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ORGANIZATION OF *PLETHODON* SALAMANDER COMMUNITIES: GUILD-BASED COMMUNITY ASSEMBLY

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Abstract. A long-standing goal in evolutionary ecology is to determine whether the organization of communities is reflective of underlying deterministic processes. In this study, I examined patterns of species co-occurrence among eastern *Plethodon* salamanders and determined whether they were consistent with predictions from a guild model of competition-based community assembly. Using a database of 45 species and 4540 geographic sites, I found that patterns of co-occurrence were significantly nonrandom at both a regional and continental scale, and species of different size guilds were distributed more evenly in sites than was expected by chance. Sites with the highest species richness had consistent patterns of community composition, and with few exceptions, the same five species were present at all sites. Taken together, these results imply that larger *Plethodon* communities are assembled from simpler communities in a manner consistent with what is predicted through competitive mechanisms and suggest that stable species combinations are possible to achieve at various levels of species richness. These results also provide strong evidence consistent with the hypothesis that competitive-based community assembly is a general phenomenon in *Plethodon* and that interspecific competition is prevalent among the eastern species of this group.

Key words: *community assembly rules; functional groups; interspecific competition;* Plethodon.

Introduction

A fundamental question in evolutionary ecology is whether communities are random assemblages of species or whether they are the result of deterministic biotic and abiotic processes. Two rather different empirical approaches are used to address this question. First, manipulative field experiments are conducted to measure the effect of processes operating in natural communities, such as competition and predation. Such studies have proven enormously successful at documenting the relative strength and generality of species interactions across a diverse set of ecological communities (reviewed in Gurevitch et al. 1992, 2000, Sih et al. 1998). Second, species compositions are examined across sets of communities to determine whether species co-occur more or less frequently than expected by chance (e.g., Diamond 1975, Weiher et al. 1998, Brown et al. 2002). If nonrandom co-occurrence patterns are encountered, they are interpreted as the result of deterministic processes, such as interspecific competition, resource exploitation, or other effects.

When first proposed, comparing community patterns and the "community assembly rules" these patterns implied (Diamond 1975) sparked a contentious debate in which the significance, and even the existence, of assembly rules were questioned (for a review see Wiens 1989). Much of the debate focused on the appropriate methods for constructing null-model communities and how much biological information should be incorporated (e.g., Connor and Simberloff 1979, Stone et al. 1996, Simberloff et al. 1999, Gotelli 2000). This debate resolved many of the methodological issues and provided community ecologists with a rigorous quantitative framework in which null models may be used to identify patterns of community organization (see Gotelli and Graves 1996). Further, a recent meta-analysis of the available data found that nonrandom species co-occurrence patterns are in fact common (Gotelli and McCabe 2002), suggesting that patterns of community organization are at least concordant with assembly rule predictions. However, while nonrandom patterns are frequently treated as evidence of competitive-based community assembly, other processes such as habitat heterogeneity (Schoener and Adler 1991, Bell 2001), and even stochastic processes (Ulrich 2004, Bell 2005), can also generate spatial nonrandomness. Thus, attributing nonrandom co-occurrence patterns to a particular ecological process must be done with care. Despite this challenge, when independent evidence of an ecological process (such as competition) is combined with nonrandom co-occurrence patterns, these patterns can provide strong corroborating evidence suggesting that a particular process is prevalent across a set of communities (see, e.g., Gotelli and Ellison 2002).

The terrestrial salamanders of the genus *Plethodon* (see Plate 1) provide an excellent opportunity to examine the mechanisms responsible for community organization. *Plethodon* are widely distributed in the forests of North America, and extensive ecological research

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suggests that interspecific competition may be widespread (Anthony et al. 1997, Marshall et al. 2004). Similarly sized species often replace one another ecologically (e.g., Hairston 1951, Jaeger 1970), and competition for resources such as food (Adams and Rohlf 2000) and space (Hairston 1980*a*) have been documented. Territorial aggression is prevalent in *Plethodon* (reviewed in Jaeger and Forester 1993), and in some instances, appears to have restricted the geographic ranges of potential competitors (e.g., Jaeger 1970, Hairston 1980*a*). Additionally, competition between juveniles of large species and adults of small species may also occur (Fraser 1976*a*, Lancaster and Jaeger 1995, Price and Secki Shields 2002). Finally, *Plethodon* communities often contain numerous species (up to five), and throughout eastern North America it is common to find a large species sympatric with a small species (Grobman 1944, Highton 1995).

Examining the spatial distributions of species of *Plethodon* in light of experimental ecological data suggests that competition may be important in structuring *Plethodon* communities. Nevertheless, while competition is widely assumed to be prevalent (e.g., Highton 1972, Jaeger 1974), this hypothesis has not been rigorously tested. In this study, I therefore explored whether the observed patterns of species co-occurrence were consistent with those predicted under models of competitive-based community assembly. Using a database of eastern United States *Plethodon*, I determined whether *Plethodon* communities exhibited nonrandom species co-occurrence patterns and whether these patterns were consistent with what was expected under interspecific competition. I also examined whether patterns of community composition were consistent across sites with similar levels of species richness.

Materials and Methods

Community selection and functional-group designation

To test these hypotheses I compiled a database of eastern United States *Plethodon* communities based on the collections of the National Museum of Natural History, Washington, D.C., USA. This repository contains >160 000 *Plethodon* specimens, the vast majority of which were collected by Richard Highton and colleagues for taxonomic, systematic, and life history research (e.g., Highton 1972, 1999, Highton and Peabody 2000). These specimens were collected from the 1950s through the early 2000s from nearly 4800 distinct geographic localities (sites). More than 1650 sites were visited multiple times (mean = 3.53), and nearly 300 sites were visited five or more times. For each visit, ~1 h was devoted to collecting salamanders (see Highton 2005), usually by multiple field researchers. Thus, it is likely that assessments of species' occurrences at these sites are reasonably accurate.

From this database, I eliminated specimens of uncertain species designation, sites without specific geographic locality information, and sites where hybrids were known to occur. The final data set contained 45 *Plethodon* species and 4540 geographic sites (Appendix A; Plate 1). These sites varied in species richness from one to five species per site. I then assembled a species co-occurrence matrix, in which species presence or absence at each site was indicated. In this matrix, rows represented communities (sites) and columns represented species. Only multispecies sites were used to construct the co-occurrence matrix (1741 multispecies sites were in the data set). Species were assigned to one of two functional groups or size guilds (Appendix B). Eastern *Plethodon* are frequently described as belonging to two size guilds, small *Plethodon* and large *Plethodon* (e.g., Dunn 1926, Grobman 1944, Highton 1972, 1995), and there is ample evidence that these represent functional groups of species with similar biology. For instance, aggressive behavior between species of the same size guild is common (e.g., Jaeger 1974, Nishikawa 1985, Anthony et al. 1997). Additionally, interspecific competition has been documented between species within size guilds (e.g., Jaeger 1970, Hairston 1980*a*, *b*, Adams and Rohlf 2000). Finally, species within size guilds overlap in various ecological requirements and tend to utilize similar food resources (e.g., Fraser 1976*b*, Hairston et al. 1987, Adams 2000), similar shelter sites (e.g., Griffis and Jaeger 1998), and burrows.

Favored-states analysis, null models, and regional source pools

To test the first hypothesis, I used a guild-based community assembly model and the method of favored states to determine whether the observed pattern of species co-occurrence was different from expected under random assemblages (Fox 1987, 1989). The model predicts that species are added to a community sequentially from different guilds before additional members of the same guild are incorporated. Communities generated in this manner would be even or uniform in their distribution of species among guilds. Communities that are perfectly even or differ by no more than one taxon from evenness are defined to be in a "favored state" (Fox 1987). For the analysis, I calculated the number of communities exhibiting favored states for the entire co-occurrence matrix. I then compared the observed pattern of favored states to those generated from random assemblages using null-model approaches employed in EcoSim (Gotelli and Entsminger 2001*a*). Null-model methods generate pseudocommunities at random with respect to particular processes, and patterns in these communities are then compared to the pattern in the observed communities. If the observed pattern is uncommon when compared to the distribution of randomly generated patterns, it is likely that the observed pattern did not arise by random chance (see Gotelli and Graves 1996).

To assess the observed pattern of favored states in *Plethodon* communities I used two null-model approaches. First, the elements in the co-occurrence matrix were shuffled to generate null-model communities, for which

the number of favored states among sites was calculated (Gotelli and Graves 1996, Gotelli 2000). Each matrix was shuffled using the Independent Swap algorithm (Gotelli and Entsminger 2001*b*) with fixed row and column sums. The procedure was performed 1000 times to generate a distribution of possible values, which were then used to determine whether the observed number of favored states was extreme relative to chance (i.e., the proportion of times the observed exceeded the randomly generated values).

The above procedure preserved species richness among sites and preserved differences in the occurrence frequencies among species (see Connor and Simberloff 1979). This method also exhibited good statistical properties (see Gotelli 2000). However, these constraints may inadvertently incorporate competition into random assemblages, because they are generated by sampling post-competition communities (the so called "Narcissus effect": see Colwell and Winkler 1984). Thus, the approach may actually underestimate the effect of competition on community organization. To circumvent this difficulty, a second approach was used in which guild labels were randomly shuffled and assigned to species, and the number of favored states for the sites was calculated. This approach left the co-occurrence matrix unchanged and thus preserved species' geographic ranges and the original incidence pattern (see Stone et al. 1996). The procedure was performed 5000 times to generate a distribution of possible values, which were then used to determine whether the observed number of favored states was extreme relative to chance (e.g., Feeley 2003, McCay et al. 2004).

The analyses described above examined species co-occurrence patterns relative to null-model communities generated from the entire data set. However, utilizing the entire eastern United States as the source pool for null-model communities is unrealistic, because some species are widely separated both spatially and ecologically and thus do not have a reasonable probability of co-occurrence (see Schoener 1988, Gotelli and Graves 1996). To account for this, I generated 14 regional source pools from this database using USGS physiographic regions (divisions and provinces) for the eastern United States (Appendix A). Using ArcMap 9.1 (ESRI 2005), the geographic coordinates of each site were linked to a map of physiographic regions (Appendix A). I then assigned each site to a regional source pool based upon its presence in a specific physiographic region. Co-occurrence patterns in each regional source pool were then evaluated using both null-model procedures described above to determine whether the observed pattern of co-occurrence and favored states differed from that generated from random species assemblages.

Finally, the two most widely distributed eastern *Plethodon* species, the small species *P. cinereus* and the large species *P. glutinosus*, were found in nearly half of all multispecies sites in the database (886 and 765 sites, respectively) and co-occurred at 549 sites. It was therefore possible that these two species had an undue influence on the resulting co-occurrence patterns. To address this, I eliminated them from the global co-occurrence matrix and reran the favored states analysis using the guild labels approach described previously.

Spatial analysis and description of community patterns

One possible complication with analyses of co-occurrence matrices is that sites are assumed to be independent (Gotelli and Graves 1996). If sites are found in close geographic proximity, it is possible that the same community is sampled multiple times (i.e., spatial pseudo-replication). To assess whether this was an issue, I determined the degree of spatial autocorrelation in species composition across sites using spatial correlograms (Sokal and Oden 1978). For all multispecies sites in a favored state, I calculated the matrix of geographic distances between sites. I also calculated a matrix representing similarity in species composition, coding whether sites had the same or different species composition. I then used a spatial correlogram to determine the degree of spatial autocorrelation of species composition at various spatial scales. I set the lower distance classes for this analysis at 90 m and 300 m, which correspond to the maximum dispersal distance observed for most species and the maximum dispersal distance ever recorded for *Plethodon* (Smith and Green 2005). Thirteen additional distance classes were used that ranged from 1 to >250 km. Spatial analyses were performed in Passage 1.1 (Rosenberg 2004).

I also performed several additional analyses to better understand the observed patterns of community composition. I assembled a matrix of species identity × site richness, and for each species I noted whether it was present in sites of different species richness. From this matrix the maximum species richness (community size) for each species was calculated. The matrix was also examined to establish whether species present in sites with high levels of species richness were also present in sites containing all lower levels of species richness. Finally, to determine whether community composition was consistent across sites, I calculated the number of unique combinations of species found in all favored state communities. I also examined all sites containing five species and determined the unique species combinations in those sites.

Results

Using the guild-based assembly model, I found that 79% of all multispecies sites (1381 of 1741) were in a favored state (Table 1, Fig. 1). When regional source pools were examined, in all but one physiographic region, at least 86% of the multispecies sites were in a favored state. The remaining region, Blue Ridge South, contained 51% of its multispecies sites in a favored state.

When null-model communities were generated through random shuffling of the co-occurrence matrix (Gotelli 2000), I found that the observed number of

TABLE 1. Results of null-model analyses for the entire data set and regional source pools.

Region	No. sites		No. favored states			
	Total	Multispecies	Observed	Expected	Pr_I	Pr_{II}
Total data set	4540	1741	1381	871	0.001	0.04
Appalachian Plateau: Allegheny Mountains	165	118	113	59	0.029	0.001
Appalachian Plateau: Catskill/southern New York	41	23	23	12	0.001	0.001
Appalachian Plateau: Cumberland Plateau/Mountain	56	22	19	11	0.022	0.001
Appalachian Plateau: Kanawha	342	209	198	105	0.001	0.013
Atlantic Coastal Plain	556	47	47	24	0.001	0.001
Blue Ridge North	178	92	87	46	0.001	0.05
Blue Ridge South	1734	635	325	317	0.001	0.39NS
Interior/Central Lowlands	52	15	14	8	0.005	···†
New England	19	2	2	1	···†	···†
Ouachita	44	22	22	11	0.001	0.001
Ozarks	18	7	7	4	0.001	0.001
Piedmont	502	94	88	47	0.008	0.034
Valley and Ridge Prov.: middle	723	402	389	201	0.001	0.001
Valley and Ridge Prov.: Tennessee	110	53	47	27	0.002	0.044

Notes: For each analysis, the total number of sites (communities), the number of multispecies sites, the number of sites in a favored state, the expected number of favored states, the significance based upon the null-model community method (Pr_I; Gotelli 2000), and the significance based on the guild label exchange method (Pr_{II}; Stone et al. 1996) are listed.

† Analyses could not be performed due to small sample sizes.

favored states was greater than expected by chance for the entire data set and for all 13 physiographic regions that could be evaluated (Table 1). With the guild label exchange method (Stone et al. 1996), I found that the observed number of favored states was greater than expected by random chance for the entire data set, as well as for 11 of the 12 physiographic regions that could be evaluated (Table 1). Only the Blue Ridge South region did not display a significant pattern. Two physiographic regions could not be statistically evaluated (New England, Interior/Central Lowlands), because subdividing the total data set into regions reduced the

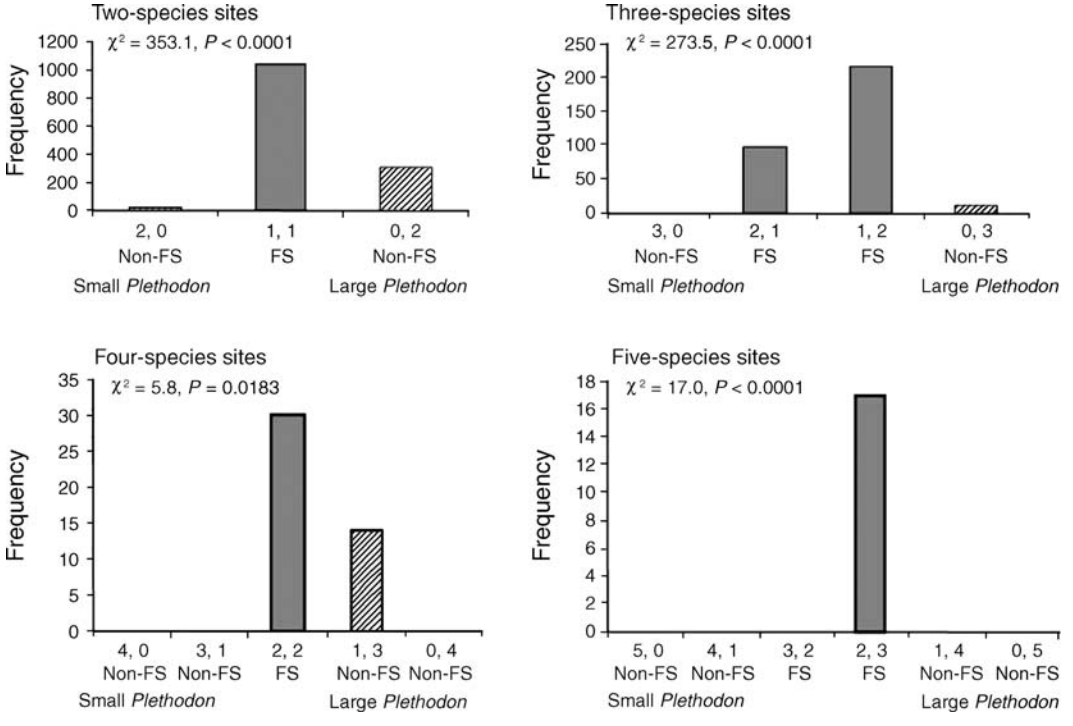


FIG. 1. Frequency distributions of the number of sites in favored states (FS; shaded bars) and nonfavored states (non-FS; hatched bars) for each class of species richness. Values on the *x*-axis refer to the number of small and large *Plethodon* in each community, respectively (e.g., "2, 0" indicates communities with two small and no large *Plethodon* species). Favored state communities are those in which the number of small and large *Plethodon* species are even or differ by no more than one species from evenness. Chi-square tests compare the number of favored vs. unfavored state communities relative to expectations.

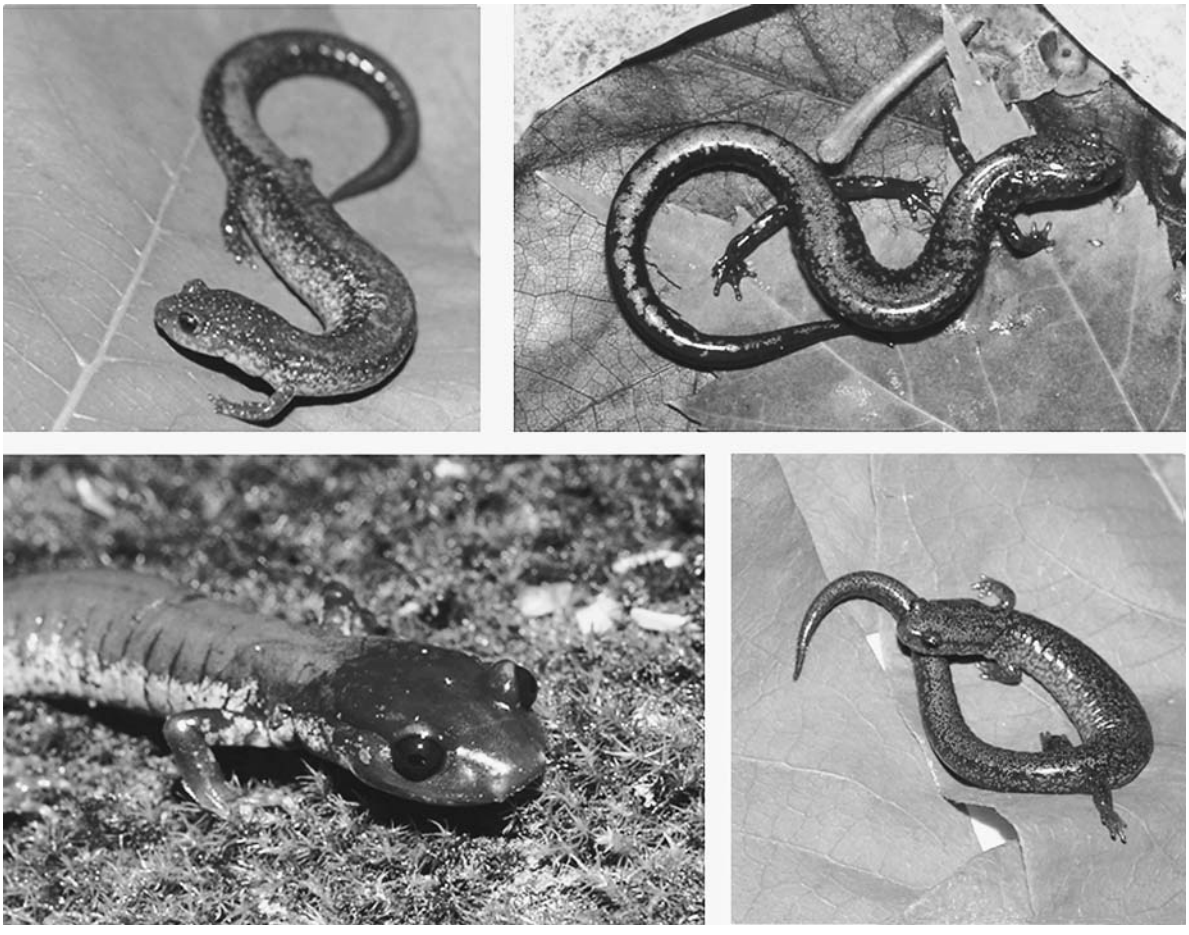


PLATE 1. Adult salamanders from representative *Plethodon* species from communities in the eastern United States (top, left to right, *P. cincereus* and *P. hubrichti*; bottom, *P. yonahlossee* and *P. electromorphus*). Photo credits: Top left and bottom right, D. Adams; top right and bottom left, Carl D. Anthony.

number of multispecies sites or the number of species in a guild to levels that prohibited analysis. However, in these regions, nearly all of the multispecies communities were in a favored state (2 of 2 and 14 of 15, respectively), implying that the pattern was at least qualitatively consistent with that found in other geographic regions. Additionally, when the two most common species were eliminated, patterns of co-occurrence were still significantly nonrandom ($P = 0.035$). Considered simultaneously, these results revealed that species co-occurrence patterns at both the regional and continental scales were highly nonrandom and displayed more evenness than expected from chance, a pattern consistent with what was predicted under the competitive-based community assembly model.

When patterns of spatial autocorrelation were examined, I found little evidence that spatial pseudoreplication was responsible for the observed pattern. For sites within the known range of maximum *Plethodon* dispersal (90 m and 300 m), there was essentially no autocorrelation in species composition ($r = 0.003$ and $r = 0.006$, respectively). Further, for sites in all distance classes up to 5 km, the autocorrelation of species composition was less than $r = 0.062$. This implied that pseudo-replication through oversampling sites in close geographic proximity was not responsible for the highly nonrandom patterns of community composition.

When the community composition was examined, I found that favored states communities exhibited 105 unique species combinations. Thus, while it was common to find *Plethodon* communities with an even number of small and large species, which species were present at particular sites was more variable. However, inspecting these patterns in more detail revealed considerable consistency in sites with high species richness. For example, in sites containing five species, 14 of the 17 sites contained the same five species (*P. cinereus*, *P. cylindraceus*, *P. montanus*, *P. richmondi*, and *P. yonahlossee*). Further, at the remaining three sites, four of these five species were also found, with only one species of small *Plethodon* replaced at two sites (*P. welleri* for *P. richmondi*) and only one species of large *Plethodon* replaced at the final site (*P. glutinosus* for *P. cylindraceus*). There was less consistency in species

composition in the four-species sites, but patterns were still evident. For example, 26 of the 44 sites consisted of subsets of species from the five-species sites, and roughly half of these were in a favored state. The 18 remaining four-species sites were more varied in their species composition, but interestingly, 17 of these sites (94%) were found to be in a favored state. Finally, I found a highly consistent pattern of site occupation for each species. Species present in sites with high levels of species richness were also present in sites containing all lower levels of species richness (Appendix B).

Discussion

Understanding whether deterministic mechanisms are responsible for community organization or whether communities assemble randomly is a long-standing goal of ecological research. In this study, I examined whether patterns of species co-occurrence among eastern *Plethodon* species were consistent with what was predicted under a guild model of competitive-based community assembly. I found that at both the regional and continental scales, patterns of co-occurrence were significantly nonrandom and species of different size guilds were distributed more evenly across sites than was expected by chance. I also found that sites with the highest species richness had consistent patterns of community composition, and with few exceptions, the same five species were present at all sites. These results revealed that *Plethodon* co-occurrence patterns were highly nonrandom and were consistent with what was predicted under a model of guild-based competitive community assembly. Additionally, because results were consistent between two different null-model approaches, inadvertent inclusion of competition in the randomly generated null communities (the Narcissus effect) was not responsible for the observed patterns (see Stone et al. 1996). When these broad comparative patterns are combined with experimental evidence from select *Plethodon* communities (e.g., Jaeger 1970, Hairston 1980*a*, *b*, Adams and Rohlf 2000), they provide strong evidence that competitive-based community assembly is likely a general phenomenon in *Plethodon* and that interspecific competition is prevalent among the eastern species of this group.

From the patterns of species co-occurrence examined here, I hypothesize that larger *Plethodon* communities are assembled from simpler communities in accord with predictions from the guild-based model. This hypothesis is based on several observations. First, species co-occurrence patterns were highly nonrandom across both regional and continental scales, a pattern consistent with the guild-based community assembly model. Second, while favored-state communities exhibited many unique species combinations, community composition in the most species-rich sites was highly consistent. Finally, species found in larger communities were also present in smaller communities. Taken together, these observations suggest that larger *Plethodon* communities are assembled from simpler communities and suggest that stable species combinations are possible to achieve at various levels of species richness. This hypothesis is speculative and is based solely on observed patterns of species co-occurrence. Nevertheless, it is a hypothesis that is testable through manipulative experimental approaches (see *Introduction*) in which species composition are manipulated to examine the degree of stability in *Plethodon* communities.

Considering the results of this study in light of known phenotypic variation between populations suggests that *Plethodon* may also be a useful model for understanding the mechanisms of microevolutionary change. In this study, I found that interspecific competition likely produced *Plethodon* communities containing even distributions of species from different size guilds. Previous studies have shown that ecologically relevant morphological traits in *Plethodon* (both body size and head shape) have evolved as a response to interspecific competition (e.g., Adams 2000, Adams and Rohlf 2000), generating patterns consistent with ecological character displacement. Thus, it appears that interspecific competition in *Plethodon* plays a role in both the evolution of quantitative morphological characters as well as the evolution of community composition. Additionally, while species of *Plethodon* can be categorized into specific size guilds, size variation between species does exist. Interestingly, one species present in all of the five species communities (*P. montanus*) is intermediate in body size (Highton and Peabody 2000). This suggests that species in larger communities may be arranged somewhat evenly along a continuous body size axis (community-wide character displacement; Strong et al. 1979, Dayan and Simberloff 2005). Combining these observations, I hypothesize that interspecific competition in *Plethodon* has generated patterns of community-wide character displacement of body size across multispecies communities. If such a pattern is identified, it provides an important link between the processes operating to structure communities and the selection processes that drive microevolutionary change.

Species co-occurrence patterns have long fascinated community ecologists, as they suggestively hint at the underlying mechanisms responsible for structuring ecological communities. While such hypotheses were initially made descriptively and qualitatively, the vigorous debate over community assembly rules provided much-needed quantitative rigor to the field. Null models are now used to provide a quantitative means for determining whether co-occurrence patterns are different from random, and when nonrandom patterns are identified, hypotheses concerning the underlying processes responsible for generating such patterns may be proposed. Using this approach, I tested the long-standing suggestion that interspecific competition was prevalent in communities of *Plethodon* salamanders. When combined with experimental ecological data (e.g., Hairston 1980*a*, Griffis and Jaeger 1998, Jaeger et al.

2002), the observed nonrandom patterns of co-occurrence would suggest that interspecific competition may be widespread. Together, these results provide strong evidence that competitive-based community assembly is likely a general phenomenon in *Plethodon* and that interspecific competition is prevalent among the eastern species of this group.

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APPENDIX A

Maps of the geographic localities of sites used in this study and of USGS physiographic regions used as regional source pools for the co-occurrence analyses (*Ecological Archives* E088-081-A1).

APPENDIX B

A list of species of eastern *Plethodon* used in this study including guild assignment, number of sites occupied, and maximum species richness (*Ecological Archives* E088-081-A2).