

Predators alter the scaling of diversity in prey metacommunities

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Although predator effects on the number of locally coexisting species are well understood, there are few formal predictions of how these local predator effects influence patterns of prey diversity at larger spatial scales. Building on the theory of island biogeography, we develop a simple model that describes how predators can alter the scaling of diversity in prey metacommunities and compares the effects of generalist and specialist predators on regional prey diversity. Generalist predators, which consume prey randomly with respect to species identity, are predicted to reduce α -diversity and increase β -diversity thereby maintaining regional diversity (γ -diversity). Alternatively, specialist predators, which filter out prey species intolerant of predators, are predicted to reduce both α -diversity and β -diversity by causing the same prey species to be extirpated in each locality, resulting in regional prey species extinctions and lower γ -diversity. These distinct effects of generalist and specialist predators on prey diversity at different spatial scales are uniquely shaped by the extent of predation within those metacommunities. Overall, our model results make general predictions for how different types of predators can differentially affect prey diversity across spatial scales, allowing a more complete understanding of the possible implications of predator eradication or introductions for biodiversity.

All organisms consume or are consumed by other organisms, making predation fundamental to the organization of communities (Wellborn et al. 1996, Duffy 2002) and often the numbers of species that can coexist locally and regionally (Paine 1966, Polis 1991). While the effects of predators on the number of locally coexisting species (i.e. α -diversity) have been well studied (reviewed by Sih et al. 1985, Holt and Lawton 1994, Menge 1995, Abrams et al. 1996, Proulx and Mazumder 1998, Chase et al. 2002), more recent focus has shifted toward understanding how these local effects of predators scale-up to alter regional diversity (γ -diversity) of prey metacommunities (Shurin and Allen 2001, Kneitel and Miller 2003, Chase et al. 2009). Knowing how predators alter prey diversity at different spatial scales, however, requires knowledge of how predators alter prey community assembly and the structure of species composition from site-to-site, known as β -diversity (Chase et al. 2009).

Although both stochastic (e.g. ecological drift; Hubbell 2001) and deterministic (e.g. niche differentiation; Chase and Leibold 2003) processes contribute simultaneously to community assembly (Gravel et al. 2006, Leibold and McPeck 2006, Adler et al. 2007), external factors that influence the size of the realized species pool can alter the relative importance of those processes (Chase 2007, 2010, Chase et al. 2009, Chase and Myers 2011). For example, top predators can potentially alter the relative importance of stochastic and deterministic processes in

prey community assembly, leading to changes in patterns of β -diversity by altering prey community size, colonization and extinction rates, and the pool of species available for colonization (Chase et al. 2009). Predators can increase β -diversity by increasing the relative importance of stochastic contributions to assembly through reductions in local population and community size (Orrock and Fletcher 2005, Ryberg and Chase 2007), or decrease β -diversity by selectively filtering the regional species pool (Chase et al. 2009). Thus, the net effect of predators on β -diversity should depend largely on the degree of predator selectivity within the prey regional species pool, as well as the magnitude of consumptive effects on overall community size.

Different types of predators vary substantially in their degree of prey selectivity (Cooper et al. 1985, Osenberg and Mittelbach 1989, Sih and Christensen 2001), with important implications for community structure (Jiang and Morin 2005, Östman and Chase 2007, Worsfold et al. 2009). Here, we use a simple modeling approach to theoretically explore how generalist and specialist predators might influence β -diversity and the scaling of diversity in prey metacommunities. We do this by first incorporating the effects of these different types of predators into a simple depiction of community assembly idealized by MacArthur and Wilson's (1963, 1967) equilibrium theory of island biogeography (ETIB) (see also Ryberg and Chase 2007). Next, using an island analogue of metapopulation models, we expand the predictions of the ETIB to describe how

differences in the spatial scale of predator population dynamics can alter their effects on the scaling of diversity in prey metacommunities. It is important to note that this model is a heuristic depiction of how different predator types affect prey diversity at different spatial scales, and therefore lacks some realism (Brown 1981, Rosenzweig 1995, Whittaker 1998). Our primary goal is to achieve generality while maintaining mathematical tractability, so our results might allow a more complete understanding of the possible implications of predator eradications or introductions for biodiversity (Myers and Worm 2003, Borrvall and Ebenman 2006, Heithaus et al. 2008, Terborgh and Estes 2010). Nevertheless, we recognize that relaxing the fundamental assumptions of our trophic extension of the ETIB can lead to qualitatively different results, and we explore some of these assumptions below.

The model

The ETIB predicts that the equilibrium number of species ($\hat{S}$) on an island will be a function of the immigration rate (I), extinction rate per species (E), and number of species in the mainland pool (P), resulting in

$$\hat{S} = \frac{IP}{I + E} \quad (1)$$

To explore β -diversity under the ETIB, we first re-define $\hat{S}$ as α -diversity and P as γ -diversity. When diversity is partitioned additively ($\gamma = \alpha + \beta$; Lande 1996, Veech et al. 2002), β -diversity becomes the difference between P and $\hat{S}$ ($\beta = \gamma - \alpha$), which yields the following simplified mathematical expression:

$$\hat{\beta} = \frac{EP}{I + E} \quad (2a)$$

Under this modeling approach, the species pool is assumed to be external to the metacommunity (i.e. an open metacommunity). For simplicity, we begin to incorporate predation into the model by assuming that predator population dynamics are determined by processes operating at a spatial scale larger than the spatial extent of the prey metacommunity (i.e. a mobile predator; Holt 1996, Holt and Hoopes 2005). Under this assumption, the metacommunity of interest has no predator-free space. We later relax this assumption. Building on the approach of Ryberg and Chase (2007), we distinguish the effects of different types of predators on the idealized community assembly of prey species under the ETIB model framework by expanding the meaning of the terms generalist and specialist predation beyond their traditional descriptions of prey selectivity to include the impact of predators on prey populations and thus community structure.

Beginning with generalist predation in a large metacommunity, we assume that generalist predators impose a neutral contribution to prey community assembly such that all prey species are equally susceptible to predators, and that by reducing prey population sizes, these predators increase the extinction rates of prey species (Fig. 1a; Ryberg

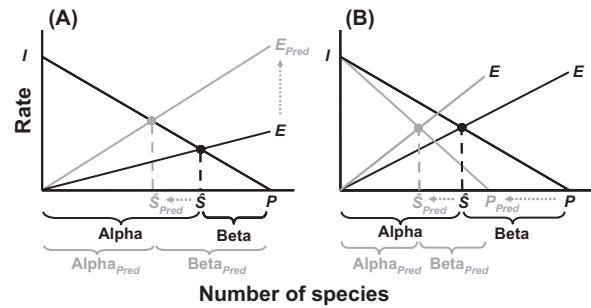


Figure 1. Generalist and specialist predation incorporated into the equilibrium theory of island biogeography (model parameters are defined in the text). (A) Stochastic contributions of generalist predators to prey community assembly through increases in the prey maximum extinction rate decrease α -diversity and increase β -diversity while maintaining the regional species pool (γ -diversity). (B) Deterministic contributions of specialist predators to prey community assembly through selective filtering of the regional species pool decrease α -diversity and β -diversity simultaneously.

and Chase 2007). The total extinction rate of prey species is the sum of environmental (E) and predator-induced (E_{Pred}) contributions to extinction. When $E_{Pred} > 0$, the overall extinction rate increases and results in a simultaneous reduction in α -diversity and increase in β -diversity (Fig. 1A) and is given by

$$\hat{\beta}_G = \frac{P(E + E_{Pred})}{I + E + E_{Pred}} \quad (2b)$$

When generalist predators are present, $E_{Pred} > 0$, and the negative effect of predators on α -diversity is distributed across all localities randomly with respect to species identity, β -diversity among localities is higher than when generalist predators are absent. This negative effect of generalist predators on α -diversity produces an increase in β -diversity, because the diversity of the region (γ -diversity) is determined by the species pool. In other words, generalist predators reduce the community size of their prey, and thus increase the degree to which stochasticity contributes to local community assembly (Orrock and Fletcher 2005). Increasing the strength of generalist predation (increasing E_{Pred} ; Fig. 2A) enhances this effect.

To explore the effects of specialist predators on β -diversity, we incorporate the assumption that predators deterministically filter the prey regional species pool. With no predator-free space in the prey metacommunity, P is decreased by the number of species in the region that cannot coexist with predators, P_{Filter} , to give P_{Pred} (Fig. 1B). Prey immigration (I) and extinction rates (E) remain unchanged as P is decreased to P_{Pred} , because, as in the ETIB, these parameters are assumed to be related to biogeographic features such as island isolation or size that are unaffected by the presence of predators. This causes local prey species richness to decrease ($\hat{S}$ to $\hat{S}_{Pred}$; Fig. 1B), which yields the following mathematical expression for β -diversity,

$$\hat{\beta}_s = \frac{(P - P_{Filter})E}{I + E} \quad (2c)$$

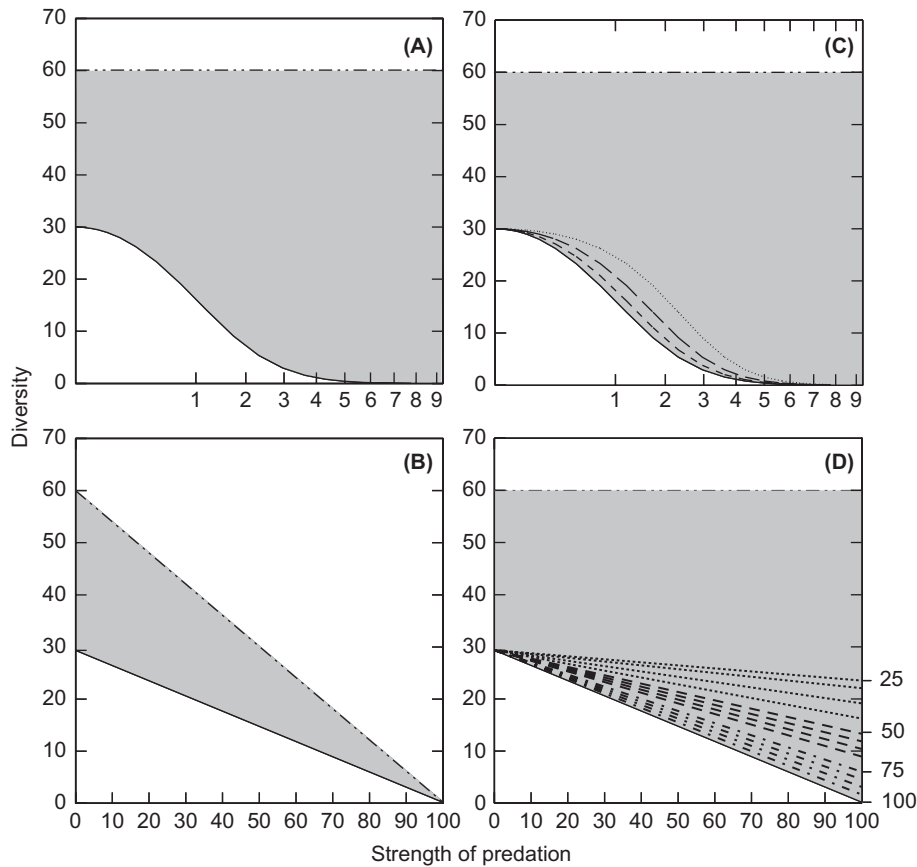


Figure 2. Effect of increasing the strength of generalist and specialist predation on equilibrium prey α -(solid line), γ -(dash-dot-dot line), and β -diversity (shaded). Prey community parameter values are: $I = 15$, $E = 15$, $P = 60$, yielding an equilibrium α -diversity of 30 prey species without predation (y-axis). (A) Numerical runs of the ETIB model with increasing strength of generalist predation ($E_{Pred}/E \times 100$) generate greater decreases in α -diversity and increases in β -diversity while γ -diversity remains unchanged. (B) Increasing the strength of specialist predation (P_{Filter}/P) erodes β -diversity more extensively than α -diversity resulting in the substantial loss of regional diversity (γ -diversity). Under the metapopulation model formulation, increasing the strength of both (C) generalist and (D) specialist predation increases β -diversity, but decreasing predator occupancy (100 $\rightarrow$ 75 $\rightarrow$ 50 $\rightarrow$ 25%; solid $\rightarrow$ dash-dot $\rightarrow$ dash $\rightarrow$ dotted lines, respectively) weakens this relationship. Higher values for E_{Pred} (c_y , lower lines in occupancy quartets) mitigate this occupancy effect for specialist predators.

When specialist predators are present, $P_{Filter} > 0$, the negative effect of predators on γ -diversity is greater than their negative effect on α -diversity, and β -diversity is reduced. As the strength of specialist predation increases (increasing P_{Filter} ; Fig. 2B), prey γ -diversity erodes to a larger degree than α -diversity (i.e. predators cause more regional prey extinctions than local prey extirpations), and β -diversity decreases more substantially. Thus, specialist predators reduce prey diversity at all spatial scales.

Predator occupancy

Predator population dynamics might also be determined by processes operating at a spatial scale that subdivides the prey metacommunity, resulting in variable amounts of predator-free space within that metacommunity (Holt and Hoopes 2005). Under such a scenario, predators would only increase local prey extinction rates when and where they were present. Such variation in the ubiquity of predators across the prey metacommunity should generate changes in the effects of predators on prey. In order to examine the influence of predators on prey β -diversity when predator populations are dynamic, we expand our

modeling approach using an island analogue of metapopulation models to include descriptions of the colonization and extinction dynamics of each species (Holt 2010). First, we re-derive Eq. 1 by tracking the occupancy of each prey species within an open metacommunity using the following equation:

$$\frac{dX}{dt} = c(1 - X) - eX \quad (3a)$$

where X is the proportion of patches occupied, c is the colonization rate, and e is the extinction rate of a prey species leading to an equilibrium occupancy of $X^* = c/(c + e)$. If we assume that there are P prey species in the regional pool with identical colonization and extinction rates, then the expected number of prey species on an island ($\hat{S}$) becomes $P \cdot X^*$. If we substitute X^* from above and allow $c = I$ and $e = E$, then the resulting equation is identical to Eq. 1, and Eq. 2a follows from $\beta = P - \hat{S}$.

Next, we incorporate generalist predation into the model by adding a predation term to Eq. 3a giving

$$\frac{dX}{dt} = c_x(1 - X) - e_x X - c_y XY \quad (3b)$$

Here c_x and e_x are colonization and extinction rates of a prey species, respectively. Y is the proportion of patches occupied by the generalist predator, and c_y is the colonization rate of the generalist predator. We assume that Y is driven by extrinsic factors and not by the occupancy of particular prey species. Equilibrium occupancy of X is now $X^* = c_x / (c_x + e_x + c_y Y)$. Again, if we assume that there are P prey species in the regional pool with identical colonization and extinction rates and equal susceptibility to generalist predation, then the expected number of prey species on an island ($\hat{S}$) becomes $P \cdot X^*$. If we substitute X^* and allow $c_x = I$, $e_x = E$, and $c_y = E_{pred}$, then the resulting simplified expression for β -diversity ($\beta = P - \hat{S}$) under generalist predation becomes:

$$\hat{\beta}_g = \frac{P(E + E_{pred} Y)}{I + E + E_{pred} Y} \quad (4a)$$

When generalist predators are absent ($Y = 0$), Eq. 4a collapses to Eq. 2a. When generalist predators are present everywhere ($Y = 1$), Eq. 4a is equivalent to Eq. 2b and the results from above apply. When generalist predators occupy a fraction of sites ($0 < Y < 1$), prey β -diversity increases under all model parameter combinations, as it did when ($Y = 1$), but the magnitude of that increase diminishes as generalist predators occupy fewer sites within the metacommunity (Fig. 2C).

To incorporate specialist predation into the model, we split the prey assemblage into two groups ($P\gamma = P_1 + P_2$) and model the dynamics of those prey species that cannot coexist with predators, X_1 , independently from the dynamics those prey species that do not respond to predators, X_2 . Following this approach, we add a predator occupancy parameter to the first term of Eq. 3b to get:

$$dX_1/dt = c_x(1 - X_1 - Y) - e_x X_1 - c_y X_1 Y \quad (3c)$$

Prey species that do not respond to predators (X_2) are modeled according to Eq. 3a. Here, there are $P\gamma$ prey species in the regional pool with identical colonization and extinction rates, but P_1 of them cannot coexist with specialist predators and P_2 of them do not respond to the predators. As such, the expected number of prey species on an island ($\hat{S}$) becomes $P_1 \times X_1^* + P_2 \times X_2^*$. Following the same substitution conventions as above, the resulting simplified expression for β -diversity ($\beta = P - \hat{S}$) under specialist predation becomes:

$$\hat{\beta}_s = \frac{P_1(YI + E + E_{pred} Y)}{I + E + E_{pred} Y} + \frac{P_2 E}{I + E} \quad (4b)$$

As above, when specialist predators are absent ($Y = 0$), Eq. 4b collapses to Eq. 2a. When specialist predators are present everywhere ($Y = 1$), Eq. 4b becomes

$$\hat{\beta}_s = P_1 + \frac{P_2 E}{I + E} \quad (4c)$$

This equation is similar to Eq. 2c, describing the effect of specialist predation on prey β -diversity under the ETIB.

Indeed, the second term of Eq. 4c is identical to Eq. 2c, where $P_2 = P_{pred} = P - P_{filter}$ (Fig. 1B), and therefore the predicted effects of specialist predators on prey β -diversity without P_1 or P_{filter} are the same (i.e. prey β -diversity decreases). In the metapopulation model (Eq. 4c), however, those species in the region that cannot coexist with predators, P_1 or P_{filter} , are included in calculations of prey β -diversity, and the predicted effects of specialist predators on prey β -diversity are reversed since γ -diversity is held constant (Fig. 2D). Finally, when specialist predators occupy a fraction of sites ($0 < Y < 1$), prey β -diversity increases under all model parameter combinations, but the magnitude of that increase diminishes as specialist predators occupy fewer sites within the metacommunity (Fig. 2D). Increases in E_{pred} (c_y) within the metapopulation model mitigate this effect of specialist predator occupancy on prey β -diversity (Fig. 2D).

Discussion

We find that the presence of predators can alter the relative importance of deterministic and stochastic factors in assembly processes, but that this effect will depend on the relative selectivity and occupancy of the predators. Specifically, we find that generalist predators, by reducing the size of the local prey community through indiscriminate foraging, increase the relative importance of stochasticity in community assembly, which tends to increase β -diversity among sites (see also Orrock and Fletcher 2005, Ryberg and Chase 2007). As a result, despite having potentially strong effects on α -diversity, generalist predators tend to have relatively small effects on γ -diversity. Alternatively, specialist predators, by selectively reducing the realized size of the regional species pool, increase the relative importance of determinism in community assembly, which tends to decrease β -diversity among sites. Here, the effect of specialist predators tends to be magnified at regional (γ -diversity) relative to local (α -diversity) scales (see also Chase et al. 2009). However, when predators are not ubiquitous in the metacommunity, we find that prey species intolerant of specialist predators can persist in 'predator-free' refuges and help maintain γ -diversity (and β -diversity), and the effects of generalist and specialist predation converge.

The distinct effects of generalist and specialist predators on prey diversity at different scales are sensitive to the way in which γ -diversity and the species pool are defined. Specifically, we find that the effects of ubiquitous specialist predators on prey β -diversity can vary depending on whether predator-susceptible prey are completely filtered from the species pool, as we assume. In practice, the metacommunity species pool is typically characterized as the total set of species observed across all communities within a metacommunity (Chase et al. 2011). This is the interpretation we follow in this paper, and we assume that the elimination of a species from all communities within a metacommunity results in the elimination of that species from the species pool. However, we acknowledge that this assumption may not be realistic or desirable in all situations. For this reason we repeat the caveat of Chase et al. (2011) that the definition of the species pool should be

done thoughtfully and with respect to the question being addressed.

For simplicity, our model framework is agnostic towards some potential complexities in real-world predator–prey metacommunities that could influence the predicted effects of predators. First, our model framework assumes that prey communities assemble within an infinitely large network of similar island-like habitats. This assumption does not capture potential variation in model predictions for metacommunities of variable size that are composed of island-like habitats of variable size and connectivity. We relaxed these simplifying spatial assumptions by using a simulation approach to explore the sensitivity of our analytical predictions to model scenarios involving finite metacommunities with unique spatial attributes. We found that qualitative model predictions were robust to spatial variation in island habitat size and connectivity, and metacommunity size under most simulation conditions (Supplementary material Appendix A1). However, because the magnitude of predator effects on prey β -diversity varied with these spatial attributes, we suggest that simulation models incorporating the explicit spatial relationships of island-like habitats will be required to fully understand how predators regulate the abundance (i.e. α -diversity) and distribution (i.e. β -diversity) of prey species in real, spatially unique metacommunities.

Second, our framework implicitly assumes that prey species immigration rates are not altered by predator presence. Clearly many prey species avoid habitats with predators, which should result in lower immigration rates for those species (Sih and Wooster 1994). Incorporating prey behaviors into our model framework should generate a greater array of potential effects of predators on the scaling of prey diversity in metacommunities (Resetarits et al. 2005). For example, generalist predators might decrease β -diversity in prey metacommunities if a large subset of the regional species pool is capable of avoiding habitats with predators.

Third, our framework only considers cases where predators limit prey coexistence, though predators can also enhance prey coexistence through keystone predation effects (Paine 1966, Leibold 1996). While our model does not include the indirect interactions of keystone predation, we posit that through the suppression of competitive dominants, keystone predators would increase local prey diversity (α -diversity) and thereby increase the regional occupancy of prey species, with consequent decreases in β -diversity. Thus, it is possible that keystone predators could enhance prey diversity at local spatial scales while simultaneously eroding compositional diversity at larger spatial scales.

Alongside the empirical results of Chase et al. (2009), our theoretical results advocate an expansion of conventional views about predator effects on prey diversity to include both local and regional perspectives. Moreover, our results for patterns of prey diversity in metacommunities echo conclusions from previous research stressing the importance of considering predator identity when investigating effects of predators on prey populations and communities (Duffy 2002, Chalcraft and Resetarits 2003, Östman and Chase 2007). Predators with varying prey

selectivities and population structures can have different effects on both the abundance (i.e. α -diversity) and distribution (i.e. β -diversity) of prey species in space. Against the backdrop of global top predator declines and alien predator introductions (Myers and Worm 2003, Borrvall and Ebenman 2006, Heithaus et al. 2008, Terborgh and Estes 2010), our results address an increasingly important applied problem by extending the ecological consequences of changes in top predator presence for ecosystem structure and function to include shifting patterns of biodiversity at different spatial scales.

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Supplementary material (available online as Appendix O19620 at <www.oikosoffice.lu.se>). Appendix A1.