Ecol Res (2005) 20: 623–631
DOI 10.1007/s11284-005-0092-3

MIYADI AWARD

Tadashi Fukami

Integrating internal and external dispersal in metacommunity assembly: preliminary theoretical analyses

Received: 28 April 2005 / Accepted: 13 June 2005 / Published online: 16 July 2005

Abstract Internal dispersal, which occurs among local communities within a metacommunity, and external dispersal, which supplies immigrants from outside the metacommunity, can both have a major impact on species diversity. However, few studies have considered the two simultaneously. Here I report preliminary computer-simulation results to suggest that internal and external dispersal can interact to influence species richness. Specifically, the results show that internal dispersal did not affect species richness under frequent external dispersal, whereas it enhanced richness in local communities while decreasing richness in metacommunities under infrequent external dispersal. Conversely, external dispersal influenced species richness in local communities more greatly in the absence of internal dispersal than in its presence, while external dispersal did not affect richness in metacommunities regardless of internal dispersal. Furthermore, internal and external dispersal interactively determined the importance of community assembly history in generating and maintaining variation in local community structure. Overall, these results suggest that the two dispersal types can reciprocally provide the context in which each affects species diversity and therefore that their effects cannot be understood in isolation of the other.

Keywords Community assembly · Food web · Invasion resistance · Species coexistence · Species richness

Introduction

Dispersal of individuals across ecological communities can have a major impact on species diversity. Ecology has a long tradition in examining the role of dispersal in species coexistence (Skellam 1951; Hutchinson 1951), and dispersal studies have been increasing in number particularly over the last decade or so (Nathan 2003). Although dispersal occurs over a wide range of spatial scales (Cadotte and Fukami 2005), its effects on species diversity have generally been studied at two types of scale relative to the communities in question. Here I refer to them as "internal" and "external" dispersal.

Studies on internal dispersal are based on models in which local communities, which may be collectively called a metacommunity (Wilson 1992; Holt 1993; Leibold et al. 2004), are connected to one another by dispersal (Fig. 1a). Numerous theoretical (e.g., Levins and Culver 1971; Levin 1974; Chesson 1985; Iwasa and Roughgarden 1986; Amarasekare and Nisbet 2001; Hubbell 2001; Shurin and Allen 2001; Mouquet and Loreau 2002) and experimental (e.g., Huffaker 1958; Holyoak and Lawler 1996; Warren 1996; Burkey 1997; Forbes and Chase 2002; Kerr et al. 2002) studies have shown that, depending on its rate and extent, internal dispersal can either facilitate or destabilize species coexistence (Leibold et al. 2004).

On the other hand, studies on external dispersal are concerned with dispersal from outside the set of local communities under consideration (Fig. 1b). The most influential model of this kind is that of MacArthur and Wilson (1967) (Hanski and Simberloff 1997). More

---

Electronic Supplementary Material Supplementary material is available for this article at http://dx.doi.org/10.1007/s11284-005-0092-3

Tadashi Fukami is the recipient of the ninth Denzaburo Miyadi Award.

T. Fukami
Department of Ecology and Evolutionary Biology,
University of Tennessee, Knoxville, TN 37996-1610, USA

T. Fukami
Laboratory of Biodiversity Science,
School of Agricultural and Life Sciences, University of Tokyo,
Tokyo 113-8657, Japan

Present address: T. Fukami
Landcare Research, P.O. Box 69, Lincoln, New Zealand
E-mail: fukamit@landcareresearch.co.nz
Tel.: +64-3-3256700
Fax: +64-3-3252418

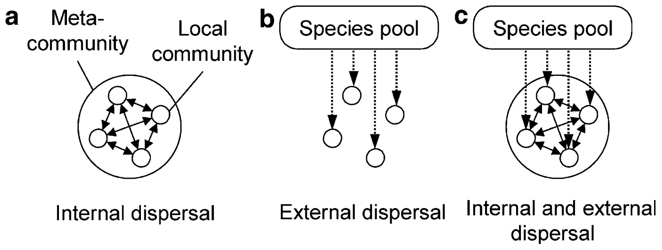

Fig. 1 Models that incorporate **a** internal dispersal, **b** external dispersal, and **c** both internal and external dispersal. *Solid* and *dashed arrows* represent the direction of internal and external dispersal, respectively

recent models more explicitly incorporate species interactions than MacArthur and Wilson did (e.g., Post and Pimm 1983; Drake 1990; Law and Morton 1996; Lockwood et al. 1997; Loreau and Mouquet 1999; Moore et al. 2001; Holt and Barfield 2003; Tokita and Yasutomi 2003). In doing so, they predict that not only the frequency of dispersal but also the sequence in which different species disperse to local communities can affect diversity in some circumstances (Chase 2003; Fukami and Morin 2003; Fukami 2004a, 2004b).

However, despite these advances in understanding the role of internal and external dispersal, surprisingly few studies have considered the two simultaneously. A notable exception is the work of Gotelli (1991) and Gotelli and Kelley (1993) (see also Rosenzweig 1995), but this work focused on populations of single species rather than communities of multiple interacting species. Much remains unknown about how internal and external dispersal may interact to influence community dynamics when local species interactions are taken into consideration. In this paper, I integrate internal and external dispersal (Fig. 1c) in a computer simulation model of metacommunity assembly. The model is built after the general Lotka–Volterra systems that have been extensively used for studying community assembly (e.g., Morton and Law 1997; Mouquet et al. 2003). The simulation assembles metacommunities through random sequential dispersal of species, both internal and external. My aim here is to provide an initial assessment of whether internal and external dispersal can interact to affect species diversity in the presence of local competition and predation.

Materials and methods

I simulated the assembly of local communities and metacommunities with seven replicates of species pools. In each simulation, each local community was assembled by dispersal of species from a common species pool (external dispersal) and, in some cases, by dispersal of species among local communities within the metacommunity (internal dispersal). In total, I assembled 1,120 local communities, i.e., 7 independently created species pools×2 external dispersal rates×2 internal dispersal rates×10 metacommunities per species pool×4 local communities within each metacommunity.

Constructing species pools

I assumed that the dynamics of populations within each local community are governed by general Lotka–Volterra equations defining population growths and intra- and inter-specific interactions (see section "Local community dynamics" below):

$$\mathrm{d}x_{ik}/\mathrm{d}t = x_{ik}\left(b_i + \sum_{j=1}^{m} a_{ij}x_{jk}\right). \tag{1}$$

Here, x_{ik} is the density of species i in local community k, b_i is the per capita intrinsic rate of increase or decrease of species i, and a_{ij} is the per capita effect of species j on species i. Given these equations, a set of m species that are each assigned a value of b_i and those of a_{ij} would define a species pool from which they disperse to local communities. Each species pool was created independently using a method similar to that of Law and Morton (1996, p 775), Morton and Law (1997, pp 323–325), and Fukami (2004b) (see Appendix). Although the method is not applicable to every real community possible due to the specific assumptions about body sizes and interaction strengths (see Appendix), the empirically derived method used here generates parameter values consistent with the presence of many weak and a few strong interactions in natural communities (Paine 1992; Berlow et al. 1999; McCann 2000; but see Abrams 2001; Sala and Graham 2002; see also Huisman et al. 2001).

Assembling local communities and metacommunities

External dispersal

I initiated the simulations by randomly drawing, for each local community, a species from the species pool and introducing it to the corresponding local community (i.e., external dispersal). When a predetermined period of time had passed (see "Manipulating dispersal rates" section below), a second species was chosen randomly from the species pool for each local community and introduced to the corresponding community. This process of dispersal was repeated for the entire course of the simulation. Invading species were introduced with a low abundance ($x_{ik} = 1.0\times10^{-3}$). This initial abundance was several orders of magnitude lower than carrying capacities of basal species in a local community, which could range between 9.09×10^{3} [i.e., 100 biomass units divided by the maximum body size possible = $100/(0.1\times1.1)$] and 1.11×10^{4} [i.e., 100 biomass units divided by the minimum body size possible = $100/(0.01\times0.9)$] (see Appendix). In keeping with the methods in previous assembly modeling (e.g., Law and Morton 1996; Morton and Law 1997), species already present at a given time in a given local community were not allowed to be chosen as the newly invading species for that community at that time.

Internal dispersal

Where appropriate (see "Manipulating dispersal rates" section below), species in local communities were also allowed to disperse among the local communities within a metacommunity (i.e., internal dispersal). Once in 10 days, total abundance summed across the four local communities in the metacommunity was measured for each species. Whether a species dispersed to a community was determined probabilistically as a linear function of its total abundance in the metacommunity. For basal species, the dispersal probability was set so that a species that had the maximum total abundance possible would have a dispersal probability of 0.25. The maximum total abundance possible was calculated as: the number of local communities in a metacommunity (4)×the maximum biomass units possible in a local community (100)/ the minimum body size possible $(0.01\times0.9)=4.44\times10^4$. For consumer species, dispersal probability was set so that a species that had 5% of the maximum total abundance possible for basal species would have a dispersal probability of 0.25. Placing the 5% (same as the value of the conversion efficiency, c_2) here was done on the assumption that consumers should tend to have a better ability to disperse between local communities than basal species do, so that consumers can efficiently forage basal species within a metacommunity. Species dispersing among local communities were introduced to the target communities with the same abundance as those dispersing from the species pool ($x_{ik}=1.0\times10^{-3}$). Species were allowed to disperse to a local community regardless of whether they were already present or absent in that community.

Local community dynamics

Throughout the simulation, the abundance of each species in each local community was calculated by numerically integrating the Lotka–Volterra equations (Eq. 1) using the commercially available algorithm d02ejc (Numerical Algorithms Group 2002), which implements backward differentiation formulae (see Hall and Watt 1976). This method more accurately and more explicitly tracks population dynamics than do other methods used in most earlier assembly studies, including those based on local asymptotic stability (Post and Pimm 1983; Drake 1990), Euler integration approximation (Law and Morton 1996; Lockwood et al. 1997; Wilmers et al. 2002), and permanence theory (Law and Morton 1996; Morton and Law 1997) (see Morton et al. 1996 for discussion on relevant technical issues). A species was removed from the local community if its abundance fell below an extinction threshold, $x_{ik}=1.0\times10^{-3}$, which is the same as the initial density of dispersing species.

Invasion resistance

For each metacommunity, the following measures of invasion resistance were recorded 1.0×10^4 and 5.0×10^4 days after the first external dispersal and every 1.0×10^5 days afterwards to determine when to terminate the simulation (see below): (1) R averaged over the four local communities in a metacommunity, $\bar{R}$, and (2) proportion of local communities, in a metacommunity, for which R is 1 (P). Here, R of a local community is defined as the proportion of species absent from the community, but present in the species pool, which would become extinct after a certain time (1.0×10^3 days) had passed if it were introduced to the community. To obtain R, I first introduced one of the species absent from the local community to the community, followed community dynamics using the same numerical integration algorithm and extinction criterion as above for 1.0×10^3 days without introducing any more species, and determined if the introduced species had a density greater than the threshold, 1.0×10^{-3}. If it did not, I counted it as an unsuccessful colonizer. I then introduced a second species from the species pool to the community of original species composition and abundance and determined if this species was an unsuccessful colonizer. I repeated this process for all species in the pool to obtain the total number of unsuccessful colonizers. R was the number of unsuccessful colonizers divided by the number of species absent from the community but present in the species pool. Therefore, when R is 1, the community is resistant to invasion by any species present in the species pool, but absent from the community.

Terminating simulations

The simulations were terminated when either of the following was satisfied: (1) the value of P had been 1 for four consecutive samplings, or (2) the assembly had been simulated for 2×10^6 days. These two criteria maximized the possibility that the dynamics of community assembly had reached an equilibrium state, be it a stable point or a more complex attractor, by the time the simulations were terminated. Therefore, the measures of communities obtained at the end of the simulations (see below) reflect a consequence of long-term dynamics over an ecologically important time-scale rather than initial stages of community development toward persistent states.

Manipulating dispersal rates

I used two rates of external dispersal: once in 10 days and once in 1,000 days. I also used two rates of internal dispersal: potential dispersal of species once in 10 days subject to the dispersal probability specified above and no internal dispersal. I did not allow dispersal among metacommunities in order to ensure that metacommunities could be treated as statistically independent replicates of community assembly.

Measurements and analyses

For each metacommunity, I obtained six measures of species richness at the end of each simulation: (1) mean number of basal species in a local community, averaged over the four local communities in the metacommunity, $\overline{n_{\mathrm{BL}}}$, (2) number of basal species in the metacommunity, n_{BM}, (3) local community dissimilarity in basal species composition ($n_{\mathrm{BM}} - \overline{n_{\mathrm{BL}}}$ as an index of dissimilarity), (4) mean number of consumer species in a local community, averaged over the four local communities in the metacommunity, $\overline{n_{\mathrm{CL}}}$, (5) number of consumer species in the metacommunity, n_{CM}, and (6) local community dissimilarity in consumer species composition ($n_{\mathrm{CM}} - \overline{n_{\mathrm{CL}}}$).

I performed ANOVAs to test for the effects of species pool, external dispersal, internal dispersal, and all interaction terms among them on species richness. When ANOVAs detected significant effects, I performed Tukey–Kramer HSD pairwise comparisons to determine which treatment groups differed significantly. All analyses were done with SYSTAT version 10 (SPSS 2000).

Results

Species richness appeared to reach equilibrium by the time the simulations were terminated (Electronic supplementary material Figs. 1 and 2). Under frequent external dispersal, local communities within metacommunities converged to a similar state (Electronic supplementary material Fig. 1). Under infrequent external dispersal, local communities experienced continued species turnover, with no long-term increase or decrease in richness (Electronic supplementary material Fig. 2).

There were strong interactive effects of internal and external dispersal on basal species richness (see rows for external×internal dispersal in Table 1). Local richness, $\overline{n_{\mathrm{BL}}}$, was highest under frequent external dispersal, intermediate under infrequent external dispersal and with internal dispersal, and lowest under infrequent external dispersal and without internal dispersal (Fig. 2a, b). Metacommunity species richness, n_{BM}, was not as strongly affected by dispersal as was local richness, $\overline{n_{\mathrm{BL}}}$ (Fig. 2a, b). This scale-dependent pattern was caused by changes in local community dissimilarity, $n_{\mathrm{BM}} - \overline{n_{\mathrm{BL}}}$, with dispersal rate (*X* and *Y* in Fig. 2c, d). In this simulation, random variation in the sequence in which species dispersed to local communities was the only source of variation in species composition among the local communities within a metacommunity. Therefore, the results (Fig. 2c, d) indicate that external and internal dispersal jointly regulated the importance of assembly sequence in creating and maintaining local community dissimilarity.

Consumer richness was not significantly affected by interaction between the two dispersal types, although strongly affected by external dispersal (Table 2, Fig. 3).

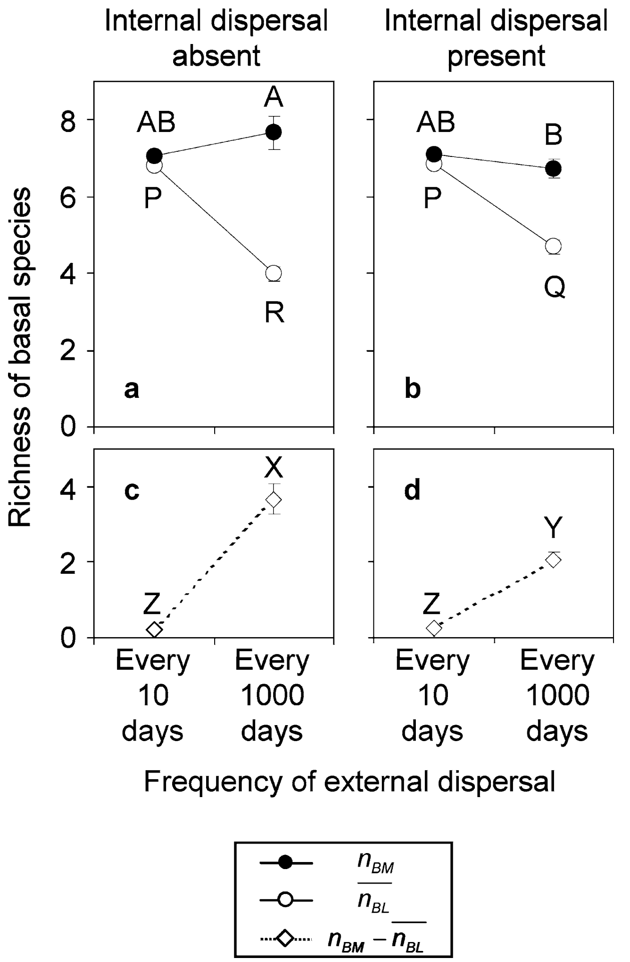

Fig. 2a–d Basal species richness at the end of the simulations. Data points are the mean of 70 replicates (7 species pools×10 metacommunity replicates for each species pool). *Bars* represent SEMs. Values labeled with *different letters* differ significantly (Tukey–Kramer HSD pairwise comparisons with $\alpha = 0.05$ except between A and B, for which $P = 0.065$; comparisons were made separately for mean number of basal species in a local community, averaged over the four local communities in the metacommunity, $\overline{n_{\mathrm{BL}}}$, number of basal species in the metacommunity, n_{BM}, and local community dissimilarity in basal species composition $n_{\mathrm{BM}} - \overline{n_{\mathrm{BL}}}$)

Discussion

Interpretation of results

To my knowledge, this study is the first to theoretically demonstrate that the effects of internal dispersal on species diversity can depend on external dispersal, and vice versa. What biological interpretations could be given to these results? Population dynamics (Electronic supplementary material Figs. 1 and 2) and prior theoretical studies on metacommunity dynamics suggest the following interpretation.

Under infrequent external dispersal, internal dispersal enhances species richness in local communities through a source–sink effect (Pulliam 1988; Loreau and Mouquet 1999; Amarasekare and Nisbet 2001). This

Table 1 Summary of ANOVAs on basal species richness

Response variable	Source of variation	*df*	*F*	*P*
Species richness in local communities ($\overline{n_{\mathrm{BL}}}$)	Species pool (S)	6	95.408	< 0.0005*
	External dispersal (E)	1	1,338.226	< 0.0005*
	Internal dispersal (I)	1	28.495	< 0.0005*
	S×E	6	67.548	< 0.0005*
	S×I	6	2.809	0.012*
	E×I	1	22.681	< 0.0005*
	S×E×I	6	2.951	0.008*
Species richness in metacommunities (n_{BM})	Species pool (S)	6	47.030	< 0.0005*
	External dispersal (E)	1	0.888	0.347
	Internal dispersal (I)	1	9.158	0.003*
	S×E	6	44.404	< 0.0005*
	S×I	6	11.914	< 0.0005*
	E×I	1	11.717	< 0.0005*
	S×E×I	6	11.993	< 0.0005*
Local community dissimilarity in species composition ($n_{\mathrm{BM}} - \overline{n_{\mathrm{BL}}}$)	Species pool (S)	6	71.264	< 0.0005*
	External dispersal (E)	1	657.944	< 0.0005*
	Internal dispersal (I)	1	60.778	< 0.0005*
	S×E	6	77.166	< 0.0005*
	S×I	6	20.708	< 0.0005*
	E×I	1	63.522	< 0.0005*
	S×E×I	6	20.693	< 0.0005*

**P*-value significant ($\alpha = 0.05$)

Table 2 Summary of ANOVAs on consumer species richness

Response variable	Source of variation	*df*	*F*	*P*
Species richness in local communities ($\overline{n_{\mathrm{CL}}}$)	Species pool (S)	6	52.619	< 0.0005*
	External dispersal (E)	1	4,418.630	< 0.0005*
	Internal dispersal (I)	1	4.072	0.045*
	S×E	6	159.783	< 0.0005*
	S×I	6	2.714	0.014*
	E×I	1	2.962	0.086
	S×E×I	6	3.034	0.007*
Species richness in metacommunities (n_{CM})	Species pool (S)	6	35.236	< 0.0005*
	External dispersal (E)	1	459.655	< 0.0005*
	Internal dispersal (I)	1	0.164	0.686
	S×E	6	36.405	< 0.0005*
	S×I	6	4.099	0.001*
	E×I	1	0.003	0.954
	S×E×I	6	4.889	< 0.0005*
Local community dissimilarity in species composition ($n_{\mathrm{CM}} - \overline{n_{\mathrm{CL}}}$)	Species pool (S)	6	24.595	< 0.0005*
	External dispersal (E)	1	254.796	< 0.0005*
	Internal dispersal (I)	1	0.713	0.399
	S×E	6	26.701	< 0.0005*
	S×I	6	3.467	0.003*
	E×I	1	1.714	0.192
	S×E×I	6	4.309	< 0.0005*

**P*-value significant ($\alpha = 0.05$)

increase in local species richness leads to greater homogenization of local communities. Consequently, local communities are more similar in species composition and therefore in the species to which they are resistant when new species attempt to invade (Fukami 2004b). This greater similarity leads to lower species richness in metacommunities. Local communities do not reach complete R and continue to experience cyclic changes in species composition probably due to trophic interactions (Schreiber and Rittenhouse 2004; Steiner and Leibold 2004).

In contrast, under frequent external dispersal, a greater number of species are able to coexist in local communities after transient cyclic changes in community structure (Electronic supplementary material Fig. 2), eventually resulting in local communities that are almost completely resistant to invasion by the species remaining in the species pool (Fukami 2004b; Schreiber and Rittenhouse 2004). However, frequent external dispersal leaves little room for variation in assembly history among local communities to contribute to local community dissimilarity. At both local and metacommunity

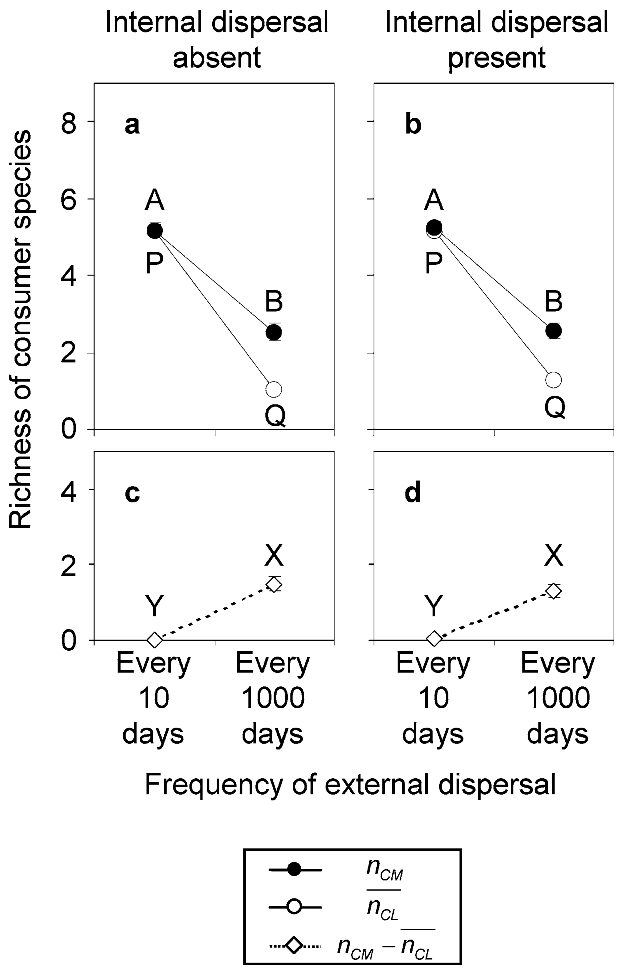

Fig. 3a–d Consumer species richness at the end of the simulations. Comparisons were made separately for mean number of consumer species in a local community, averaged over the four local communities in the metacommunity, $\overline{n_{\mathrm{CL}}}$, number of consumer species in the metacommunity, n_{CM}, and local community dissimilarity in consumer species composition ($n_{\mathrm{CM}} - \overline{n_{\mathrm{CL}}}$). *Symbols* are as in Fig. 2

scale, external dispersal is so frequent that it overwhelms any effects of internal dispersal.

Future directions

My results suggest several research directions regarding interactive effects of internal and external dispersal. First, consequences of dispersal over narrower ranges of dispersal rates may differ from the patterns found here. In this study, internal dispersal was sufficiently frequent to allow for source–sink dynamics, while there were no source–sink dynamics by external dispersal even when it was frequent (i.e., dispersal by species already present in local communities was ignored). It remains to be investigated whether dispersal shows interactive effects when these assumptions about dispersal rate are altered. Furthermore, previous work shows that there may be non-linear effects of dispersal, which can be revealed only by studying more than two rates of dispersal (Loreau and Mouquet 1999; Mouquet and Loreau 20002).

Second, this study deliberately omitted environmental heterogeneity to focus on the role of dispersal. However, heterogeneity both in space (see, e.g., Tilman and Pacala 1993; McLaughlin and Roughgarden 1993; Amarasekare and Nisbet 2001; Snyder and Chesson 2003) and time (see, e.g., Chesson 1994, 2000; Holt and Barfield 2003) can alter the role of internal dispersal in species coexistence. It remains to be seen to what extent external dispersal alters this interaction between internal dispersal and environmental heterogeneity. Likewise, tradeoffs between internal dispersal ability and other species traits (e.g., competitive ability, reproductive rate, and predation resistance) can play a major role in maintaining species diversity (Levins and Culver 1971; Amarasekare and Nisbet 2001; Kisdi and Geritz 2003; Kondoh 2003). Impacts of external dispersal on the role of these tradeoffs are another unexplored issue.

Third, the simulation results suggest that whether external dispersal interacts with internal dispersal may depend on the trophic level at which species diversity is observed (Figs. 2 vs. 3). However, it should be noted that the difference between the trophic levels might not reflect anything about trophic level per se, but merely the difference in internal dispersal rate between the trophic levels. Consumer species was less abundant than basal species throughout simulations (Electronic supplementary material Figs. 1 and 2), which may have been responsible for different diversity patterns. In future work, the parameters that define the differences between basal and consumer species can be altered to ascertain the factors causing interactive effects of internal and external effects to differ depending on the trophic levels observed.

Conclusions

This study has shown that internal and external dispersal can reciprocally provide the context in which each influences species diversity. There seems considerable scope for studies on such interactive effects, and I have discussed some future directions. Understanding these effects is not only academically interesting, but is also vitally important to biological conservation. That internal dispersal can have both negative and positive effects on species persistence has fueled much debate over the use of habitat corridors that may promote internal dispersal among nature reserves (Simberloff et al. 1992; Beier and Noss 1998; Earn et al. 2000). In the meantime, much interest has focused on the role of external dispersal in ecological restoration, in which species are introduced from external sources (Lockwood 1997; Young et al. 2000; Temperton et al. 2004), and in biological invasions, in which external dispersal rate can be a key to predicting which exotic species become invasive (Levine 2000; Mack et al. 2000). However, many of these issues remain unresolved. The results presented here suggest that it may not be easy to understand effects of internal and external dispersal in isolation of the other. Unifying the two dispersal types in a coherent framework for species diversity remains a rewarding challenge for both basic and applied ecology.

Acknowledgements I would like to thank the Ecological Society of Japan for awarding me a Denzaburo Miyadi award. I also thank Aaron King for numerous discussions that improved this paper, and Marc Cadotte, Jim Drake, Mac Post, Susan Riechert, Dan Simberloff, Chris Steiner, and an anonymous reviewer for helpful comments. This research was supported by the U.S. National Science Foundation and the Department of Ecology and Evolutionary Biology and the Yates Dissertation Fellowship at the University of Tennessee, Knoxville, Tennessee.

Appendix: Constructing species pools

Number of species

The set of m species that constitute a species pool is divided into m_1 basal species and m_2 consumer species. I used species pools consisting of $m_1 = 20$ basal species and $m_2 = 20$ consumer species. A basal species is able to grow in the absence of any other species from the species pool and does not eat other species from the pool. A consumer species eats some of the other species from the pool and cannot sustain its population in a local community without them.

Assigning body sizes

The method begins with assigning a body size (s_i) to each species i in the species pool. The logarithm of body size of species i, $\log_{10}(s_i)$, is drawn at random from a uniform distribution over the range $[-2, -1]$ for basal species and $[-1, 1]$ for consumer species. It is assumed that, if $s_i < s_j$, then species i may be eaten by species j, but not vice versa.

Assigning a_{ij} between consumers and victims

The strength of the interaction between a consumer and a victim is determined based on the empirically derived assumption that there is an optimal ratio of body size between a consumer and a victim that gives the maximum interaction strength possible (cf. Cohen et al. 1993). Thus, the mean effect of an encounter between consumer j and victim i on the per capita rate of increase of the victim is given as:

$$\overline{a_{ij}} = -0.1 * \exp\left\{-\left(\log_{10}(10 * s_i/s_j) * c_1\right)^2\right\} \quad s_i < s_j$$

$$a_{ij} = 0 \quad s_i \geqslant s_j. \tag{2}$$

Here, the maximum interaction strength is 0.1, and the optimal body size ratio is 10. The parameter c_1 measures the degree of specialization of the consumers around the optimal ratio, 10. I used $c_1 = 10$. Conversely, taking into account energetic constraints so that the loss of victim density is balanced against the gain in consumer density, the mean effect on the per capita rate of increase of the consumer is given as:

$$\overline{a_{ji}} = -\overline{a_{ij}} * c_2 * s_i/s_j \quad s_i < s_j$$

$$a_{ji} = 0 \quad s_i \geqslant s_j. \tag{3}$$

The parameter c_2 measures conversion efficiency. I used $c_2 = 0.05$, which lies within the biologically feasible range (Humphreys 1979). Note that, with this method of defining consumer–victim interactions, consumer species, i.e., those from m_2 species, can also be victims of other consumer species, depending on their body sizes.

Assigning a_{ij} between basal species

The method assumes an upper limit to total biomass, or the carrying capacity of basal species (K_i) within a local community. Assuming that the limit, K_i, is 100 biomass units for each basal species i, a self-limitation term for basal species i is:

$$\overline{a_{ii}} = -b_i * s_i/100. \tag{4}$$

When different basal species occur together, they compete for limited resources such that the mean effect of basal species j and basal species i is:

$$\overline{a_{ij}} = -c_3 * b_i * s_j/100. \tag{5}$$

The dimensionless parameter $c_3$measures the similarity of the basal species in their resource use. Species do not affect each other if $c_3 = 0$; they are identical if $c_3 = 1$. I used $c_3 = 0.9$, as in Morton and Law (1997). Consumers are limited only by victim density, and their self-limitation term is zero.

Assigning b_i

Based on an empirical relationship between body size and the per capita intrinsic rate of increase, b_i, of basal species (Fenchel 1974; Blueweiss et al. 1978), it is assumed that:

$$\log_{10} \overline{b_i} = -1 - 0.25 * \log_{10} s_i. \tag{6}$$

Here, units are day^{-1} for b_i and g for s_i. It is less clear how b_i of consumers should be scaled with body size. Following Morton and Law (1997), I assume it is constant, with units of day^{-1} :

$$\overline{b_i} = -0.1. \tag{7}$$

Allowing random variation around means

The above ecological parameters, a_{ij} and b_i, are unlikely to be solely determined by body size. Morton and Law (1997) assume there are random variables with mean values set by Eqs. 2, 3, 4, 5, 6, and 7, and I follow this assumption. Thus, letting $\bar{p}$ be the mean value of a given parameter from Eqs. 2, 3, 4, 5, 6, and 7, the parameter p itself is taken as a random variable from a normal distribution $N(\bar{p}, 0.1 * \bar{p})$, truncating the distributions to ensure that p has the same sign as $\bar{p}$.

References

Abrams PA (2001) Describing and quantifying interspecific interactions: a commentary on recent approaches. Oikos 94:209–218

Amarasekare P, Nisbet RM (2001) Spatial heterogeneity, source–sink dynamics, and the local coexistence of competing species. Am Nat 158:572–584

Beier P, Noss RF (1998) Do habitat corridors really provide connectivity? Conserv Biol 12:1241–1252

Berlow EL, Navarrete SA, Briggs CJ, Power ME, Menge BA (1999) Quantifying variation in the strengths of species interactions. Ecology 80:2206–2224

Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978) Relationships between body size and some life history parameters. Oecologia 37:257–272

Burkey TV (1997) Metapopulation extinction in fragmented landscapes: using bacteria and Protozoa communities as model ecosystems. Am Nat 150:568–591

Cadotte MW, Fukami T (2005) Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. Ecol Lett 8:548–557

Chase JM (2003) Community assembly: when should history matter? Oecologia 136:489–498

Chesson P (1985) Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. Theor Popul Biol 28:263–287

Chesson P (1994) Multispecies competition in variable environments. Theor Popul Biol 45:227–276

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31:343–366

Cohen JE, Pimm SL, Yodzis P, Saldaña J (1993) Body sizes of animal predators and animal prey in food webs. J Anim Ecol 62:67–78

Drake JA (1990) The mechanics of community assembly and succession. J Theor Biol 147:213–233

Earn DJD, Levin SA, Rohani P (2000) Coherence and conservation. Science 290:1360–1364

Fenchel T (1974) Intrinsic rate of natural increase: the relationship with body size. Oecologia 14:317–326

Forbes AE, Chase JM (2002) The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. Oikos 96:433–440

Fukami T (2004a) Assembly history interacts with ecosystem size to influence species diversity. Ecology 85:3234–3242

Fukami T (2004b) Community assembly along a species pool gradient: implications for multiple-scale patterns of species diversity. Popul Ecol 46:137–147

Fukami T, Morin PJ (2003) Productivity–biodiversity relationships depend on the history of community assembly. Nature 424:423–426

Gotelli NJ (1991) Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. Am Nat 138:768–776

Gotelli NJ, Kelley WG (1993) A general model of metapopulation dynamics. Oikos 68:36–44

Hall G, Watt JM (eds) (1976) Modern methods for ordinary differential equations. Clarendon Press, Oxford

Hanski I, Simberloff D (1997) The metapopulation approach, its history, conceptual domain, and application to conservation. In: Hanski IA, Gilpin ME (eds) Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, Calif., pp 5–26

Holt RD (1993) Ecology at the mesoscale: the influence of regional processes on local communities. In: Ricklefs R, Schluter D (eds) Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Ill., pp 77–88

Holt RD, Barfield M (2003) Impacts of temporal variation on apparent competition and coexistence in open ecosystems. Oikos 101:49–58

Holyoak M, Lawler SP (1996) Persistence of an extinction-prone predator–prey interaction through metapopulation dynamics. Ecology 77:1867–1879

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, N.J.

Huffaker CB (1958) Experimental studies on predation: dispersion factors and predator–prey oscillations. Hilgardia 27:343–383

Huisman JA, Johansson M, Folmer EO, Weissing FJ (2001) Towards a solution of the plankton paradox: the importance of physiology and life history. Ecol Lett 4:408–411

Humphreys WF (1979) Production and respiration in animal populations. J Anim Ecol 48:427–453

Hutchinson GE (1951) Copepodology for the ornithologist. Ecology 32:571–577

Iwasa Y, Roughgarden J (1986) Interspecific competition among metapopulations with space-limited subpopulations. Theor Popul Biol 30:194–214

Kerr B, Riley MA, Feldman MW, Bohannan BJM (2002) Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. Nature 418:171–174

Kisdi É, Geritz SAH (2003) On the coexistence of perennial plants by the competition–colonization tradeoff. Am Nat 161:350–354

Kondoh M (2003) High reproductive rates result in high predation risks: a mechanism promoting the coexistence of competing prey in spatially structured populations. Am Nat 161:299–309

Law R, Morton RD (1993) Alternative permanent states of ecological communities. Ecology 74:1347–1361

Law R, Morton RD (1996) Permanence and the assembly of ecological communities. Ecology 77:762–775

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7:601–613

Levin SA (1974) Dispersion and population interactions. Am Nat 108:207–228

Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854

Levins R, Culver D (1971) Regional coexistence of species and competition between rare species. Proc Natl Acad Sci USA 68:1246–1248

Lockwood JL (1997) An alternative to succession: assembly rules offer guides to restoration efforts. Restor Manage Notes 15:45–50

Lockwood JL, Powell RD, Nott MP, Pimm SL (1997) Assembling ecological communities in time and space. Oikos 80:549–553

Loreau M, Mouquet N (1999) Immigration and the maintenance of local species diversity. Am Nat 154:427–440

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, N.J.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

McCann KS (2000) The diversity–stability debate. Nature 405:228–233

McLauglin JF, Roughgarden J (1993) Species interactions in space. In: Ricklefs R, Schluter D (eds) Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Ill., pp 89–98

Moore JL, Mouquet N, Lawton JH, Loreau M (2001) Coexistence, saturation and invasion resistance in simulated plant assemblages. Oikos 94:303–314

Morton RD, Law R (1997) Regional species pools and the assembly of local ecological communities. J Theor Biol 187:321–331

Morton RD, Law R, Pimm SL, Drake JA (1996) On models for assembling ecological communities. Oikos 75:493–499

Mouquet N, Loreau M (2002) Coexistence in metacommunities: the regional similarity hypothesis. Am Nat 159:420–426

Mouquet N, Munguia P, Kneitel JM, Miller TE (2003) Community assembly time and the relationship between local and regional species richness. Oikos 103:618–626

Nathan R (2003) Seeking the secrets of dispersal. Trends Ecol Evol 18:275–276

Numerical Algorithms Group (2002) NAG C library, mark 7. Numerical Algorithms Group, Oxford

Paine RT (1992) Food-web analysis through field measurement of per capita interaction strength. Nature 355:73–75

Pulliam HR (1988) Sources, sinks and population regulation. Am Nat 132:652–661

Post WM, Pimm SL (1983) Community assembly and food web stability. Math Biosci 64:169–192

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Sala E, Graham MH (2002) Community-wide distribution of predator–prey interaction strength in kelp forests. Proc Natl Acad Sci USA 99:3678–3683

Schreiber SJ, Rittenhouse S (2004) From simple rules to cycling in community assembly. Oikos 105:349–358

Shurin JB, Allen EG (2001) Effects of competition, predation, dispersal on local and regional species richness. Am Nat 158: 624-637

Simberloff D, Farr JA, Cox J, Mehlman DW (1992) Movement corridors: conservation bargains or poor investments? Conserv Biol 6:493–504

Skellam JG (1951) Random dispersal in theoretical populations. Biometrika 38:196–218

Snyder RE, Chesson P (2003) Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. Ecol Lett 6:301–309

SPSS (2000) SYSTAT. Version 10. SPSS, Chicago, Ill.

Steiner CF, Leibold MA (2004) Cyclic assembly trajectories and scale-dependent productivity–diversity relationships. Ecology 85:107–113

Temperton VM, Hobbs RJ, Nuttle T, Halle S (eds) (2004) Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, Washington, D.C.

Tilman D, Pacala S (1993) The maintenance of species richness in plant communities. In: Ricklefs R, Schluter D (eds) Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Ill., pp 13–25

Tokita K, Yasutomi A (2003) Emergence of a complex and stable network in a model ecosystem with extinction and mutation. Theor Popul Biol 63:131–146

Warren PH (1996) The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scales. Oecologia 105:132–140

Wilmers CC, Sinha S, Brede M (2002) Examining the effects of species richness on community stability: an assembly model approach. Oikos 99:363–367

Wilson DS (1992) Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology 73:1984–2000

Young TP, Chase JM, Huddleston RH (2000) Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. Ecol Restor 19:5–18