



# Predator selectivity alters the effect of dispersal on coexistence among apparent competitors

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While the majority of studies on dispersal effects on patterns of coexistence among species in a metacommunity have focused on resource competitors, dispersal in systems with predator–prey interactions may provide very different results. Here, we use an analytical model to study the effect of dispersal rates on coexistence of two prey species sharing a predator (apparent competition), when the traits of that predator vary. Specifically, we explore the range in immigration rates where apparent competitors are able to coexist, and how that range changes with predator selectivity and efficiency. We find that if the inferior apparent competitor has a higher probability of being consumed, it will require less immigration to invade and to exclude the superior prey as the predator becomes more opportunistic. However, if the inferior apparent competitor has a lower probability of being consumed (and lower growth rates), higher immigration is required for the inferior prey to invade and exclude the superior prey as the predator becomes more opportunistic. We further find that the largest range of immigration rates where prey coexist occurs when predator selectivity is intermediate (i.e. they do not show much bias towards consuming one species or the other). Increasing predator efficiency generally reduces the immigration rates necessary for the inferior apparent competitor to invade and exclude the superior apparent competitor, but also reduces the range of immigration rates where the two apparent competitors can coexist. However, when the superior apparent competitor has a higher probability of being consumed, increased predator efficiency can increase the range of parameters where the species can coexist. Our results are consistent with some of the variation observed in the effect of dispersal on prey species richness in empirical systems with top predators.

Ecologists have increasingly recognized the need to consider larger spatial scales in their studies of interspecific interactions and coexistence (reviewed by Amarasekare 2003, Holyoak et al. 2005). In many cases, higher rates of dispersal among sites will allow species to coexist that otherwise could not; mechanisms for this include rescue-effects (Brown and Kodric-Brown 1977, Hanski 1999), source-sink processes (Loreau and Mouquet 1999, Schmidt et al. 2000, Amarasekare and Nisbet 2001, Mouquet and Loreau 2002, 2003), and/or tradeoffs between competitive ability and colonization ability (Tilman 1994, Yu and Wilson 2001). Alternatively, some of these same mechanisms can sometimes lead to regional homogenization, decreasing the probabilities of coexistence

with higher rates of dispersal (Schmidt et al. 2000, Amarasekare and Nisbet 2001, Mouquet and Loreau 2002, 2003, Amarasekare et al. 2004). Thus, increased dispersal among localities can have positive or negative effects on species coexistence when species compete for limiting resources.

Although the majority of theoretical and empirical studies on the effects of spatial processes and dispersal have focused on interspecific competition (Leibold et al. 2004), several notable exceptions have considered how dispersal might alter patterns of coexistence when species are embedded within a food web (Holt 1993, 1996, 2002, Holyoak 2000, Shurin and Allen 2001, Shurin 2001, Kneitel and Miller 2003, Holt and Hoopes 2005). Like the results from interspecific

competitive situations, those on the role of dispersal in food webs have also shown mixed results. For example, in artificial ponds, Shurin (2001) found that immigration of zooplankton from a regional species pool increased their local species richness when predators (fish and insects) were present, but not when predators were absent. In contrast, in pitcher-plant inquilines, Kneitel and Miller (2003) showed that experimentally imposed dispersal had no effect on local species richness of protists when predatory mosquito larvae were present, but increased local species richness when predators were absent. Thus, it is unclear as to when dispersal of prey organisms is expected to have positive, negative, or no effects on patterns of coexistence and species richness in communities of species that share predators.

Many species that share predators do not share resources (reviewed by Holt and Lawton 1994). Thus, they are dynamically linked in a food web through 'apparent competition' (sensu Holt 1977). Such apparent competitive systems are widespread, and include predatory insects that consume multiple types of insects which themselves do not share resources (Evans and England 1996, Müller and Godfray 1997), fishes that consume both pelagic and benthic prey (Witman et al. 2002), and predatory insects, mammals, reptiles, and birds that consume both terrestrial and aquatic prey species (Power et al. 2002). In an apparent competitive system, Holt et al. (1994) theoretically showed that all else being equal, the species that is a better apparent competitor (i.e. that which could tolerate higher levels of predators) would outcompete the other species, and exist alone. Holt et al. (1994) termed this the  $P^*$  rule as an analog to Tilman's (1982)  $R^*$  rule for competitive exclusion in resource competition systems. However, coexistence in apparent competitive systems is widespread (Holt and Lawton 1994), and thus there must be other factors that allow species to coexist in apparent competitive situations.

One mechanism that can lead to coexistence among apparent competitors even when one species has a higher  $P^*$  than the other (a better apparent competitor) is when apparent competitors have differential dispersal rates (Bonsall and Hassell 2000, Holt 2002, 2004, Holt and Barfield 2003). Specifically, if the inferior apparent competitor is immigrating into a locality, this can allow species to coexist. However, variation in the diet breadth and selectivity of predators for different prey species (i.e. specialists or generalists) can play a large role in the effects of predators on the coexistence among prey (Janzen 1970, Connell 1971, Grover 1995). As a result, it is possible that variation in predator selectivity can alter the influence of prey dispersal on patterns of coexistence in the presence of shared predators. In this paper we analytically examine the effect of predator selectivity and prey immigration on prey coexistence

where prey species are apparent competitors through a shared predator. Specifically, we ask 1) does variation in predator selectivity change the effect of immigration on the probabilities of prey coexistence? 2) What effect does the overall efficiency of predators has on the probability of coexistence when prey dispersal also varies?

## A model for apparent competition in a closed system

The population dynamics of a system of two prey species and one predator in a closed community can be described by the following equation system:

$$\begin{aligned} \frac{dP}{dt} &= P(a_1b_1N_1 + a_2b_2N_2 - m - qP) \\ \frac{dN_1}{dt} &= N_1(r_1 - a_1P) \\ \frac{dN_2}{dt} &= N_2(r_2 - a_2P) \end{aligned} \quad (1)$$

where  $P$  is the density of the predator population, while  $N_1$  and  $N_2$  the density of the prey species,  $r$  is the intrinsic growth rate of the prey species,  $a$  is the predator attack rate on the prey,  $b$  the conversion rate of prey into new predators and  $m$  predator mortality rate. For simplicity, the system is stabilized by interference competition ( $q$ ) among predators (sensu Holt 2004).

The equilibrium densities of one prey species ( $N_1$ ) and the predator ( $P$ ) becomes  $N_1^* = (m + qr_1/a_1)/(a_1^2b_1)$  and  $P^* = r_1/a_1$ . In order for a second prey species ( $N_2$ ) to invade such a system  $r_2/a_2 > r_1/a_1$  (Holt et al. 1994). Hence, for  $N_2$  to invade, it must tolerate higher predator abundance than  $N_1$ , but if  $N_2$  can invade it will increase predator densities such that  $N_1$  will have a negative population growth rate and go extinct. In a closed system, the species that is able to tolerate the highest density of predators (highest  $P^*$ ) will exist alone (Holt et al. 1994). In the special case where both species have equal  $P^*$ , the species that ultimately wins will depend on a random walk.

## Immigration and coexistence among apparent competitors

We add immigration into the dynamics of each apparent competitor and the predator using following equation system:

$$\frac{dP}{dt} = P(a_s b_s N_s + a_i b_i N_i - m - qP) + I_p$$

$$\frac{dN_s}{dt} = N_s(r_s - a_s P) + I_s$$

$$\frac{dN_i}{dt} = N_i(r_i - a_i P) + I_i \quad (2)$$

where  $I_x$  is the immigration rate of individuals of species  $x$  ( $P$ ,  $N_s$ , or  $N_i$ ) into the locality. The subscript  $s$  denotes the (locally) superior apparent competitor and  $i$  the (locally) inferior apparent competitor (i.e.  $r_s/a_s > r_i/a_i$ ). Because the immigration terms do not affect the signs in the community matrix, they do not change the stability of the system. If  $I_x > 0$ , that implies there is immigration from the region outside of the local community (i.e. from the metacommunity); there is no reciprocal feedback from the local community to the metacommunity, since there is no emigration.

For simplicity, we consider how varying immigration of each species alters the predictions of coexistence when immigration of the other two species is zero. First, immigration of the predator ( $I_p > 0$ ,  $I_s = I_i = 0$ ) will not affect coexistence between the two prey species; as above, only the superior apparent competitor ( $N_s$ ) with the higher  $P^*$  will exist, and the equilibrium densities will be  $N_s^* = (m + r_1 q/a_1)/a_1 b_1 - I_p/b_1 r_1$  and  $P^* = r_s/a_s$ . Hence, immigration of predators from an outside source will decrease prey density and predator density will be unaffected by immigration until  $I_p > (r_1/a_1)(m + r_1 q/a_1)$ , at which point predators will drive the superior apparent competitor ( $N_s$ ) extinct. Similarly, immigration of  $N_s$  ( $I_s > 0$ ,  $I_p = I_i = 0$ ) will not affect coexistence, but only it will exist with  $P$  at equilibrium:

$$N_s^* = \frac{m}{2a_s b_s} + \frac{r_s q}{2a_s b_s} + \frac{\sqrt{4a_s^2 b_s q I + (a_s m - r_s q)^2}}{2a_s^2 b_s}$$

$$P^* = \frac{r_s}{2a_s} - \frac{m}{2q} + \frac{\sqrt{4a_s^2 b_s q I + (a_s m - r_s q)^2}}{2a_s q} \quad (3)$$

The equilibrium densities of both  $N_s$  and  $P$  will increase with immigration of  $N_s$ .

In contrast, immigration of the inferior apparent competitor ( $N_i$ ) ( $I_i > 0$ ,  $I_p = I_s = 0$ ) allows coexistence of the two prey species when  $r_i < a_i P^*$ . The equilibrium is  $N_i^* = I_i/|f|$ , where  $f$  is the population growth rate in absence of immigration, i.e.  $f < 0$  (Holt 2004). The equilibrium density of the predators will still be  $P^* = r_s/a_s$ , and hence independent of  $I_i$ . The density of the  $N_i$  will increase with  $I_i$ ,  $N_i^* = I_i a_s / (r_s a_i - r_i a_s)$ , whereas density of  $N_s$  will decrease (Holt 2004):

$$N_s^* = \frac{1}{a_s b_s} \left( m + \frac{q r_s}{a_s} - \frac{b_i I_i}{\left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right)} \right) \quad (4)$$

At some sufficiently high immigration rate of the inferior apparent competitor the superior apparent competitor will go extinct. This will occur at:

$$I_i = \frac{1}{b_i} \left( m + \frac{q r_s}{a_s} \right) \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) \quad (5)$$

The immigration rate ( $I_i$ ) of the inferior apparent competitor ( $N_i$ ) required to exclude the superior apparent competitor ( $N_s$ ) increases with increasing  $m$  and  $q$ , and with decreasing  $b_i$ , hence the immigration rate increases with decreasing predator efficiency. Further, it increases with increasing differences between  $r_s/a_s$  and  $r_i/a_i$ , increasing  $a_i$ , and decreasing  $a_s$  (Appendix 1). That is, a higher immigration rate of  $N_i$  is required to exclude  $N_s$  in presence of a specialist predator than a generalist predator if  $a_s < a_i$  (Fig. 1a), and vice versa if  $a_s > a_i$  (Fig. 1b). An increase in overall predator capture efficiency (an increase in both  $a_s$  and  $a_i$ ) will result in a lower immigration rate of  $N_i$  needed to exclude the superior apparent competitor when (1)  $a_s < a_i$ , or (2) there is a large difference between  $r_s/a_s$  and  $r_i/a_i$  (Fig. 1, Appendix 1). Alternatively, if  $a_s > a_i$ ,  $r_s > r_i$ , and  $r_s/a_s$  is close to  $r_i/a_i$ , then an increase in both  $a_s$  and  $a_i$  can result in an increased immigration rate needed to exclude  $N_s$  (Fig. 1b).

## Extinction threshold

In this section, we consider the case where there is a threshold density that an immigrating prey species must achieve in order for it to persist as a population. This threshold is likely in cases where a minimum immigration rate is required for a species with an otherwise negative population growth rate to persist in a habitat. Such an effect can occur for at least one of two reasons: (1) immigrants come in discrete entities, and thus rare immigration events will not sustain populations with large negative population growth rates, and (2) in small populations, Allee-effects can diminish the effects of immigration (Brown and Kodric-Brown 1977, Holt et al. 2004). We assume that  $N_i^*$  must be larger than some extinction threshold  $E$ , to establish in a community. As such, using equation system 2 with  $I_i > 0$ ,  $I_p = I_s = 0$ , the minimum immigration rate for  $N_i$  to establish is:

$$I_i = E a_i \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) \quad (6)$$

The immigration rate of the inferior apparent competitor ( $N_i$ ) to establish in a community increases with increasing differences between  $r_s/a_s$  and  $r_i/a_i$ , and the

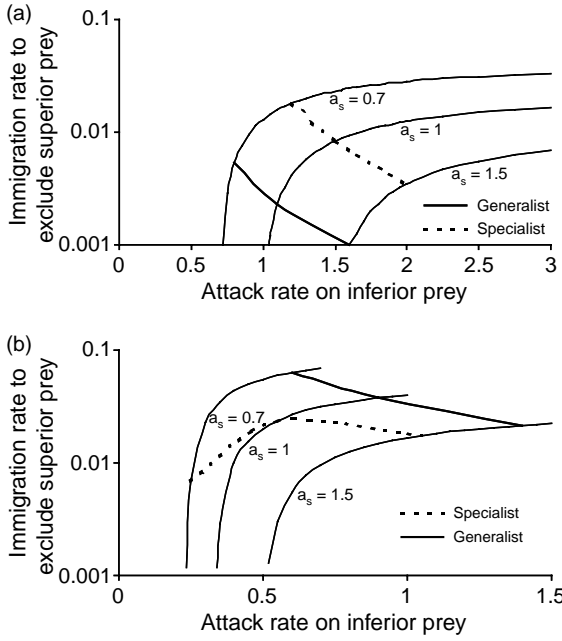


Fig. 1. The immigration rate of the inferior apparent competitor required to exclude the superior apparent competitor always increases with increasing attack rate on the inferior prey and decreasing attack rate on the superior prey. That is, a higher immigration rate is required to exclude the superior prey in presence of a specialist predator if  $a_s < a_i$  (a) but less in presence of a specialist predator if  $a_s > a_i$  (b). If  $a_s < a_i$  an increased predator capture efficiency (increase in both if  $a_s$  and  $a_i$ ) decreased the immigration rate required to exclude superior prey, but if  $a_s > a_i$  it can increase with increasing capture efficiency. Parameter values used: (a)  $r_s = r_i = 0.25$ ,  $m = q = 0.005$ ,  $b_i = 0.1$ . Thick lines show combinations of  $a_s$  and  $a_i$  where the difference is 0.1 (generalist) and hatched lines where the difference is 0.5 (specialist). (b)  $r_s = 0.6$ ,  $r_i = 0.2$ . Difference between  $a_s$  and  $a_i$  are 0.1 (generalist) and 0.45 (specialist).

derivative of Eq. 6 is always negative with respect to  $a_s$  and positive with respect to  $a_i$ . Hence, a lower immigration rate of  $N_i$  is required for it to establish in presence of a generalist predator than with a specialist predator, so long as  $a_s < a_i$  (Fig. 2a), and vice versa (Fig. 2b). An increase in predator efficiency (both  $a_s$  and  $a_i$  increase) will result in a decreased immigration rate needed for the inferior apparent competitor to establish if  $a_s < a_i$ , and an increased immigration rate needed if  $a_s > a_i$  (Fig. 2, Appendix 1).

## Range of coexistence

The range in immigration rate of  $N_i$  where the two prey species are able to coexist,  $\hat{I}_i$ , is the difference between the exclusion and immigration thresholds:

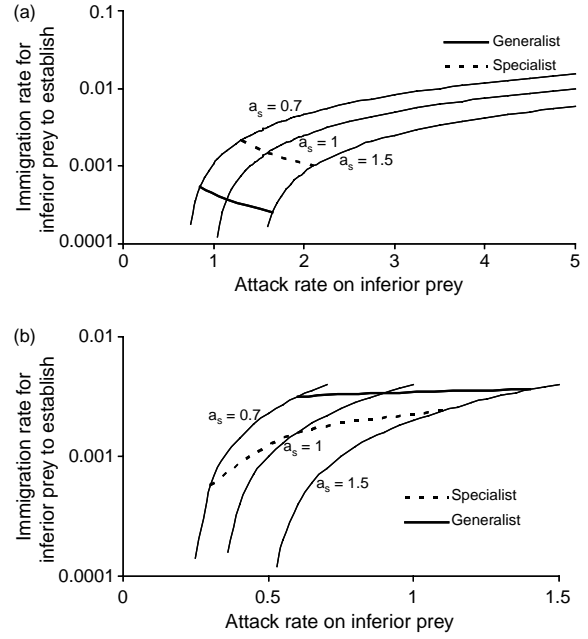


Fig. 2. The immigration rate of the inferior apparent competitor required to invade always increases with increasing attack rate on the inferior prey and decreasing attack rate on the superior prey. That is, a higher immigration rate is required to invade in presence of a specialist predator if  $a_s < a_i$  (a) but less in presence of a specialist predator if  $a_s > a_i$  (b). If  $a_s < a_i$  an increased predator capture efficiency (increase in both if  $a_s$  and  $a_i$ ) decreased the immigration rate required to invade, but if  $a_s > a_i$  it increased the immigration rate required to invade with increasing capture efficiency.  $E = 0.01$ , other parameter values used as in Fig. 1 except difference between  $a_s$  and  $a_i$  in (a) is 0.15 (generalist) and 0.6 (specialist) and in (b) is 0.1 (generalist) and 0.4 (specialist).

$$\hat{I}_i = \frac{1}{b_i} \left( m + \frac{r_s q}{a_s} - a_i b_i E \right) \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) \quad (7)$$

Because we derive Eq. 7 directly from Eq. 5 and 6, we assume the extinction threshold does not affect the superior apparent competitor ( $N_s$ ). However, incorporating an extinction threshold for  $N_s$  will decrease  $\hat{I}_i$ , but not alter the qualitative results (Appendix 1).

The range in immigration rate of  $N_i$  where the species coexist decreases with increasing values of the extinction threshold ( $E$ ), increases with increased density independent mortality of predators ( $m$ ) and predator interference ( $q$ ), decreases with increasing predator conversion rate of the inferior apparent competitor ( $b_i$ ), and increases with larger difference between  $r_s/a_s$  and  $r_i/a_i$ . Hence, in general, the range in immigration of  $N_i$  where the two species coexist is larger for a weaker predator (high  $m$  and  $q$ , low  $a_s$ ,  $a_i$  and  $b_i$ ) than a more efficient predator. Because the derivative of Eq. 7 with respect to  $a_s$  is always negative within the plausible range (Fig. 3, Appendix 1), the

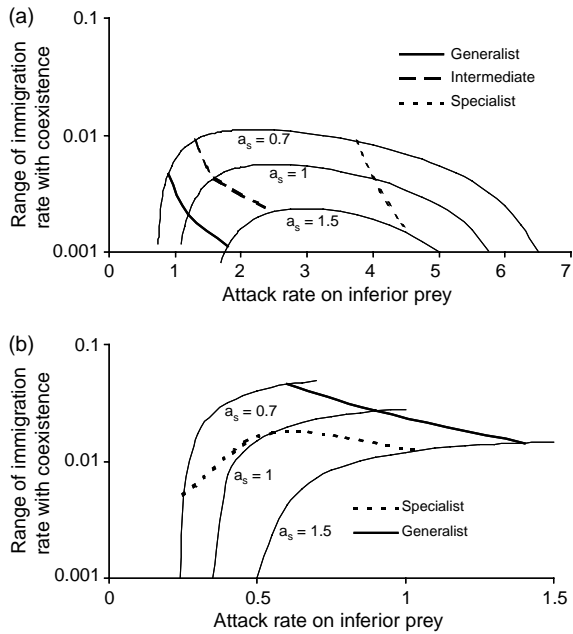


Fig. 3. The range of immigration rate of the inferior prey where coexistence is possible always increases with decreasing attack rate on the superior prey, and show a humpshaped relation with the attack rate on the inferior prey. If  $a_s < a_i$  (a) an increased predator capture efficiency (increase in both if  $a_s$  and  $a_i$ ) decreased the range of coexistence, but if  $a_s > a_i$  the range of coexistence can increase with increasing capture efficiency. Parameter values used as in Fig. 1 except difference between  $a_s$  and  $a_i$  in (a) is 0.2 (generalist), 0.6 (intermediate), and 3 (specialist), and in (b) 0.1 (generalist) and 0.45 (specialist).

range of coexistence decreases with increasing  $a_s$ . The derivatives of Eq. 7 with respect to  $a_i$  changes sign (Fig. 3c, Appendix 1), hence, the effect of changed  $a_i$  on the range of coexistence first increases, and then declines.  $\hat{I}_i$  is more likely to decrease with increasing  $a_i$  when there is a large difference between  $r_s/a_s$  and  $r_i/a_i$ , when  $b_i$ ,  $a_i$ , and  $E$  are high, and when  $m$  and  $q$  are low (Fig. 3, Appendix 1). An increase in predator capture efficiency ( $a_s$  and  $a_i$  increase) will generally decrease the range of coexistence, but the range of coexistence can increase with increasing  $a_s$  and  $a_i$  if  $a_s > a_i$  and there is a small difference between  $r_s/a_s$  and  $r_i/a_i$ , (Fig. 3b, Appendix 1).

It is important to note that while the qualitative results of our model are not dependent on specific values of the parameters, the quantitative results are. For Fig. 1–3, parameter values were arbitrary chosen, but not necessarily exceptional in any way. For reference, an immigration in the order of 0.0001 (Fig. 2) required for an inferior apparent competitor to establish when  $E = 0.01$  means that the proportion of immigrants in the population is in the order of 1%. Similarly, an immigration in the order of 0.01 (Fig. 1) required for an inferior apparent competitor to exclude the locally

superior apparent competitor requires that the proportion immigrants in the population is around 10–50%, increasing with increasing predator attack rates.

## Discussion

The key message from our analyses is simple: in an open metacommunity, the effect of dispersal (immigration) rate on the coexistence of apparent competitors that share a common predator depends on the degree of specialization, as well as the efficiency, of that predator. However, the specific results of how predator selectivity and efficiency influence patterns of coexistence among apparent competing prey species are more complex. Some of these results were anticipated by Holt and Barfield (2003) and Holt (2004), although their analyses were primarily focused on other issues, and they did not explicitly consider the influence of the degree of predator specialization on apparent competitor coexistence in open systems. Further, our results extend those previously presented by adding a more realistic extinction threshold

If predators preferentially consume the inferior apparent competitor ( $a_s < a_i$ ), the immigration rate of the inferior prey required to invade and exclude the superior prey increases with increased predator selectivity (Fig. 1a, 2a). Alternatively, if predators preferentially consume the superior apparent competitor (and  $r_s > r_i$ ), the inferior apparent competitor invades and excludes the superior prey at lower immigration rates with increased predator selectivity (Fig. 1b, 2b). In all, the effect of immigration on the range in immigration rates where coexistence of superior and inferior apparent competitors is possible will depend on the degree of predator selectivity, showing first an increase, and then a decline, with varying predator selectivity on the inferior and superior apparent competitors (Fig. 3). That is, with small differences in local net population growth rates between the superior and inferior apparent competitors ( $r_i/a_i$  close to  $r_s/a_s$ ), the range of coexistence is mainly determined by the inferior apparent competitor's ability to invade. With larger differences in local net population growth rates, the inferior apparent competitor's ability to exclude the superior apparent competitor becomes relatively more important.

Our model is clearly simplified, and can only represent a caricature of most real world situations. For example, our model omits non-linearities in the functional response of the predator (i.e. functional responses type II or III) and density dependent growth rates of the prey (i.e. carrying capacity). Therefore our predictions are most likely approximate situations at relatively low productivity, when predator satiation and prey density-dependence are less likely to be important. Adding these non-linearities will in many cases, make

analytical solutions impossible, and are beyond the scope for this article. However, while these non-linearities will certainly change the quantitative predictions, they will only change the qualitative predictions if the two apparent competitors have differential shapes to the non-linearities (i.e. predator satiation differs between the two apparent competitive prey species).

Although the above analytical analyses only consider two species coexistence, and thus can not directly apply to more diverse communities, we can derive some lessons that might help in the interpretation of empirical patterns of species richness in response to predator specialization and the effects of immigration. In essence, our analyses suggest that inferior apparent competitive prey species should more easily establish in communities connected by dispersal with non-selective (generalist) predators than with specialist predators (when assuming inferior apparent competitors have higher risk of being consumed). Furthermore, the locally superior apparent competitor should also be more easily excluded from communities with non-selective predators. That is, we predict there should be higher turnover of species coexisting with increasing dispersal when the predator is a generalist than when the predator is a specialist. Although there are no empirical studies available for directly testing this prediction, the results from Shurin's (2001) experiments on dispersal and coexistence among zooplankton in the presence and absence of predators give some guidance. When experimental communities of zooplankton were compared with and without dispersal, the identity of the predator strongly influenced the final outcome of community structure (Fig. 2 in Shurin 2001). Specifically, when the predator was the bluegill sunfish (*Lepomis macrochirus*), a more generalized predator species (Hall et al. 1970, Mittelbach 1981, Harrel and Dibble 2001, Olson et al. 2003), eight zooplankton species that were absent without dispersal were able to establish in communities connected by dispersal from an external source. Alternatively, only four zooplankton species were able to establish with dispersal from an external source when the predator was the backswimmer (*Notonecta undulata*), which is a more specialized predator (Scott and Murdoch 1983, Murdoch and Scott 1984, Murdoch et al. 1984). Furthermore, there was higher species turnover with and without dispersal in the treatments with the bluegill as the top predator than in those with the backswimmer as the top predator; three zooplankton species were lost in the former treatment, and only one in the latter treatment.

In all, we conclude that the type of predator (specialist – generalist, efficient – weak) in a community can influence the role of habitat connectance (i.e. varying dispersal rates) on patterns of coexistence (and possibly species richness) among prey species that share

that predator. Although it is often assumed – from simple metapopulation theory – that increases in the dispersal rate among habitats will increase the probability of species' coexistence (and richness), when interactions among species in a metacommunity are considered, the results are more complicated (Holt 1993, Amarasekare 2003). Our results show that the type of predator, and in particular whether it is a specialist or generalist, can alter predicted patterns of coexistence among prey species when dispersal rates vary. This emphasizes the necessity not only to consider whether species interactions occur, but to understand that nature by which species interact, when discerning the responses of community structure to variation in dispersal rates.

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## Appendix 1.

The derivative of the right side of Eq. 5 with respect to  $a_s$  is:

$$\dot{I}_{ia_s} = -\frac{r_s}{a_s^2 b_i} \left( m + \frac{r_s q}{a_s} + q \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) \right) \quad (\text{A.1})$$

which is always negative because  $r_s/a_s - r_i/a_i$  per definition is positive. The derivative of the right side of Eq. 5 with respect to  $a_i$  is:

$$\dot{I}_{ia_i} = \frac{r_i}{a_i^2 b_i} \left( m + \frac{r_s q}{a_s} \right) \quad (\text{A.2})$$

which is always positive. An increase of  $a_s$  will be perfectly compensated with an identical increase in  $a_i$ , i.e. the immigration rate of the inferior prey to exclude the superior prey remains constant, when:

$$\frac{r_s q}{a_s^2 b_i} \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) + \frac{r_s}{a_s^2 b_i} \left( m + \frac{r_s q}{a_s} \right) = \frac{r_i}{a_i^2 b_i} \left( m + \frac{r_s q}{a_s} \right) \quad (\text{A.3})$$

The right side of Eq. A.3 can only be larger than the left hand side if  $a_s > a_i$  and  $r_s/a_s$  is close to  $r_i/a_i$  so that the first term on the left side is close to zero.

An identical change in  $a_s$  and  $a_i$  will perfectly counteract each other on the immigration rate for the inferior apparent competitor to establish (inequality 6) when  $r_s a_i E / a_s^2 = r_s E / a_s$  which simplifies to  $a_s = a_i$ .

The derivative of Eq. 7 with respect to  $a_s$  is:

$$\hat{I}'_{a_s} = -\frac{r_s}{a_s^2 b_i} \left( q \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) - \left( m + \frac{r_s q}{a_s} - a_i b_i E \right) \right) \quad (\text{A.4})$$

which can only be positive if  $m + r_s q / a_s - a_i b_i E$  is negative, which can only be negative if Eq. 7 is negative and hence not relevant in our case (implies the superior prey is excluded at lower immigration rates than the inferior prey can establish). The derivative of Eq. 7 with respect to  $a_i$  is:

$$\hat{I}'_{a_i} = \frac{r_i}{a_i^2 b_i} \left( m + \frac{r_s q}{a_s} - a_i b_i E \right) - E \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) \quad (\text{A.5})$$

In order for compensate for a decreased range of coexistence with increasing  $a_s$  with an identical increase in  $a_i$  the following condition must be fulfilled:

$$-\frac{1}{b_i} \left( m + \frac{r_s q}{a_s} - a_i b_i E \right) \left( \frac{r_s}{a_s^2} - \frac{r_i}{a_i^2} \right) - \left( \frac{r_s q}{a_s^2 b_i} + E \right) \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) = 0 \quad (\text{A.6})$$

Equation A.6 can only be positive if  $a_s$  is larger than  $a_i$  (but not a necessary condition). Because  $m + r_s q / a_s - a_i b_i E$  is assumed to be positive and  $r_s / a_s - r_i / a_i$  is per definition positive,  $r_s / a_s^2 - r_i / a_i^2$  must be negative which is only possible if  $a_s > a_i$ .

Assuming also an extinction threshold for the superior prey will only affect the results quantitatively, not qualitatively.  $I_i$  required to exclude the superior prey would be

$$I_i = \frac{1}{b_i} \left( m + \frac{q r_s}{a_s} - E a_s b_s \right) \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) \quad (\text{A.7})$$

which would lower  $I_i$  required to exclude superior prey, but not change the sign of the derivative with respect to  $a_s$ , and decrease the derivative with respect to  $a_i$  but both positive and negative signs are still possible. The range in immigration where prey can coexist would be

$$\hat{I}_i = \frac{1}{b_i} \left( m + \frac{r_s q}{a_s} - E(a_i b_i + a_s b_s) \right) \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) \quad (\text{A.8})$$

which would lower  $\hat{I}_i$ , and the derivative A.8 with respect to  $a_s$  is

$$\hat{I}'_{a_s} = -\frac{r_s}{a_s^2 b_i} \left( q \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) - \left( m + \frac{r_s q}{a_s} - E(a_i b_i + a_s b_s) \right) \right) \quad (\text{A.9})$$

and with respect to  $a_i$  is

$$\hat{I}'_{a_i} = \frac{r_i}{a_i^2 b_i} \left( m + \frac{r_s q}{a_s} - E(a_i b_i + a_s b_s) \right) - E \left( \frac{r_s}{a_s} - \frac{r_i}{a_i} \right) \quad (\text{A.10})$$

Hence, an extinction threshold for the superior prey affects the value of the derivatives but not the possibility for changing the signs of the derivatives.