical models of both types, there is typically an assumption of separation of time scales between local community dynamics and colonization events (Law and Leibold 2005). Consequently, dispersal does not play any role in maintaining mass effects among patches and is instead important because it fuels the process of community assembly. In the species-sorting view, where random extinctions are ignored, such dispersal eventually leads to local communities being dominated by the species that are best suited to local environmental conditions because they drive less suited species to extinctions via competitive exclusion. In the patch dynamics view, random extinctions (due either to demographic stochasticity or to local disturbances; Lande 1993) disrupt this process and dispersal is important because it allows local populations to recover and be maintained despite such extinctions (Levins and Culver 1971, Horn and MacArthur 1972, Hastings 1980). An additional complication in comparing models of species sorting with patch dynamics is that most previous work in patch dynamics ignores the possible effects of environmental differences among patches (but see Horn and MacArthur 1972, Holt 1997, Shurin et al. 2004, Gross 2008, Nagelkerke and Menken 2013). Consequently patch dynamics approaches have so far been hard to compare with models of species sorting where such environmental differences are critical.

Examples of cases where patch dynamics and environmental filters interact are probably common. An excellent example, with many of the features we highlight in our model, comes from work on a three species *Daphnia* assemblage in rock pools in the Baltic Sea (e.g., Pajunen and Pajunen 2003, 2007). These involve large numbers of rock pools that differ in local conditions (size, water chemistry, etc.) that favor different species of *Daphnia*. Although different *Daphnia* species can coexist in some pools for some period of time, they are largely seen to be mutually exclusive of each other. Background extinctions are common (approximately 20% per year) and they are balanced by colonizations with occupancy rates roughly fixed at 30%. Over a period of 17 years however, 70% of pools were occupied at least once, indicating that the large majority of patches can support *Daphnia* populations at least to some degree. Colonization rates by the three species are largely proportional to the product of occupied and empty patches as predicted by patch

dynamic models (e.g., Levins and Culver 1971, Hastings 1980) but otherwise similar for all three species and dispersal is likely constrained to relatively short distances ( $<10$  m) although long distance dispersal almost certainly also happens. We suspect that similar features are common in many other systems (e.g., Ellis et al. 2006).

Here, we ask how stochastic extinctions like those that characterize patch dynamics models affect the process of species sorting. To do this, we elaborate on the work by Horn and MacArthur (1972) to combine the main elements of species sorting (community assembly, niche partitioning in relation to habitat, and habitat heterogeneity) and patch dynamics (background extinctions due to stochastic factors) in a simple two-species–two-patch-type setting. Previous work has focused on conditions for coexistence and diversity in the metacommunity (Horn and MacArthur 1972, Holt 1997, Shurin et al. 2005, Gross 2008, Nagelkerke and Menken 2013). Here, however, we instead focus on the degree to which patches in this model are occupied by local competitive dominants as a function of the magnitude of extinctions using both analytical and simulation methods. As expected, the results show that background extinctions strongly erode the environmental regulation of patch occupancy predicted by species sorting. We then study effects on partitioning of community composition in relation to environment vs. space by modeling a similar dynamic on a lattice and consider the additional effects of environmental spatial autocorrelation and dispersal. Our results confirm that environmental regulation of community composition declines with the extinction rate. This is associated with both an increase in spatial patterning and in random variation (unexplained by either spatial or environmental effects). These findings indicate that colonization–extinction dynamics in harlequin metacommunities could explain the common observation that environmental and spatial patterning jointly explain community composition in metacommunities that seem to be dispersal limited.

#### THE MODEL

To investigate the interaction between patch dynamics and species sorting, we analyze a minimal model that includes the critical elements of both of these perspectives. We do so first with an analytical model in which we model space implicitly using the basic metapopulation approach of Levins and Culver (1971), Horn and MacArthur (1972), and Hastings (1980). We then develop a spatially explicit version of the model in which patches occur in a lattice and use simulations to examine how environmental, spatial, and stochastic effects are generated in our model.

We start with a metacommunity consisting of an infinite number of two patch types inhabited by two competing species each of which is dominant in a different patch type. The two patch types exist in the metacommunity in proportions  $h_a$  and  $h_b$ . In each case, the patch can be colonized at a rate  $c$  by either species when the patch is

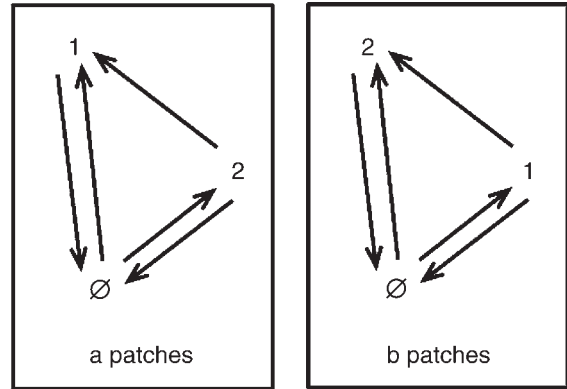


FIG. 1. Assembly graphs for the two-patch model. Different assembly graphs apply to each patch type (a vs. b). Patches can be empty ( $\emptyset$ ), occupied by species 1, or occupied by species 2. Upward arrows denote colonization events (in this case, by the species at the end of the arrow) and downward arrows denote background extinctions (by the species at the root of the arrow). Colonization by a superior competitor of a patch occupied by the inferior competitor implies extinction of that inferior competitor. Patches thus fall into six categories depending on patch type and occupancy and arrows denote all the possible transitions among these categories.

uninhabited, but then the inferior competitor is replaced by the superior competitor when the latter colonizes an occupied patch. We assume a separation of time scales (Law and Leibold 2005) where intra-patch dynamics go to steady state on a very fast time scale relative to dispersal events. Both species go extinct in any given patch at a given rate  $e$ . We use the letters a and b to describe the patch types, the numbers 1 and 2 to refer to the species, and assume that species 1 is better adapted to patch type a and species 2 to patch type b. We model the dynamics of patch frequencies  $p_{ij}$  where  $i$  refers to the species present in the patch and  $j$  refers to the patch type. An assembly graph (sensu Law and Morton 1996) for this situation can illustrate the situation as shown in Fig. 1. The model consists of the following dynamic equations:

$$\frac{dp_{1a}}{dt} = c(p_{1a} + p_{1b})(h_a - p_{1a}) - e \times p_{1a} \quad (1)$$

$$\begin{aligned} \frac{dp_{2a}}{dt} = & c(p_{2a} + p_{2b})(h_a - p_{1a} - p_{2a}) \\ & - cp_{2a}(p_{1a} + p_{1b}) - e \times p_{2a} \end{aligned} \quad (2)$$

$$\begin{aligned} \frac{dp_{1b}}{dt} = & c(p_{1a} + p_{1b})(h_b - p_{1b} - p_{2b}) \\ & - cp_{1b}(p_{2a} + p_{2b}) - e \times p_{1b} \end{aligned} \quad (3)$$

$$\frac{dp_{2b}}{dt} = c(p_{2a} + p_{2b})(h_b - p_{2b}) - e \times p_{2b}. \quad (4)$$

We analyze the model using conventional methods as presented in Appendix A. We are interested in the effects of extinction on occupancy patterns and on how this

differs from the species-sorting case where the background extinction rate is assumed to equal zero. To do so, we examine two types of deviation. In the first, we evaluate the degree to which non-empty patches are occupied by the competitive dominant vs. the subordinate species using the metric (where stars denote equilibrium values)

$$G = \frac{p_{1a}^* + p_{2b}^*}{p_{1a}^* + p_{2a}^* + p_{1b}^* + p_{2b}^*}. \quad (5)$$

As a second measure of deviation from species sorting, we examine the prevalence of empty patches in the metacommunity (there are no empty patches under species sorting) using the metric

$$Z = 1 - p_{1a}^* - p_{2a}^* - p_{1b}^* - p_{2b}^*. \quad (6)$$

Replacing with coexistence equilibrium values (see Appendix A), it is easy to show that

$$G = \frac{c}{e + c} \quad (7)$$

$$Z = \frac{e}{c} \quad (8)$$

so that  $Z$  and  $G$  are related:  $G = 1/(1 + Z)$ . This suggests that the quantity  $G - 1/(1 + Z)$  might be a good index for evaluating whether a metacommunity is actually close to its equilibrium behavior. The model thus shows that deviations from species sorting are roughly commensurate with the background extinction rate, at least until extinction thresholds are reached. We have studied modifications of this model that give a reduced extinction rate for each species in its favored habitat and obtained results that are qualitatively robust to such a change (results not shown).

This first model treats space in an implicit way, as has been done in much previous work in patch dynamics (e.g., Levins and Culver 1971, Horn and MacArthur 1972, Hastings 1980, Shurin et al. 2004, Gross 2008, Nagelkerke and Menken 2013). It shows that associations between environmental conditions and community composition are likely to decrease as the background rate of extinctions increases. It, however, seems likely that spatial effects could also be important since empty patches would be more likely to be colonized by immigrants from nearby patches than those further away, regardless of patch type (Ng et al. 2009, Pinto and MacDougall 2010, Leibold 2011). This could provide an explanation for the existence of metacommunities that show patterns of association of composition with both space and environment (e.g., Cottenie 2005, Ellis et al. 2006). We investigated how background extinctions in a heterogeneous landscape of patches affected how community composition related to environmental, spatial, and stochastic factors by simulating the process on a lattice of 30\*30 patches. We studied two types of lattices: random lattices and spatially autocorrelated

lattices, which were obtained using the “forced to be full” algorithm (Mangel and Adler 1994). Details of our method are presented in Appendix A.

As in our spatially implicit model, environmental regulation of community composition declined strongly and in a roughly proportional way to background extinction as measured by  $G$  and  $1/(1 + Z)$  (Fig. 2). As in the analytical model, when extinctions were absent,  $G$  was 1 and declined with the extinction rate ( $e$ ) in a monotonic fashion. We found that the observed value of  $G$  in our simulations was reasonably well predicted by the analytical model although the observed values tended to be a bit smaller and this was more so at high extinction rates and in random rather than autocorrelated landscapes. We found that  $G$  remained relatively high (above 0.75) even at extinction rates that approached the critical threshold for coexistence of the two species. Finally we also found that  $G$  and  $1/(1 + Z)$  were very similar to each other at equilibrium as in our analytical model although they were not identical (Pearson correlation coefficients were 0.97 and 0.93 for the random and autocorrelated landscapes respectively). In the simulations, differences between  $G$  and  $1/(1 + Z)$  can be due either to deviation from equilibrium or to effects of spatially limited dispersal but our simulations indicate that the spatial effects are small, at least in the simulations we modeled. We found that  $1/(1 + Z)$  was indeed very similar to the analytical value but that  $G$  was somewhat underestimated as predicted showing that patch dynamic models with neighbor-limited dispersal, have lower occupancy than otherwise identical infinite-patch-unlimited-dispersal Levins-type models (Roy et al. 2008).

We also used methods of variation partitioning to evaluate how distributions were predicted by purely environmental ( $[E|S]$ ), purely spatial ( $[S|E]$ ), residual ( $R$ ), and spatio-environmental effects that could not be resolved ( $[S|E]$ ) using the method of PCNM developed by Peres-Neto et al. (2006), which has become the most commonly used method (Logue et al. 2011). As might be expected from the results on  $G$ , environmental effects ( $[E|S]$ ) were very high (in excess of 0.8) when extinction rates were zero and declined as the extinction rate increased (Fig. 2). At the highest extinction rates environmental effects were very small and approached zero. This occurred in part because species increasingly used suboptimal patches (as described by measures of  $G$ ) but also because of the increasing prevalence of empty patches (as measured by  $Z$ ). Additionally we found that spatial patterning ( $[S|E]$ ) increased from levels near zero when extinctions are absent to levels of about 0.2 at high extinction rates that approach the critical threshold for metacommunity coexistence. In the random landscape joint environmental-spatial effects ( $[EwS]$ ) were small but they were more substantial in the autocorrelated landscapes as expected. These effects also declined with extinction in the autocorrelated landscapes in parallel with the purely environmental ones. Finally, we found



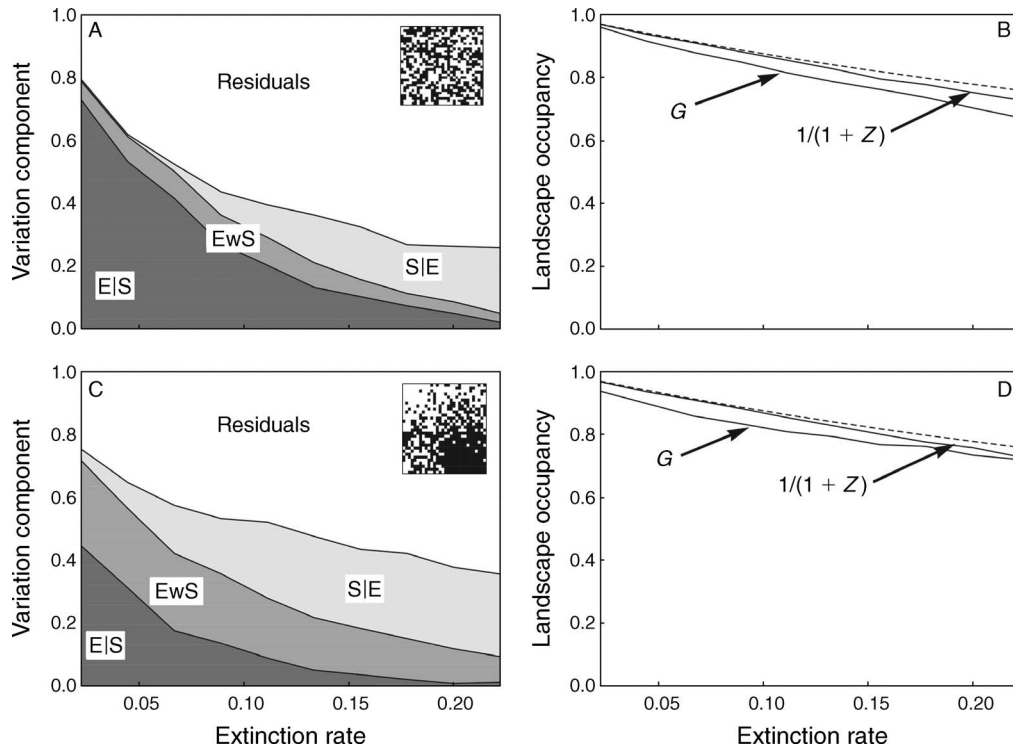


FIG. 2. Characteristics of the metacommunity, depending on the extinction rate. Panels (A) and (C) correspond to the variation partitioning, teasing apart environmental and spatial signals in the metacommunity structure. All four components add up to 1.0, where variation was characterized as purely environmental ( $E|S$ ), purely spatial ( $S|E$ ), joint environmental-spatial ( $EwS$ ), or residual and the magnitude of each component is the vertical distance in the area labeled for each category shaded separately for each component. Panels (B) and (D) show the proportion  $G$  and  $1/(1+Z)$  as well as the (identical) values of  $G$  and  $1/(1+Z)$  predicted by the non-spatial analytical model (dashed line), where  $G$  is the degree to which non-empty patches are occupied by the competitive dominant vs. the subordinate species and  $Z$  is the prevalence of empty patches in the metacommunity. Panels (A) and (B) correspond to random lattices, panels (C) and (D) to autocorrelated lattices, typical example of landscapes are shown in insets. Curves show the mean of 20 replicates for each  $e$  (extinction rate) value.

that residual ( $[R]$ ) variation increased from near zero at low extinction to being substantial (in excess of 0.7) at high extinction rates.

We examined the robustness of our simulations to a number of factors, including the probability of local dispersal, the amount of landscape evenness in the patch type frequencies, the degree of localized dispersal, the amount of spatial autocorrelation in patch distribution, the size of the landscape, and the number of patch types and species. We found that our results were qualitatively robust to all of these modifications and, in fact, were often nearly quantitatively so. These are described in Appendix B.

#### DISCUSSION

The emerging field of metacommunity ecology proposes a complex array of possible dynamics that depend in part on dispersal–connectivity relations in the landscape of the metacommunity and in part on factors that affect local dynamics within patches in the metacommunity (Leibold et al. 2004, Leibold 2011). Here, we investigated how colonization–extinction dynamics, typically studied in environmentally homoge-

neous patches, interacts with the process of species sorting that is typically studied without considering colonization–extinction processes. Although several other studies have worked with similar models (Horn and MacArthur 1972, Holt 1997, Shurin et al. 2004, Gross 2008, Nagelkerke and Menken 2013) our model specifically focuses on how these two processes interact to affect how community composition relates to environmental regulation and by extension to spatial effects vs. indeterminate variation due to stochastic assembly history.

We found that the degree of environmental regulation of community structure can be strongly reduced by colonization–extinction dynamics and that this depended quantitatively on the extinction and colonization rates in a simple way. Thus, colonization–extinction dynamics may be an important possible explanation for the relatively large amounts of variation in community composition seen that cannot be explained by environmental effects (Cottenie 2005). We also found that colonization–extinction processes could produce spatial effects that are unrelated to environment as speculated by several previous studies (Ng et al. 2009, Pinto and

MacDougall 2009, Leibold 2011). Here, we confirm these speculations but we also show that the spatial effects should also occur in the presence of high residual or random variation in such cases. Previous meta-analyses of metacommunity data (Cottenie 2005, Logue et al. 2011) show that this is very often the case.

The highly simplified way we implemented our model makes environmental sorting very simple and likely strong. If environmental gradients are more complex or if the assumption of separation of time scales is relaxed (e.g., Adler and Mosquera 2000), detecting their effects on community composition is likely to be weaker and more difficult to evaluate. In other work (Loeuille and Leibold 2014) we found no strong effect of relaxing time scales in a closely related model of niche evolution. Nevertheless, our work highlights the qualitative ways that environmental factors, spatial effects, and apparently random variation interact in harlequin landscapes.

The four paradigms of metacommunity (Leibold et al. 2004) are often perceived as independent views of ecological spatial dynamics. However, in real systems, many processes overlap or alternate in space and time, so that each of the paradigms can apply and interact in any given community. In the present work, we tackle how considering simultaneously aspects of two paradigms (species sorting and patch dynamics) can influence the composition of communities in space. To do so, we have drawn a very simple model. Many aspects of this model could be modified to account for other specific issues. For instance, it is possible to include niche construction aspects in such models (Loeuille and Leibold 2014). Also, in the context of global changes, it would be interesting to investigate how community composition changes along an environmental gradient, when this gradient is modified continuously in time (e.g., to mimic increasing temperatures, see Norberg et al. [2012], Kubisch et al. [2013]). Similarly, the investigation of fragmentation with consequent effects on local extinction rates could easily be investigated in such systems.

Although we here focus on how patch dynamics in landscapes of heterogeneous patches may affect community composition, we do not mean to imply that other processes such as mass effects and stochastic demography do not play a role (Durrett and Levin 1998). The application of these various possibilities in explaining spatial patterning and environmental determination of community composition will depend on the relative temporal and spatial scales of dispersal relative to local population dynamics (Hanski 1983, Law and Leibold 2005, Pinto and MacDougall 2009, Leibold 2011, Logue et al. 2011) and fall outside the scope of our paper. Better identifying how colonization–extinction vs. mass effects vs. stochastic demography and species sorting lead to joint spatial and environmental regulation of metacommunities would be an important contribution in providing clear links between the study

of metacommunity patterns and theories (Logue et al. 2011).

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## SUPPLEMENTAL MATERIAL

### Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-2354.1.sm>