OIKOS 103: 618–626, 2003

Community assembly time and the relationship between local and regional species richness

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Mouquet, N., Munguia, P., Kneitel, J. M. and Miller, T. E. 2003. Community assembly time and the relationship between local and regional species richness. – Oikos 103: 618–626.

Many previous studies have assumed that a linear relationship between local and regional species richness indicates that communities are limited by regional processes, while a saturating relationship suggests that species interactions restrict local richness. We show theoretically that the relationship between local and regional richness changes in a consistent fashion with assembly time in interacting communities. Communities show saturation in their early assembly stages because only a subset of the regional pool may colonize a locality. At intermediate assembly times, communities will appear unsaturated until significant competitive exclusion occurs. Finally, when communities reach equilibrium, we found saturation as a result of resource competition resulting in the dominance of a limited number of species. We show that habitat size and species fecundity are important in determining the time needed for the community to reach equilibrium and thus affect the relationship between local and regional species richness. Our results suggest the number of coexisting species is a function of local and regional processes whose relative influences might vary over time and that research using the relationship between local and regional species richness to infer mechanisms limiting species richness must have knowledge of the assembly time of the community.

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Since the work by Terborgh and Faaborg (1980), Cornell (1985a, b), and Ricklefs (1987), many ecologists have addressed the relationship between local and regional species richness (Cornell 1999, Huston 1999 and Srivastava 1999, for reviews). This issue is a key point in the debate on the relative importance of local processes (e.g. competition, niche differentiation) and regional processes (e.g. immigration/emigration) in structuring ecological communities (Ricklefs 1987, Zobel 1992, 1997, Ricklefs and Schluter 1993, Hillebrand and Blenckner 2002). To this end, many authors have attempted to interpret a plot of local versus regional species richness (Cornell 1985a). When a saturating relationship was found, they concluded that local processes like competition were limiting local species richness, and when no saturation was found, they concluded that regional factors were the important determinants of local species richness (Terborgh and Faaborg 1980, Cornell and Lawton 1992).

Many of the studies that have used this procedure have found little evidence for species saturation (see Cornell 1999 for a review), concluding that processes on regional (biogeographical) and historical (evolutionary) scales are probably more important than species interactions (e.g. competition and predation) in shaping ecological communities. However, an increasing number of studies have asked whether the 'saturation vs unsaturation' pattern can be interpreted simply as 'in-

Accepted 15 April 2003

ISSN 0030-1299

teractive' or 'non-interactive' (Huston 1999, Lawton 1999, Srivastava 1999, Loreau 2000, Valone and Hoffman 2002). The critics have asked whether the methodology used to test such relations was adequate (Cresswell et al. 1995, Srivastava 1999), whether the scales at which local and regional scales were defined were pertinent (Huston 1999, Loreau 2000, Gering and Crist 2002, Arita and Rodrigez 2002, Mouquet and Loreau 2003), and whether the processes behind the variation in species richness were clearly identified (Partel et al. 1996, Cornell 1999, Huston 1999, Loreau 2000).

In this paper, we address another factor concerning the community assembly time (Lawton and Strong 1981, Holt 1993, Morton and Law 1997, Huston 1999, Lawton 1999, Mungia in press). Most of the previous studies have assumed, either implicitly or explicitly, that sampled communities were at equilibrium (but see Huston 1999). We define community assembly time as the time elapsed between the arrival of the first successful species and the state characterized by stability in species abundances and composition. It can be analogous to successional time (McIntosh 1980, Rees et al. 2001) but also to the duration of assembly processes within a successional stage. We expect an interactive community to exhibit different relationships between local and regional species richness, depending on the time at which they are sampled for species richness (Morton and Law 1997). We assume that (1) in the first stages of community assembly, only a subset of the regional species pool may colonize a locality and (2) the process of species competitive exclusion can be relatively long and thus that sampled communities are often far from equilibrium (Hubbell 1979). We expect that the combination of these two assumptions will vary the degree of saturation during community assembly.

To this extent, we present a simple theoretical model of species competition in which we vary the size of the regional pool as well as the time of sampling of species richness since initial colonization. We also vary the size of the habitat and the fecundity of species (whose combination determines species probability of interaction) because they are important factors determining the time needed for the community to reach equilibrium (Hurtt and Pacala 1995). This model is sufficiently general to apply to a broad range of organisms from plants to animals.

Methods

We have chosen a simple niche model adapted from the generalized competition model proposed by Pacala and Tilman (1994), see also Hurtt and Pacala 1995, Mouquet et al. 2002). Originally this model was built for plant communities, but it can be applied to a broader range of organisms. We understand that community composition is also the result of other mechanisms and that our niche model is oversimplified. However, we wanted to study relative importance of local interactions and regional influences through time without interference from other processes. We point out some of the possible effects of other factors in the discussion.

Locally, we consider species to be competing for a fixed number of resource units and to vary in the probability of winning a particular resource unit (i.e. each species has a different competitive ability). Individuals reproduce only if they win a resource unit. Individuals keep a resource unit until they die, and the resource unit then becomes available again. To mimic resource heterogeneity we postulate that there are different kinds of resource units, and each species specializes in only one kind. This set of assumptions makes the model very general. It can easily be applied to competition for space by plants or marine sessile animals because for these organisms the concept of space cannot be separated from that of resource (Yodzis 1986). In this case, a resource unit is equivalent to a site that can be used by only one individual at a time. More generally, the model applies to any kind of organism if a resource unit is the minimal amount of resource (or shelters, mates, etc.) an individual must obtain to reproduce successfully.

The number of species in the regional pool is S_{reg} and the number of locally coexisting species is S_{loc}. Species abundance, N_i, is equal to the number of resource unit occupied by species i. The resource units in the community are divided equally in 20 different classes of value H_j, where H_j varies between 0 and 1 ($H_1 = 0$ and $H_j = H_{j-1} + 0.05$; j ranges from 2 to 20). Therefore each community will have the equivalence of 20 different types of resources. The probability that an individual of species i will win a resource unit is the product of the probability P_i that it will reach the unit and the probability C_{ij} of being the best competitor for a resource unit of value H_j. The probability P_i obeys a Poisson distribution that is a function of local species abundance N_i and fecundity F (equal for all species).

$$P_i = 1 - \exp\left(-F\frac{N_i}{\sum_{k=1}^{S_{loc}} N_k}\right) \tag{1}$$

Each species i is characterized by a competition parameter R_i chosen randomly between 0 and 1 from a uniform distribution. The probability C_{ij} is determined by

$$C_{ij} = 1 - |H_j - R_i| \tag{2}$$

so a species has a high competitive ability for a particular type of resource unit when its competitive parameter value (R_i) is close to the resource unit value (H_j). Individuals die with probability m, which is density independent and is the same for all species ($m = 0.3$).

Each simulation starts with an empty community. Species colonize from the regional pool with a probability I, equal for all species ($I = 0.05$): At each time step, a random number is drawn from a uniform distribution between 0 and 1 and compared to I to determine whether a particular species will colonize. When a particular species colonizes, the local abundance for that species is set to 20 individuals (i.e. 20 resource units are allocated to this species). Several species can colonize during the same time step. The colonization is limited to only one successful event per species in each simulation so as to avoid confounding the effects of time and immigration intensity on species assembly (Loreau and Mouquet 1999; see also discussion). This process assures a sequential assembly of the community but does not prevent the community from reaching equilibrium because the colonization period ends when all species have had one colonization event.

Simulations were conducted in repeated loops. Each cycle consisted of (1) estimation of species densities in each community, (2) mortality events, (3) colonization-attempt events, and (4) local recruitment procedures, where for each available resource unit the model determines (a) the probability that a juvenile (or a seed) will reach a resource unit (P_i, Eq. (1)) and (b) the probability that no better competitor will reach that unit (derived from Eq. (2)). The simulations were continued until an equilibrium was reached (all species have had a successful colonization event and species abundances were stable).

Unless specifically varied, the species fecundity was fixed at 50 and the number of resource units was 10000 (i.e. maximal total density was 10000). To study the relationship between local and regional species richness, we have assembled communities with different regional pool sizes ($S_{reg} = 2, 4, 6, 10, 15, 20, 50, 100, 150, 200$). For each value of S_{reg}, we have sampled community composition at each time step and present means over 30 replicates.

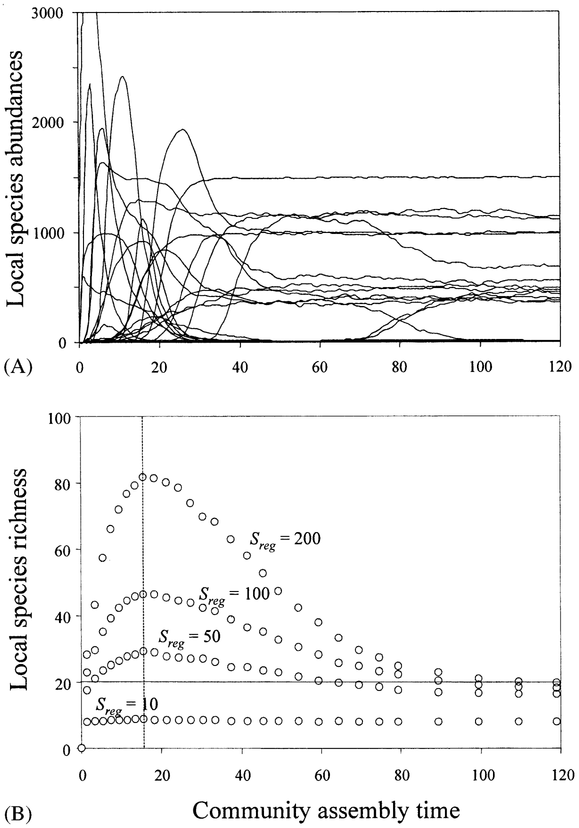

Fig. 1. (A) Dynamics of species abundances in one community with $S_{reg} = 30$. (B) Numbers of species coexisting locally for different sizes of the regional species pool as a function of time. The horizontal line denotes the maximum number of species that can coexist at equilibrium (= 20). The vertical line denotes the time when the maximum number of locally coexisting species is reached. We present mean species richness (over 30 replicates); the standard deviations are omitted for clarity and are always less than 15% of the mean.

Results

Species abundances and community composition varied in the early stage of the community assembly because colonization was a random process (Fig. 1A). After a delay, the community composition stabilized as species that specialized on the different resources dominated. The resource units were all used relatively quickly ($t \approx 3$) after the first colonization event took place, indicating that communities were highly interactive and that competition for resource units was strong. The composition of the equilibrium community appeared to be robust; repeated runs with the same species parameters but different sequence of colonization resulted in the same final community.

The number of locally coexisting species was a function of the size of the regional species pool and the community assembly time (Fig. 1B). Local species richness initially increased because of transitory coexistence after colonization events but, after a delay, declined and reached asymptote at the equilibrium number of species that could coexist locally (≈ 20) based on the number of different classes of resources units values. While not explored in this paper, we have shown that increasing the number of resources available has resulted with more species coexisting at equilibrium as well as during the transient dynamic. But, except when the number of resources equaled the number of species in the regional pool (that is biologically unrealistic), this did not qualitatively affect the results we will present below.

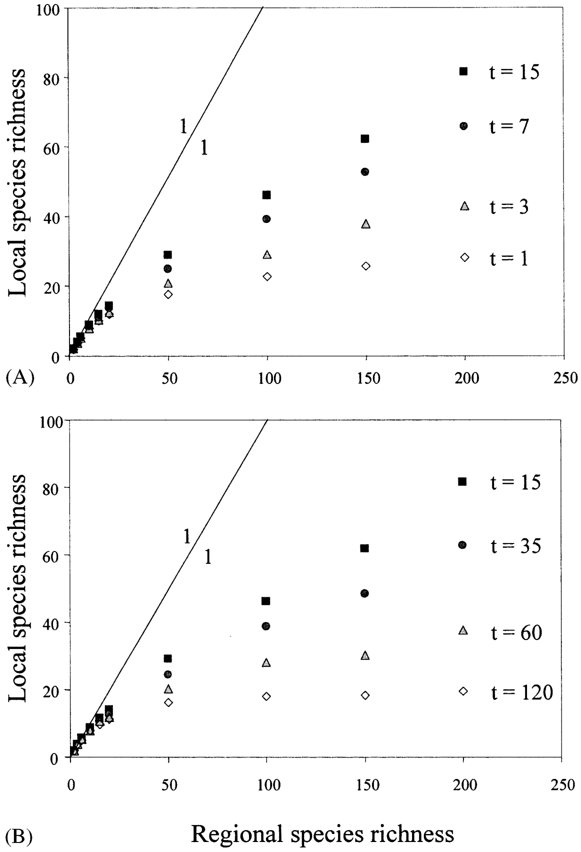

Fig. 2. Relationships between local and regional species richness obtained at different times during community assembly. (A) Early stage of community assembly, corresponding to the left side of Fig. 1B (t = 1, 3, 7, 15); (B) later stages, corresponding to the right side of Fig. 1B (t = 15, 35, 60, 120).

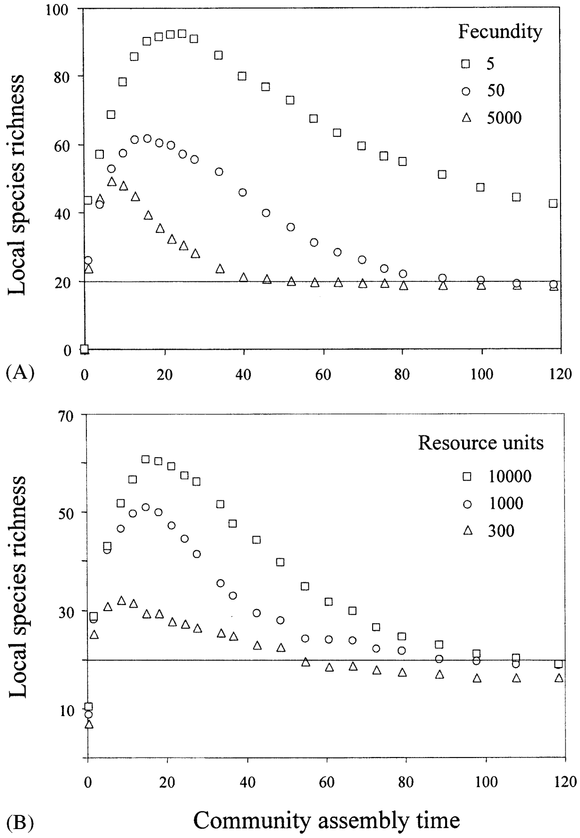

Fig. 3. Numbers of species coexisting locally as a function of time for (A) different values of species fecundity (with 10,000 resources units) and (B) different numbers of resource units (with fecundity = 50); $S_{reg} = 150$ in both cases. The horizontal line denotes the maximum number of species that can coexist at equilibrium (= 20). We present mean species richness (over 30 replicates); the standard deviations are omitted for clarity and are always less than 15% of the mean.

The relationship between local and regional species richness was clearly a function of sampling time (Fig. 2). There was almost no relationship (i.e. slope near zero) at early stages of community formation (t = 1 and 3, Fig. 2A), when local richness is largely determined by stochastic colonization events. Similarly, there is a saturating relationship during later succession near as the community nears equilibrium and competition limits local richness (t = 60 and 120, Fig. 2B). However, during intermediate periods in succession, the relationship between local and regional richness becomes nearly linear (t = 7, 15, and 35, Fig. 2A, B).

These results depended on species fecundity and the number of resource units in the community. Higher fecundity produced a more rapid build-up of density and greater competition for available resources, resulting in coexistence of fewer species in the early stages of assembly and a more rapid approach to equilibrium (Fig. 3A). Fewer resource units resulted in a lower peak of species richness and rapid saturation (Fig. 3B). Note that for a low number of resources units (300), the number of coexisting species is lower than the number of limiting resources. Such under-saturation is observed because at a low number of sites some species (including good competitors) have been lost because of stochastic extinction.

The general pattern of the relationship between local and regional species richness was robust to variation in fecundity and number of resource units. We plotted the slopes of this relationship for different sampling times and found, as previously, a progression from no relationship to a nearly linear one, then to saturation as the community assembles through succession (Fig. 4): final saturation occurs earlier at high fecundity (Fig. 4A) and low number of resources units (Fig. 4B).

Discussion

As expected (Cornell and Lawton 1992), our assembly model based on local competition ultimately constrains species richness by the number of resource types and

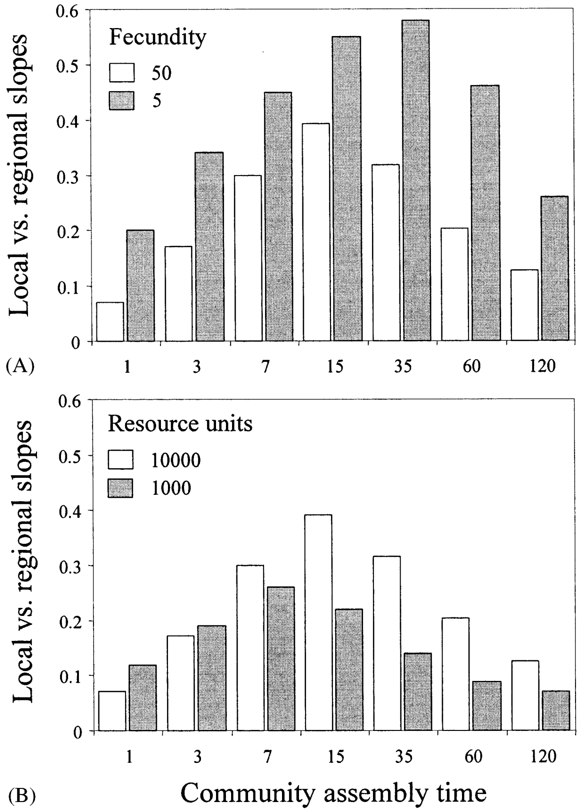

Fig. 4. Slopes of the relationship between local and regional species richness for different sampling times with (A) two levels of fecundity (with 10,000 resources units) and (B) two numbers of resources units (with fecundity = 50). For simplicity we have chosen a linear regression model.

leads to a saturated relationship between local and regional species richness at equilibrium. The variation of species richness over time corresponds to patterns of successional diversity (Odum 1969, Whittaker 1970, Huston 1994). Our results can also be interpreted as species assembly within a successional stage, in which case only species of that particular stage are concerned. Clearly, the dynamics of succession are more complex than what is described by our simple model, but the simplicity of our approach helps generalize our results to a broad variety of systems. Our results also illustrate how the relationship between local and regional species richness varies with the time at which communities are sampled. We predict that early in assembly (or succession) no relationship will be apparent between local and regional species richness. However, a nearly linear relationship, with increasing slope, will rapidly develop during intermediate stages of assembly. Finally, as the community nears equilibrium, the slope will again decrease to zero. We suggest that research using the relationship between local and regional species richness should have better knowledge of the assembly time of the community in order to infer any mechanisms limiting species richness. We do not argue that only local processes are important in shaping ecological communities since, whatever the degree of local interaction, the regional species pool always limits local species richness to the number of potentially colonizing species (Zobel 1997). The number of coexisting species is then both a function of local and regional processes whose relative influences vary over time.

Our results emphasize some previous arguments for caution in interpreting plots of regional vs local species richness in terms of saturated or unsaturated communities based on time considerations (Lawton and Strong 1981, Holt 1993, Huston 1999, Lawton 1999, Loreau 2000). We can divide the duration of assembly into three stages of community development: colonization stage, non-saturation, and saturation. The colonization stage where there is no relationship between local and regional richness is perhaps non-intuitive and does not follow the classical interpretation that local processes like competition limit species richness in local communities. It occurs when few colonization events have happened and the local community is unaffected by the regional pool size (except for very small sizes). This result reflects, at least in part, previous verbal models like the ‘pool exhaustion’ hypothesis (Lawton and Strong 1981, Cornell 1985b), or the ‘pseudo-saturation’ effect (Cornell and Lawton 1992, Lawton 1999), under which only a subset of the apparent species pool may actually be able to colonize a locality early in the assembly sequence (see also Aho 1990). The middle, unsaturated stage where there is a linear relationship between local and regional richness occurs after many species from the regional pool have successfully established themselves in the local community but before significant competitive exclusion has occurred. In our model, competition is important, as all resource units are occupied early in the assembly process. This result indicates that the linear relationship can be the result of transient dynamics of a strongly interactive community succession toward equilibrium (Morton and Law 1997), contrary to the interpretation that it is thought to occur when the effects of regional richness through migration are more important than local factors such as competitive interactions (Terborgh and Faaborg 1980, Cornell and Lawton, 1992). As the community approaches equilibrium, the late saturation stage occurs as a result of competitive exclusion, because the maximal number of coexisting species is equal to the number of different classes of resource units (here 20). This result corresponds to the classical interpretation: saturation as the result of strong local interactions (Terborgh and Faaborg 1980, Cornell and Lawton 1992).

Many previous field studies have used saturation (or its absence) as an indicator of the relative importance of local and regional processes in determining community species richness (see reviews of Cornell 1999, Huston 1999, Srivastava 1999). We provide here five examples in which the community assembly time was implicated in shaping such a relationship. Winkler and Kampichler (2000) found evidence of local species saturation in communities of surface-dwelling grassland Collembola. They pointed out that their surveys were not conducted over a sufficiently long period of time to provide insight into species turnover or species interactions. In other words, when sampled, their communities might have been at the colonization stage saturation or late saturation stage, as illustrated by our model. Kennedy and Guegan (1994) studied species richness in helminth parasite communities in 32 species of freshwater fish, which showed a linear (non-saturation) relationship between local and regional species richness, whereas the relation was curvilinear on the native species. The authors interpreted this result as a temporary situation reflecting the shorter time that had been available for community assembly on newly introduced fish species that were in the process of acquiring parasites. In a survey of forest patches, Jacquemyn et al. (2001) found that the number of species per patch and the slopes of species-area curves increase with time. They interpreted this pattern as partially the result of increased heterogeneity with time but it may also indicate that the relation between local and regional species richness is a function of time because the end points of the species-area curve are the regional scale (Rosenzweig and Ziv 1999). In a study of scleractinian corals, Cornell and Karlson (1996, Karlson and Cornell 2002) found that the local scale was unsaturated, but they point out that these communities take a long time to reach equilibrium, and one of the mechanisms to explain non-saturation is that disturbance in this system acts at a higher rate than the growth rate of organisms (see below). In another benthic system, Mungia (in press) found that depending on the life history of the species, the local-regional relationship may change with succession. At early stages of community assembly, motile species showed a saturated relationship and became unsaturated with succession, while sessile species presented an unsaturated relationship throughout the study period.

By varying the number of resource units, we are essentially varying the local habitat size. The model thus predicts that larger habitat size will result generally in higher species richness and a later decline to saturation in the relationship between local and regional richness. Recently, Loreau (2000) pointed out that such a ‘size-limitation’ argument might be used to explain local species richness saturation. The result we found for low habitat size (Fig. 3B, 300 resources units) confirms Loreau’s intuition. Our model provides a complementary pattern showing that habitat size is also important in constraining the number of transitory coexisting species which results in delayed saturation with increased community size.

Like any theoretical study, our model makes a set of simplifying assumptions. First, the community assembly was the result of sequential colonization events, which produces the relationship found in the colonization stage. If the model had started with all species present, species richness would have declined continuously (right part of Fig. 1B) and the tendency would therefore have been from non-saturation to saturation through assembly time (as in Fig. 2B). However, sequential species colonization seems to be a reasonable assumption supported by many field studies (Simberloff and Wilson 1969, Schoener 1974, Simberloff 1976, Jenkins and Buikema 1998). Second, we used a simple model of species competition based on earlier studies (Pacala and Tilman 1994, Hurtt and Pacala 1995, Mouquet et al. 2002), but other models of species competition might have produced different results. For example, some authors have used classical Lotka–Voltera models to demonstrate that the sequence of species assembly may be important in determining final species composition (Drake 1991, Morton et al. 1996). However, the possibility of different endpoints for the communities would not alter our conclusions because we focus on the number of different species rather than their identity (see also Morton and Law 1997). Third, we assume species have equal fecundity and similar colonization strategies. Realistically, a range of types is more likely, for instance, according to the competition-colonization trade-off hypothesis (Hastings 1980, Shmida and Ellner 1984, Tilman 1994). Taking such variation in species strategies into account would not affect our results and might even reinforce them, because the good competitors would colonize the community later and the unsaturated stage would then last longer. Fourth, a criticism that applies to all previous theoretical studies of the relationship between local and regional species richness, is that our model does not consider an explicit origin for the regional species pool. This can be done considering that some communities are connected by dispersal, the sum of which constitutes the regional scale organized in a metacommunity (Wilson 1992, Holt 1993, Mouquet and Loreau 2002, 2003). In that case a limit to local species richness is set by the degree of regional heterogeneity and the dispersal between communities (Mouquet and Loreau 2002, 2003), and the relationship between local and regional species richness will result from the balance between alpha and beta diversity, from saturated at low dispersal to unsaturated when dispersal increases (Loreau 2000, 2003, Valone and Hoffman 2002). However assembly time will still have an important role in chapping the relationship between local and regional species richness since transitory coexistence will still be possible. Note also that different definitions of the regional scale can produce qualitatively different patterns of local and regional diversity (Shurin et al. 2000).

Other mechanisms of species coexistence

Species composition in competing communities can be the result of other mechanisms (Tilman and Pacala 1993, Bengtsson 1994, Chesson 2000, for reviews) that we did not include in our model for the sake of simplicity. Our model considers a highly competitive system where the number of coexisting species at equilibrium is equal to the number of limiting resources. But in reality one can imagine a continuum between niche based communities and systems where species are competitively equivalent, as in the neutral perspective (Bell 2000, Hubbell 2001). In the case of local competitive equivalence (or quasi-equivalence), the time to reach equilibrium tends to infinity and coexistence of a high number of species is possible on few resources. Regional diversity is then a function of the balance between speciation and extinction, while local species diversity drifts due to stochastic extinctions and colonisations. In such case, the relationship between local and regional species richness will be function of the size of local communities, the distance between the communities, and the dispersal limitation of individual species (Hubbell 2001).

Disturbance can disrupt community assembly, essentially setting it back to an earlier stage, so the relationship between rate of disturbance and species richness is generally thought to be unimodal (Connell 1978, Huston 1979). In a related fashion, disturbance can cause an unsaturated relationship between local and regional species richness despite strong local interactions (Caswell and Cohen 1993, Huston 1999, Foster 2001) as illustrated in Fig. 5A (left). Under low and high disturbance rates, no relationship between local and regional richness is expected either because the community is saturated at equilibrium or because disturbance is so severe that few species can exist. In accordance with our model, however, the slope of the local-regional relationship will depend on the assembly time (Fig. 5A left). Fig. 5B illustrates the predicted local-regional relationships for different combinations of community assembly times and disturbance rates. The relationships when the disturbance rate is low and the community assembly time is variable and when the community assembly time is long and the disturbance rate variable correspond to what is expected from our model (Fig. 5A right) and the literature (Caswell and Cohen 1993, Hugueny and Paugy 1995, Huston 1999, Fig. 5A left). However these predictions are altered at intermediate disturbance rates and community assembly times (Fig. 5B, gray cells). For example, saturation is predicted even at intermediate level of disturbance (Fig. 5B, light gray cell, t > d) if the community assembly time is short (for the same reason as in our model without disturbance). Disturbance can also overwhelm the predicted relationship based on community assembly time (Fig. 5B, dark gray cell, d > t).

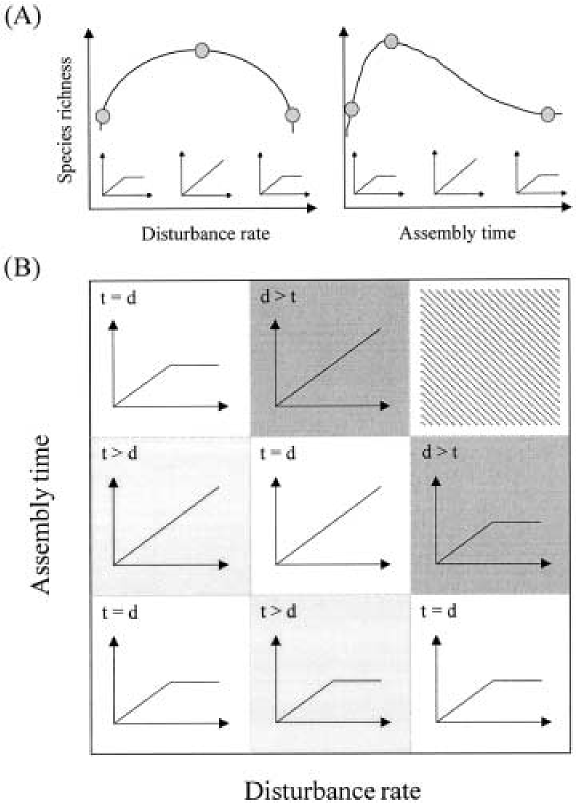

Fig. 5. Summary of the predicted relationships between local and regional species richness for different community assembly times and disturbance rates. The variation of local species richness is shown in (A), given the disturbance rate (left) and the community assembly time (right). Below the curves are the expected relationships between local and regional species richness (saturation and non-saturation) in communities corresponding to the gray circles on both curves. The predicted relationships between local and regional species richness is shown in (B) when both community assembly time and disturbance rate vary. The cells are white when the two predictions are equivalent (t = d) in shaping the relationship between local and regional species richness. The cells are light gray when the community assembly time is more important than the disturbance rate (t > d) and dark gray when the disturbance rate is more important (t < d). Note that the case with high disturbance rate and long assembly time was thought to be unrealistic and not considered.

Immigration is also an important factor determining the relationship between local and regional species richness (Shmida and Ellner 1984, Mouquet and Loreau 2002). In our model each species colonized only once and the results could differ if continuous immigration was allowed. First, if immigration was high, the probability of colonization of species from the regional species pool would increase and the period of initial increase in species richness. The initial colonization stage with no relationship between local and regional richness will be very short and thus probably not observed in the field. In contrast, if immigration was very low, the colonization stage would last longer and thus would more likely be observed. Second, immigration can rescue species from competitive exclusion and thus may increase realized species richness (MacArthur and Wilson 1967, Brown and Kodric-Brown 1977, Loreau and Mouquet 1999). The relationship between regional and local species richness at equilibrium would then switch from saturation to non-saturation with increasing immigration intensity in continent island models or dispersal between communities in metacommunity models (Mouquet and Loreau 2003).

Conclusion

Our study emphasizes that the relationship between local and regional species richness is not a simple indicator of the influence of local and regional forces but also changes in a predictable way during community assembly. In an interacting community, at equilibrium, the relationship should be curvilinear, indicating that local factors limit species richness to a set value and, past some threshold, is unaffected by regional richness. We have also demonstrated, however, that a similar relationship may be found during the earliest stages of community assembly, regardless of local species interactions. As the community develops through migration of new species and species sorting, the slope of the relationship between local and regional richness should first increase from near zero, reach some maximum slope at an intermediate assembly stage, then decrease to near zero again. Thus in such system, species richness is thus both a function of local and regional processes whose relative influences vary over time. Future field studies that use the relationship between local and regional species richness should either incorporate some information on the assembly stage of the community or, preferably, sample the community through time at scales appropriate (on the basis of habitat size and the potential fecundity of species involved) to the system.

Acknowledgements – We thank M. Loreau for comments on the manuscript. A. Thistle kindly edited the manuscript. This work was supported in part by School of Computational Science and Information Technology (NM), Florida State University and grants from the National Science Foundation (DEB-0091776 and DEB-0083617 to TEM).

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