

## ON THE RELATIONSHIP BETWEEN REGIONAL AND LOCAL SPECIES RICHNESS: A TEST OF SATURATION THEORY

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**Abstract.** What are the local community consequences of changes in regional species richness and composition? To answer this question we followed the assembly of microarthropod communities in defaunated areas of moss, embedded in a larger moss “region.” Regions were created by combining moss from spatially distinct sites, resulting in regional species pools that differed in both microarthropod richness and composition, but not area. Regional effects were less important than seasonality for local richness. Initial differences in regional richness had no direct effect on local species richness at any time along a successional gradient of 0.5–16 months. The structure of the regional pool affected both local richness and local composition, but these effects were seasonally dependent. Local species richness differed substantially between dates along the successional gradient and continued to increase 16 months after assembly began. To the best of our knowledge, this is the first critical test of saturation theory that experimentally manipulates regional richness. Further, our results failed to support the most important mechanisms proposed to explain the local richness–regional richness relationship. The results demonstrate that complicated interactions between assembly time, seasonality, and regional species pools contribute to structuring local species richness and composition in this community.

*Key words:* community composition; dispersal; local richness; mites; regional richness; saturation; seasonality; source pool.

### INTRODUCTION

Much research in community ecology aims to understand the factors structuring species diversity in any local area (MacArthur 1972, Ricklefs 1987, Holyoak et al. 2005). Classically, local species richness has been explained by referring to local or regional processes. Local processes have been most strongly invoked through niche theory (Pianka 1966, MacArthur and Levins 1967, Schoener 1974), where strong competition for niche space limits the number of species that can locally coexist. Such a limitation of local richness is referred to as species saturation. Regional processes, on the other hand, can result from evolution through time (Jablonski and Sepkoski 1996, Ricklefs 2004), or at ecological time scales through dispersal to the local community from a larger region (MacArthur and Wilson 1967). Numerous experimental studies show the importance of biotic interactions in structuring local communities (e.g., Paine 1966, Connell 1983, Carpenter et al. 1995, Brown et al. 2001). By contrast, there are few studies examining how differences in regional richness structure local species richness through processes like

dispersal (e.g., Fukami 2004a, Cadotte 2006). There are, however, a number of empirical studies where the relationship between local and regional richness is interpreted using regressions of local richness on regional richness (reviewed by Hillebrand and Blenckner 2002, Shurin and Srivastava 2005). Generally, linear relationships between local and regional richness have been understood to indicate a dominant role for regional processes such as dispersal. A decelerating curvilinear line, where maximum local species richness is reached at a low level of regional species richness, indicates that local processes like competition are dominant, and this is typically interpreted as evidence for saturation.

Tests for species saturation have been largely observational (e.g., Terborgh and Faaborg 1980, Cornell 1985, 1999, Ricklefs 1987, Kiflawi et al. 2003). The observational approach has been criticized on many fronts (Srivastava 1999, Hillebrand and Blenckner 2002, Shurin and Srivastava 2005). Many of these critiques concern confounding covariates of regional richness. For example, some regions may contain more species than others simply because they are larger (Rosenzweig 1995). Similarly, locations may differ in richness because of extent of, or time since, disturbance. Several models have shown that variation in either local or regional area (Srivastava 1999, Hillebrand and Blenckner 2002, He et al. 2005, Shurin and Srivastava 2005) or time since disturbance (Caswell and Cohen 1993) can lead to misleading results when using the graphical method.

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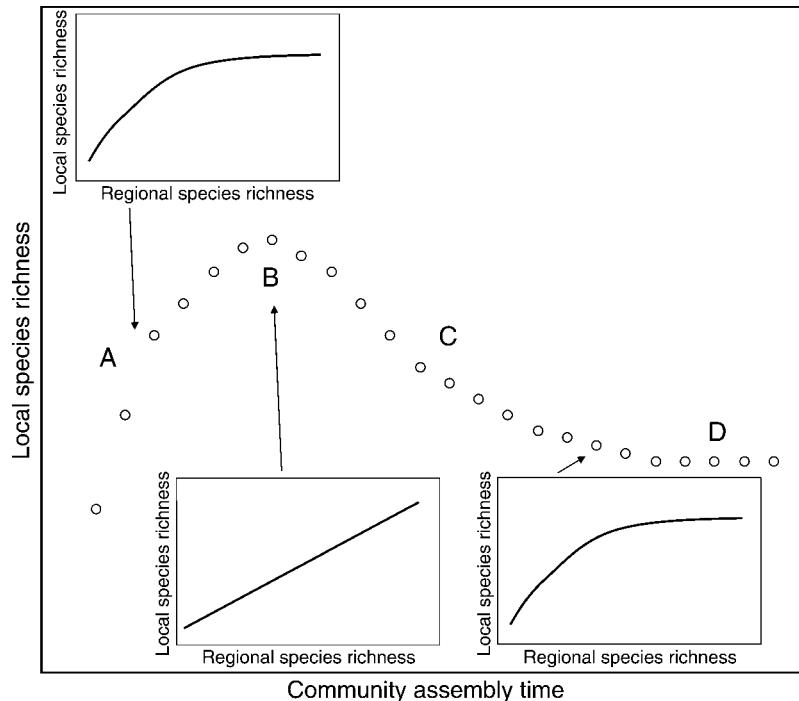


FIG. 1. Predictions for the pattern of local species richness with assembly time in an interactive community, with expected relationships between local and regional richnesses at three points along the community assembly trajectory. Point A shows the result of early colonization effects, where local species richness is largely independent of regional richness because only the fastest colonizers have arrived. Point B shows the point of transitory coexistence, where both good colonizers and good competitors coexist before competition goes to completion. Eventually competition will exclude the early colonizers that are poor competitors, beginning at point C, where early competitive effects are seen, and concluding at point D.

The problems with observational approaches to testing saturation theory may be solved by experimentally manipulating regional species richness. Nevertheless, there are few experimental manipulations of regional richness, save for seed addition experiments (Turnbull et al. 2000) and coral reef manipulations (Abele 1984). There are even fewer that change regional species composition (Cadotte 2006). We expand on these studies by constructing a gradient of regional richness and composition without changing regional area. We then account for time since disturbance by following the assembly of local communities through time.

Several theoretical and observational studies have looked at the interacting effects of assembly time and regional species richness on local species richness (Mouquet et al. 2003, Fukami 2004a, b, Munguia 2004). In the species competition model of Mouquet et al. (2003) the size of the regional pool is varied, and the relationship between local and regional richness changes depending on the time when sampled (Fig. 1). Local communities appear saturated early in the assembly process because only a subset of the regional pool is able to quickly colonize any local patch ("pseudosaturation": Lawton and Strong 1981). At intermediate time periods communities appear unsaturated because competitive exclusion has not gone to completion. At equilibrium, competitive exclusion causes saturation. Local richness

thus has a predictable relationship with regional richness through time, moving from dominance by regional (dispersal) processes early in community assembly, to dominance by local processes (competitive interactions) late in assembly. In an observational study of the fouling community colonizing pen shells in Florida, Munguia (2004) demonstrated different relationships between local and regional richness developed through time, depending on the dispersal ability of species: motile species arrived first and showed a saturating relationship, while sessile species arrived more slowly and remained unsaturated. This suggests that, when the community has had little time to assemble relative to dispersal rates, unsaturated relationships between local and regional richness are expected. As time along the assembly trajectory increases, the relationship becomes saturated (Munguia 2004).

Local composition as well as richness may be affected by the regional species pool, but the mechanisms are just beginning to be explored. Fukami (2004b) showed that in interactive communities, the effects of assembly history can cause local communities to increase in dissimilarity as regional pool size increases. If assembly history is unimportant, strong local interactions would instead cause communities to converge on a similar composition as long as all component species were present in the species pool (i.e., especially in the richest

regions). In the absence of local interactions, community similarity may depend more on the similarity of the regional pools.

One potential problem with all attempts to examine regional richness effects on local communities is that regional richness is not independent of regional composition. The composition of the regional species pool may also impact the assembly of communities (Drake 1991), leading to disparate local communities through time, due to better competitors or colonists being present in one regional pool and not another. Composition may thus have important implications for the relationship between local and regional richness, especially if, as recently suggested, community assembly is more strongly a function of species traits (Fukami et al. 2005) or idiosyncratic dispersal (Cadotte 2006), than number of species.

Here we experimentally test the impact of changes in regional species richness and composition using the microarthropod community of a moss-based ecosystem. In this system, microarthropods, predominantly mites (Acari) and springtails (Collembola), are found at high abundance and species richness (Gonzalez and Chanton 2002, Hoyle 2004, Starzomski and Srivastava 2007; see Plate 1). By combining moss from multiple sites kilometers apart, we are able to compress the natural  $\beta$  diversity into a few hundred square centimeters, creating identically sized regions differing in species richness and composition.

We predict that the assembly of local microarthropod communities will be affected by both the richness and composition of the regional species pool. Specifically, we expect local richness and composition to reflect strong interactions between time and regional richness/composition. Early in the successional process, transitory relationships between local and regional richness may occur (Fig. 1), due to early arrival of fast dispersing species (pseudo-saturation) or insufficient time for competitive exclusion (pseudo-proportional). If local processes predominate, any proportional relationship should be transitory, and local communities should converge on a common richness due to competitive interactions (i.e., saturate; Fig. 1). If regional processes continue to dominate, the proportional relationship should persist indefinitely.

#### METHODS

The experiment was conducted outdoors on the south campus of the University of British Columbia, Vancouver, British Columbia, Canada (49°16'12" N, 123°15'36" W), using the microarthropod community of Roadside rock moss, *Racomitrium canescens* (Hedw.) Brid. This moss species is commonly found growing on cliff faces and exposed bedrock in coastal British Columbia, and during collection, we ensured that samples were as similar as possible in moisture level, aspect, and exposure, and composed entirely of *R. canescens*.

We collected Roadside rock moss along a latitudinal gradient (Fig. 2) between West Vancouver and Whistler in southwestern British Columbia (between 49°18' N, 123°7'48" W and 50°4'12" N, 123°4'48" W; Fig. 2). Distances between individual sites ranged from 4.5 km to 71.5 km. It is well known that communities of species in similar habitats, sampled at increasing distance from one another, tend to have progressively fewer species in common (Whittaker 1970, Rosenzweig 1995). This turnover in species richness between sites, known as  $\beta$  diversity (Whittaker 1970), allows us to sample several different sites to collect different communities in similar habitat. Later these communities can be combined to create treatments of different regional richness.

We manipulated regional richness independently of region area by creating large patches of moss (35.5 cm diameter "regions") through combining moss collected from the different sites (labeled A through H). Regional richness treatments were created from moss originating from one, two, four, or eight sites (Fig. 2). These treatments followed the random assembly method of biodiversity-ecosystem function studies (Schmid et al. 2002), since we were unable to examine all combinations of sites. We randomly drew sites from eight possible locations for each treatment. Thus, the one-site treatment was represented by three site origins (C, F, and H), the two-site treatment was represented by three site combinations (AB, AH, and BD), the four-site treatment was represented by site combinations CDEG, CDEH, and DFGH, and the eight-site treatment had three replicates of the full eight-site combination (ABCDEFGH). To construct the treatments, eight "pie-slices" of moss were placed in a 35.5 cm diameter plastic planting tray. The center of the moss circle consisted of a 10 cm diameter plug of moss collected from a ninth location (Fig. 3). This plug of moss was defaunated in a Tullgren funnel (for 72 hours) prior to being placed in the center of the tray (Kethley 1991).

Each of these 12 site combinations (nine different site combinations plus three ABCDEFGH) was reproduced seven times to allow destructive harvesting through time. Thus, 84 plastic planting trays, each with a 5 cm lip, were placed on flat particle board, spaced a minimum of 20 cm apart. A gap of even 1 cm between moss habitat patches constitutes an effective barrier to dispersal (Gonzalez et al. 1998); the combination of the 5-cm lip and the 20 cm of bare particle board prevented most terrestrial dispersal between replicates. To look for other modes of dispersal, we later test whether arrival of microarthropods via wind currents was a substantial source of colonists.

To determine the regional species richness and composition that resulted from the creation of each regional treatment, we extracted and sorted microarthropods from additional pie slices of moss from each collection site. A total of 44 samples were taken across all regions, including four replicates of region A, four of B, eight of C, four of D, four of E, eight of F, four of G,

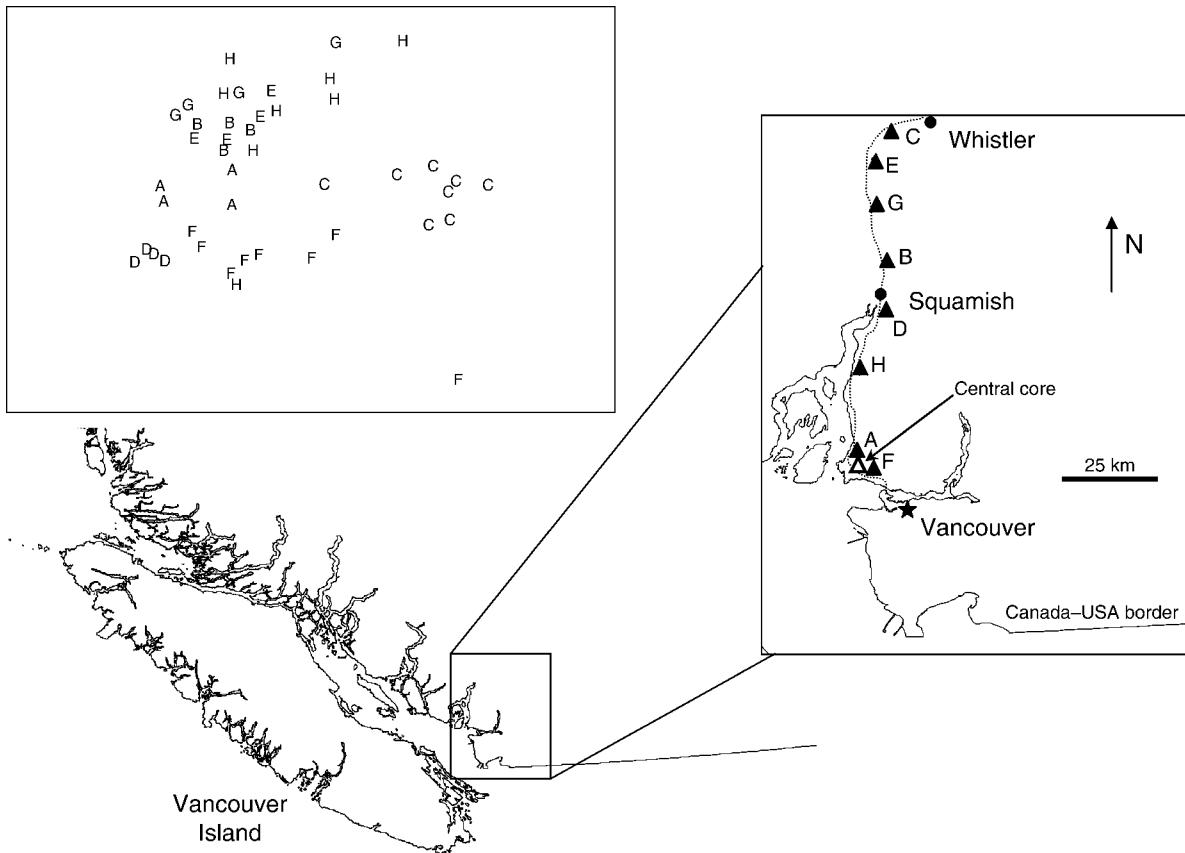


FIG. 2. Locations in southwestern British Columbia, Canada, of collection sites for moss used in the experiment (sites A–H). Also shown is a nonmetric multidimensional scaling (NMDS) plot illustrating the differences in community structure among moss samples from different sites (each sample = one-eighth of a region in the experimental setup shown in Fig. 3). Stress = 0.20.

and eight of region H. This initial estimate of regional richness required identification of 20 079 microarthropods, a Herculean task that could not be repeated for subsequent time periods.

The experiment was run for 16 months to permit population turnover of microarthropods, as well as to ensure coverage of both wet and dry seasons. Generation times of microarthropods vary from 2 to 4 weeks (collembola, many mesostigmatid mites) to months and occasionally years (oribatid mites). Wet-season months included September through April, with average monthly precipitation of  $123.2 \pm 9.9$  mm (mean  $\pm$  SD). Dry season months included May through August, with average monthly precipitation of  $45.1 \pm 38.6$  mm. Previous studies have shown that mite species can move between 1 and 10 cm/d (Berthet 1964, Starzomski and Srivastava 2007; K. Venter, *unpublished data*), and thus the time scale of our experiment should provide more than enough time for full dispersal of all species. To examine community assembly, the center plug of the moss circles was destructively sampled from each treatment at 0.5 months, 2 months, 3 months, 4 months, 8 months, 11 months, and 16 months after the beginning of the experiment. We chose these sampling dates to

capture the assembly of the community, reasoning that colonization of the defaunated plugs would be just starting at 0.5 months and equaling extinction by 16 months. To sample a plug of moss, the center 10-cm plug of a treatment was cut out of the plastic planting tray, and placed in a Tullgren funnel for 41 hours (17 hours at low intensity, and 24 at mid intensity) under a 40 W light bulb. The microarthropods were collected and fixed in a solution of 70% ethanol, 20% glycerol, and 10% water, and manually sorted with a 60 $\times$  dissecting scope. Microarthropods with distinct morphological characteristics were described as individual morphospecies, using various keys (Krantz 1978; unpublished keys provided by the Ohio State University Acarology Summer Program), and identification by experts (D. Walter, H. Proctor, H. Klompen, V. Behan-Pelletier, and J. Addison). These communities of mites and other microarthropods form a complex set of detritivores/herbivores (particularly of detritus and fungal hyphae), and predators that feed on these lower trophic levels. Rapid population growth rates may be observed in some herbivore/detritivore species, which may be rapidly followed by predator population increases (Chen and Wise 1999). These increases appear to track the seasons

(e.g., fungal growth is rapid at the onset of the wet season, followed by increases in some species of Collembola [B. M. Starzomski, *personal observation*]).

Linear regression was used to assess the relationship between number of sites represented in the region and initial regional species richness; a tight linear relationship would allow us to use number of sites as a proxy for regional richness.

We predicted that local richness would be jointly determined by regional richness, regional composition, and time, with the exact relationship between local and regional richness changing over the course of the experiment. We first examined how local species richness was affected by the combined influence of regional treatments (either number of sites represented, or identity of sites represented) and time using a two-way analysis of variance (ANOVA). We then used one-way ANOVAs to test for overall effects of time on local richness, and for regional richness (number of sites) effects on local richness within each date. In all cases, species richness data was log-transformed to conform to ANOVA assumptions. Various measures of species diversity were also examined, with no qualitative difference in the results. We also used linear regression to examine, for each date, the relationship between local richness and either number of sites represented or initial regional richness. As both linear (unsaturated) and nonlinear (saturated) relationships were predicted, we tested the following functions: linear, quadratic, exponential, and power. All ANOVAs and regression analyses were conducted using R version 2.0.1 (*available online*).<sup>2</sup>

We predicted that local species composition would also be jointly determined by regional richness, regional composition, and time. Species composition data were analyzed using the analysis of similarity (ANOSIM) procedure of PRIMER 5 for Windows (Plymouth Marine Lab, Plymouth, UK). The ANOSIM procedure uses a randomization routine to test for differences in community composition between groups of samples. We examined microarthropod composition in central plugs for differences between dates, regional richness levels, and regional composition treatments. We also tested for differences in the microarthropod species pool of moss collected in different sites using both ANOSIM and NMDS (nonmetric multidimensional scaling). In all cases, abundance data were square-root transformed before constructing Bray-Curtis similarity matrices.

## RESULTS

Two-hundred thirty-four species were originally present in the regional pool, of which 205 were subsequently found in at least one of the experimental treatments. Roadside rock moss microarthropod communities were significantly different among sites span-

ning Vancouver and Whistler, British Columbia (ANOSIM,  $R = 0.797$ ,  $P = 0.001$ ; Fig. 2). The number of species found in pie-slice-shaped samples (each sample is one-eighth of a region) from each of the eight collection sites ranged from 26 to 83 species per 314 cm<sup>2</sup> of moss, with a mean of 50. Consequently, when moss from differing sites was assembled into "regions," regional species richness varied between 34 and 234 species (Fig. 3). In general, the regional species richness increased in a linear fashion with increased number of sites represented by moss pie slices (Fig. 3). Therefore, in the remainder of the results, we use number of sites per region as a proxy for regional richness.

Local species richness changed over time ( $F_{6,76} = 20.74$ ,  $P < 0.0001$ ; Fig. 4). Species richness increased quickly from June to August 2003, after which it rapidly decreased to a low in September 2003, and then increased through to the end of the experiment in August 2004. Local richness did not significantly differ between regional richness treatments on any date (Table 1). There were also no significant linear or non-linear relationships in the directions predicted between local richness and regional richness on any date, whether regional richness was approximated by the number of sites represented (results not shown) or initial regional richness (Fig. 5). Finally, neither regional richness (number of sites represented in region) nor regional composition (identity of sites represented in region) determined changes in local richness over time (two-way ANOVA;  $F_{3,56} = 0.85$ ,  $P = 0.47$  for number of sites  $\times$  time;  $F_{9,70} = 0.82$ ,  $P = 0.60$  for identity of site  $\times$  time).

Temporal differences in species richness followed seasonal patterns. We therefore divided the dates into the wet season (September–April) and the dry season (May–August). Local species richness was affected by the composition of the original regional community in the wet season (ANOVA,  $F_{9,14} = 2.89$ ,  $P = 0.04$ ), though not in the dry season ( $F_{9,49} = 0.55$ ,  $P = 0.83$ ). By contrast, local richness was not affected by the regional richness treatments in either the wet ( $F_{3,20} = 1.10$ ,  $P = 0.31$ ), or dry ( $F_{3,55} = 0.75$ ,  $P = 0.39$ ) season. Local areas contained more species in the dry season of 2004 compared to that of 2003 (single-tailed  $t$  test with unequal variance,  $P < 0.0001$ ).

We examined how local community composition was affected by regional richness, regional composition, and time. Overall, local community composition was significantly different between dates (ANOSIM,  $R = 0.303$ ,  $P = 0.001$ ), and affected by regional composition ( $R = 0.166$ ,  $P = 0.002$ ) and regional richness ( $R = 0.084$ ,  $P = 0.001$ ). In the wet season, differences in regional composition did not cause differences in local composition ( $R = 0.031$ ,  $P = 0.406$ ). In the dry season, however, regional composition did cause a significant difference in local community composition ( $R = 0.14$ ,  $P = 0.013$ ).

To assess the impact of species arriving with wind currents (as part of the so-called "aerial plankton" [Hardy and Milne 1938]), we calculated, for each local

<sup>2</sup> (r-project.org)

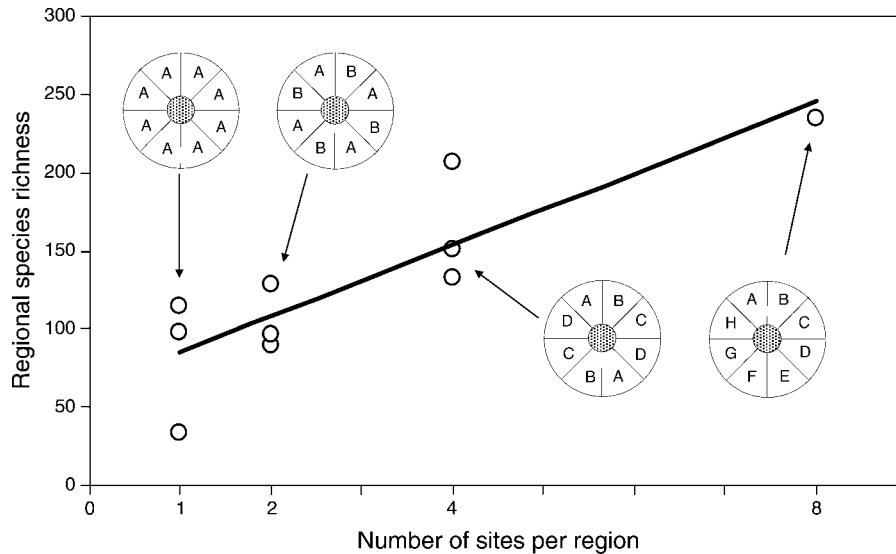


FIG. 3. Experimental design and the relationship between number of sites represented in region treatments and number of species present (regression,  $y = 25.6x + 49.8$ ;  $R^2 = 0.78$ ). Within the enlarged circles, white areas represent the different regions collected. Gray-shaded areas represent the defaunated central core. Letters refer to the different collection sites (shown in Fig. 2), from one site represented (all A's), to eight sites represented (sites A–H, the locations of which are randomly determined). There are three replicates of each treatment. The combinations shown are for illustrative purposes only.

sample, the proportion of species not originally recorded in the surrounding region (“new species”). We would always expect some new species, as even within the same region treatment there will be some variation in the exact composition of the regional pool between replicates. If only such sampling effects are important, the probability of finding a new species should be constant over time. By contrast, if aerial plankton is an important contributor of new species, we would expect the proportion of new species to increase with time. The proportion of new species, however, was constant through time (regression  $R^2 = 0.34$ ,  $P = 0.30$ ), suggesting

that aerial plankton had minimal effect on species richness over the duration of the experiment.

DISCUSSION

We predicted that local richness would be dependent on regional richness at some point in the experiment, either because communities were unsaturated by species, or because competitive exclusion had yet to occur (Mouquet et al. 2003). Our results do not support this: there was no effect of regional richness on local richness at any of our sampling dates. One potential explanation is that community assembly happens so quickly that local areas may have been fully saturated with species in just two weeks (Cadotte and Fukami 2005). Species richness continued to increase, however, more than a year after the beginning of the experiment (significant difference between dry seasons of 2003 and 2004; Fig. 4), suggesting that community assembly is actually quite slow. This explanation would also mean that even our most depauperate region (with 34 species) contained enough species to saturate the central plug. However,

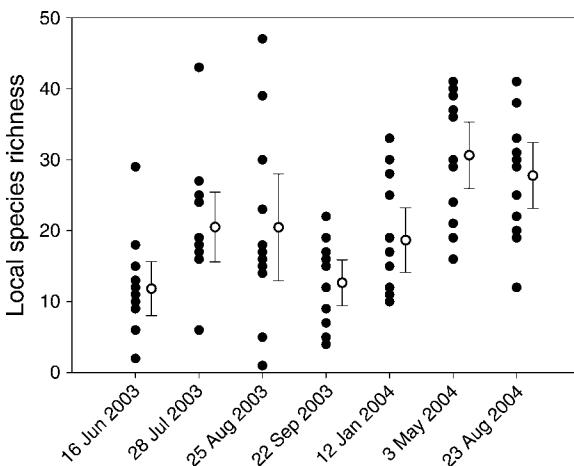


FIG. 4. Local species richness vs. time. Solid black circles show all data; open circles are means  $\pm$  SE.

TABLE 1. Summary of ANOVA results for the effects of regional richness on local species richness at each date.

Date	F	P	df
16 June 2003	1.10	0.32	3, 8
28 July 2003	0.11	0.75	3, 8
25 August 2003	0.03	0.86	3, 8
22 September 2003	0.44	0.52	3, 8
12 January 2004	0.91	0.37	3, 8
3 May 2004	2.33	0.16	3, 8
23 August 2004	0.0004	0.98	3, 8

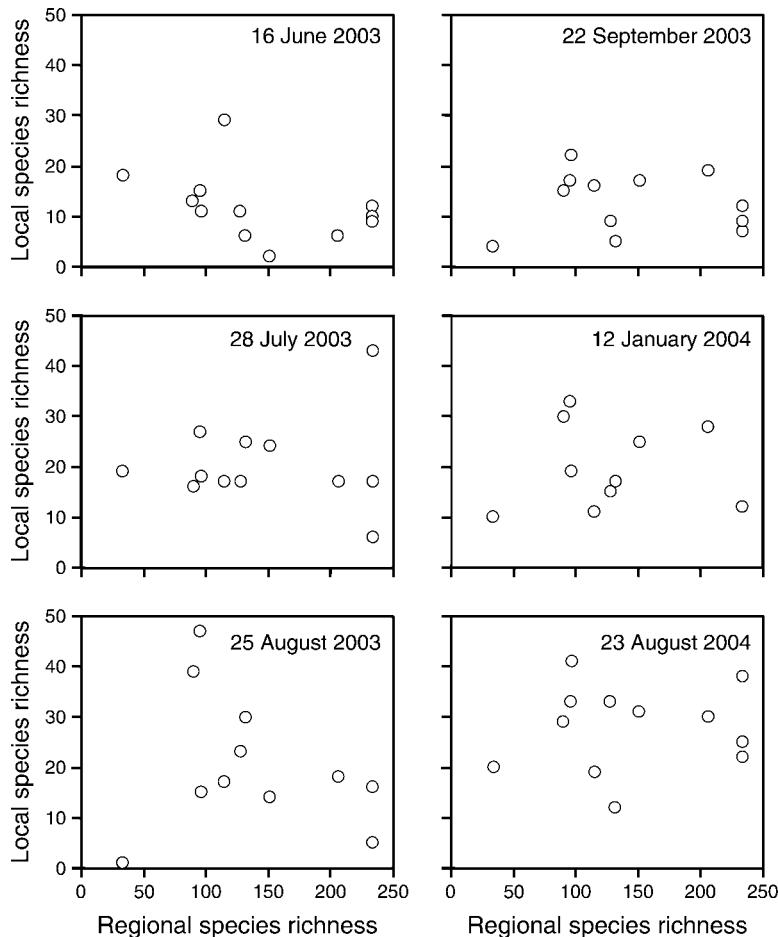


FIG. 5. Plots of local and regional species richness at sampling points in time.

the central plugs in other regions sometimes contained more than 40 species (Fig. 3). A second explanation is that the regional richness gradient collapsed. Local extinctions will eventually feed back to affect regional richness, and we cannot discount the possibility that our regional richness gradient changed over the course of 16 months. However, the lack of a regional richness effect on any date would require the gradient to collapse within the first two weeks of the experiment, an unlikely scenario. A more plausible explanation is a continual effect of “pseudosaturation” (the appearance of a ceiling to local richness in the absence of strong competitive exclusion). Several authors (Lawton and Strong 1981, Cornell 1985, Mouquet et al. 2003) have predicted that when only a subset of the species pool can quickly colonize an area, the initial pattern will be pseudosaturation. For example, Munguia (2004) showed that in a pen shell community in Florida, motile species initially showed a saturating relationship, while slower, more sessile species had an unsaturated relationship. Our species pool may face multiple filters, both in terms of dispersal (fast-dispersing species like collembola may

colonize quickly) and seasonality (species adapted to dry vs. wet seasons).

While local richness was independent of regional richness within sampling periods, local richness was significantly different between dates. There was a general pattern of a fast rise in species richness early in the experiment (June 2003), followed by a rapid decrease in September 2003, to a further rise in species richness through to the end of the experiment (August 2004). This pattern is contrary to theoretical predictions of convergence of local patch richness after transitory assembly dynamics. In the moss microecosystem, there are two partially distinct communities of microarthropods found in the wet and dry seasons (Gonzalez 2000; B. M. Starzomski, *personal observation*). During the wet season, greater amounts of fungal hyphae can be observed in the soil supporting the moss, and fungal feeding microarthropods may come to dominate at this time. During the dry season, fewer fungi are observed, and detritivorous microarthropods may play a larger role. Similar to differences in environmental conditions in space (Cottenie and de Meester 2004), differences in time (seasonal changes) may have a larger impact on

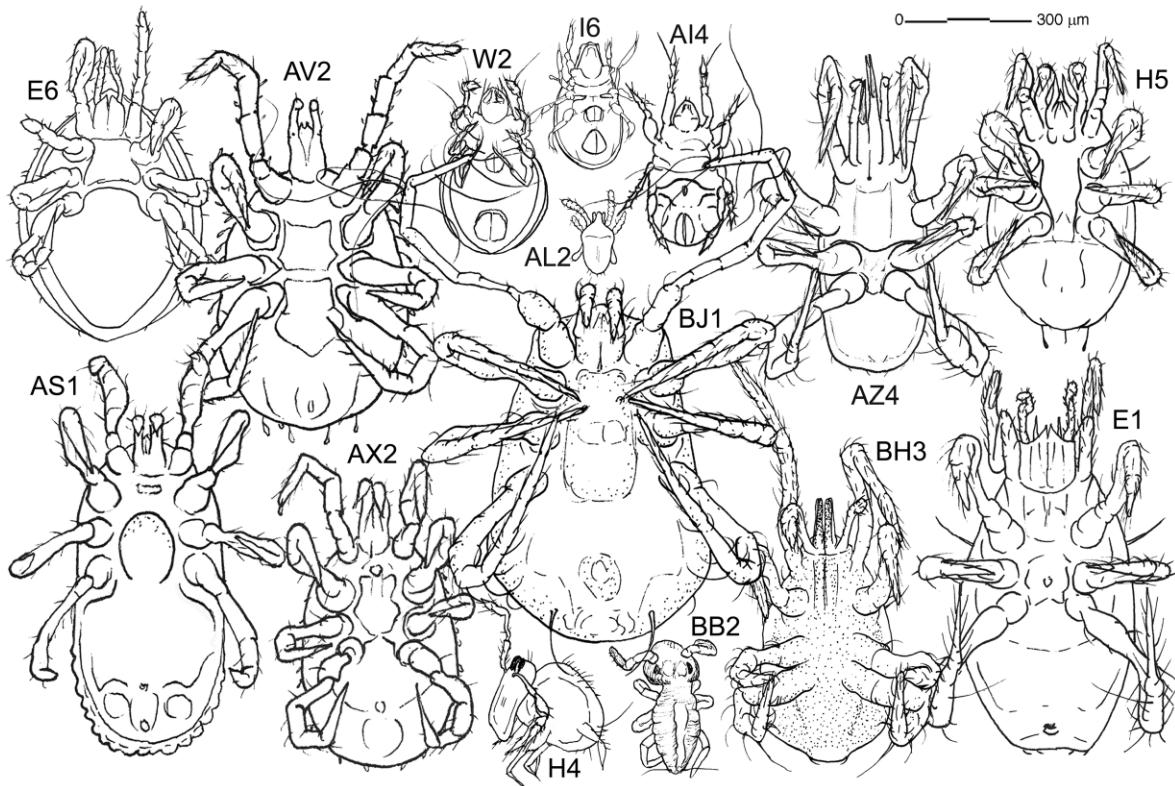


PLATE 1. Example of microarthropod diversity found in Roadside rock moss (*Racomitrium canescens*) in southwestern British Columbia, Canada, and used in this experiment. Letter-number combinations represent morphospecies codes. Original artwork by Derek Tan.

local species richness than differing regional species pools.

Although in our study regional richness does not impact local richness, regional composition does. This is a seasonally dependent process, shown strongly in the wet season (September–April). It is not clear why this pattern disappeared in the dry season. Interestingly, the pattern is opposite for local community composition: both regional richness and regional composition determined local composition, with those changes coming in the dry season (May–August). In an observational study, Munguia (2004) also found that different regions contained different local communities even when local richness was independent of regional richness. In natural systems, changes in relative abundance and identity of species in the regional pool may be more important than the number of species per se in determining the structure of local communities. As a result, saturation figures of local species richness regressed on regional species richness will under represent the role of history. Thus, even though local richness is similar between regional richnesses, this does not mean that biogeography is unimportant.

These impacts of regional composition on local richness may be related to resource pulses that occur

in the wet season in this moss system. During the dry season, the predominant resource is detritus; in the wet season fungi, nematodes, and collembola become very abundant. It is possible that this increase in local resources overwhelms the effects of local competition, allowing regional effects to be more apparent. For example, in another study in this moss–microarthropod system (Starzomski and Srivastava 2007), predator diversity and abundance increased following large wet season population increases in one collembola taxa. These predators may temporarily coexist when resource levels are very high. Predators may subsequently decrease due to interspecific competition when resource levels drop and the system returns to a detritus-dominated system in the dry season. During the dry season, the large surrounding region may provide a refuge in space for avoiding interspecific competition in the face of lower resource levels.

Assembly appears to be ongoing, 2–20 microarthropod generations after the beginning of the experiment. No local equilibrium was reached. Our analysis shows that this is not due to the influx of the so-called aerial plankton. Many microarthropods are known to disperse in air currents as part of this aerial plankton (Hardy and Milne 1938, Russell and Wilson 1996), but we could find

no evidence of an increase in new species through this mechanism. Instead, this pattern may be explained by the arrival of the poor dispersers from the region into the local patch. Some mite species are known to move between 1 and 10 cm/d (Berthet 1964; K. Venter, *personal communication*), and it may simply take many of these species weeks or months to move from the regional area to the local patch. Other experiments with this system also suggest that the immediate source of mite species is contiguous moss habitat rather than aerial plankton (Gonzalez 2000, Starzomski and Srivastava 2007).

We expect that differences in species dispersal ability and the existence of two distinct seasonal communities (one adapted to wet season conditions, the other to dry) would prevent the moss-microarthropod system from ever settling to a local equilibrium, as seasonal changes would favor different species and communities. This illustrates an important point in the interpretation of local-regional regressions: environmental changes may obscure the overall impact of the regional community on the local, due to the transition between community states. This is largely born out by our figures showing local vs. regional species richness: we never see a classic straight or decelerating curvilinear line. Rather, the relationship between local and regional richness is varied, reflecting the combined effects of seasonality and community assembly in filtering species from the region into any local patch.

In summary, various processes, not simply the richness or composition of the regional pool, contribute to structuring local species richness in local patches embedded within regions of differing species richness and composition (MacArthur 1972, Drake 1991, Ricklefs and Schluter 1993, Shurin et al. 2000, Fukami 2004a, b, Holyoak et al. 2005, Shurin and Srivastava 2005, Cadotte 2007). Our results show the effects of regional composition in structuring local species richness and composition, but further demonstrate that these effects are seasonally dependent, with no overall saturating relationship (i.e., competitive exclusion) observed. In our moss-microarthropod system, there are at least two distinct seasonal communities (wet, dry) and rates of community assembly are modified by these seasonal dynamics. We demonstrate that the effects of time and space, in the forms of community assembly and seasonality, are responsible for dispersing and resident individuals, and can dramatically impact the interpretations of processes responsible for the formation of local species richness and composition, as well as the interpretation of local-regional species richness figures.

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