

Quantifying the importance of regional and local filters for community trait structure in tropical and temperate zones

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Abstract. The influence of regional and local processes on community structure is a major focus of ecology. Classically, ecologists have used local–regional richness regressions to evaluate the role of local and regional processes in determining community structure, an approach that has numerous flaws. Here, we implemented a novel trait-based approach that treats local and regional influences as a continuum, rather than a dichotomy. Using hylid frogs (Hylidae), we compared trait dispersion among members of local species assemblages to the trait dispersion in the regional assemblage from which they were drawn. Similarly, we compared trait dispersion in the regional assemblages to dispersion in the continental species pool. We estimated the contributions of local and regional filters, and we compared their strength in temperate and tropical zones. We found that regional and local filters explained 80% of the total variation among local assemblages in community body size dispersion. Overall, regional filters reduced trait dispersion, and local filters increased it, a pattern driven by particularly strong antagonistic effects in temperate zones that reduced the realized total variation by more than 40%. In contrast, local and regional filters acted in concert in tropical regions. Patterns within the tropics did not differ from the random expectation based on a null model, but within the temperate zone, local community filtering was stronger than expected by chance. Furthermore, in temperate regions, antagonistic regional and local filtering masked from 76% to 90% of the total variation in trait dispersion. Together, these results suggest that there are fundamental differences in the scale and identity of the processes determining community structure in temperate and tropical regions.

Key words: *body size; community assembly; competition; environmental filtering; Hylidae; local community; regional processes; trait dispersion; trait distributions; variance partitioning.*

INTRODUCTION

Are ecological communities structured by regional or local processes? Since Ricklefs' (1987) call for a more historical/regional approach to community ecology, answering this question has been a major goal of the discipline. To date, the bulk of ecologists' attention on the topic has focused on species richness and, more specifically, whether local communities are saturated with species (Ricklefs 1987, 2006, 2007, Cornell and Lawton 1992, Ricklefs and Schluter 1993, Srivastava 1999, Loreau 2000, He et al. 2005, Harrison and Cornell 2008). In such studies, the primary tool in the ecologist's toolbox has been the local–regional richness regression, where a lack of correlation (or an asymptotic relationship; Srivastava 1999) between local and regional richness is considered indicative of local saturation, while a positive linear relationship implies regional control. In addition to the technical drawbacks associated with this method (Srivastava 1999), there is growing

evidence that detection of linear or curvilinear relationships cannot falsify the hypotheses of local or regional control (Cornell and Lawton 1992, Srivastava 1999, Loreau 2000, He et al. 2005). A third drawback is that local–regional plots take a predominantly dichotomous—local or regional—view of community assembly. However, community structure is likely the outcome of processes acting at both scales (He et al. 2005, Ricklefs 2006, 2007, Harrison and Cornell 2008) and thus the more germane question is not whether community structure is determined by regional or local processes, but rather, what is the relative contribution of each (Ricklefs 2006).

Here, we evaluate the relative importance of regional and local factors for community structure using a novel approach that allows local and regional control to be treated as two ends of a continuum rather than as dichotomous alternatives. We consider local communities to be collections of potentially interacting species of similar trophic level within a relatively small area (Hubbell 2001), and regions as relatively large areas that harbor broadly similar environments but contain species that do not necessarily interact (delineated here by World Wildlife Fund ecoregions; Olson et al. 2001).

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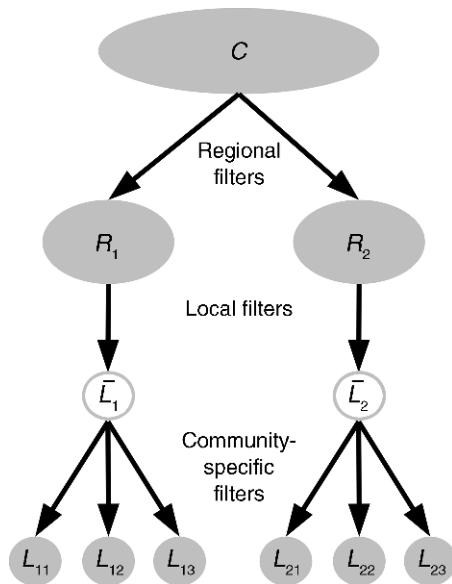


FIG. 1. The hierarchical structure of species assemblages, showing regional, local, and community-specific filters, where C is the continental species pool, R_i are regions, L_{ij} are local communities and \bar{L}_i are hypothetical average local communities.

Rather than focus on species richness, we take advantage of an alternative component of community structure: trait dispersion. While the importance of traits for community membership has long been recognized by ecologists (e.g., Hutchinson 1959, Strong et al. 1979, Ricklefs and Travis 1980, Weiher et al. 1998, McGill et al. 2006), appreciation of their importance for community assembly has recently been revitalized (e.g., Cornwell et al. 2006, McGill et al. 2006, Kraft et al. 2008, Cornwell and Ackerly 2009), in part because of the growth of a related approach: community phylogenetics (Webb 2000, Webb et al. 2002, Cavender-Bares et al. 2009). Such studies have predominantly focused on the signature left by different ecological and evolutionary processes on the distribution of trait values within species assemblages. For example, the requirement of species to tolerate particular abiotic conditions may result in phenotypes that are clustered in trait space, while competition and limiting similarity can result in dissimilar (over-dispersed) phenotypes (Weiher et al. 1998, Webb 2000, Kraft et al. 2008, Cornwell and Ackerly 2009).

Given a set of communities, our goal is to determine the proportion of community trait dispersion that is due to regional and local filters. Studies of trait and phylogenetic dispersion commonly refer to abiotic conditions that induce clustered trait values as environmental filters (e.g., Weiher et al. 1998, Webb et al. 2002, Cavender-Bares et al. 2009). However, here we consider any factor or process that alters the dispersion of a trait (or traits) within a species assemblage as a filter. We do not differentiate between patterns arising from selection or ecological sorting. For example, at local scales,

competition can act as a biotic filter by preventing species that are too similar from coexisting (competitive exclusion), or predators may act as a filter by disproportionately removing prey in a non-random portion of trait space. Alternatively, selection can lead to convergent evolution and similar trait values within communities (e.g., Cavender-Bares et al. 2006). At regional scales, time could act as a filter if traits evolve under Brownian motion and a clade has only recently colonized a region, giving little time for trait divergence among its species (e.g., Moen and Wiens 2009). Regional factors such as climate could also apply selection pressure on traits, such as increased body size, which may limit desiccation in more xeric environments (Tracy and Christian 2010). Unlike most studies of trait or phylogenetic dispersion (e.g., Weiher et al. 1998, Webb 2000, Cavender-Bares et al. 2004, Kraft et al. 2008), our goal is not to infer the processes underlying filters, but rather to quantify their relative strength and direction, i.e., the degree to which they increase or decrease trait dispersion at different scales. However, the relative strength and direction of filters at different scales could provide direction for future, more mechanistic studies aimed at identifying the dominant processes influencing community structure and how these may change, for example, along environmental gradients.

Briefly, our approach is based on nested ANOVA (Sokal and Rohlf 1995), but is tailored specifically to the effect of regional and local filters on trait dispersion. Local communities include a (possibly random) subset of the traits found in the overall species pool, potentially leading to differences in trait dispersion between the overall species pool and local communities: we refer to these differences as variation in trait dispersion. (We do not, strictly speaking, deal with variances [or covariances], as we do not quantify variation as the sum of squared departures from the mean over the number of samples minus one. Thus, we use “variation” throughout.) Our goal is to partition this variation in trait dispersion to determine the relative importance of regional and local filters. We consider a simple, hierarchical, model in which local communities are embedded within regional species assemblages which in turn are nested within continental species pools (Fig. 1). Thus, trait dispersion within a local community arises from three levels of filtering (Fig. 1): regional filters, which intercede between the continental species pool and regional assemblage; local filters, which limit the trait values from the regional assemblage that can occur in an average local community; and community-specific filters which result in differences between a particular local community and the average community within a region. For present purposes, we treat community specific filters as unexplained, or residual, variation. Filters can either decrease or increase trait dispersion and thus regional and local filters may act in concert or in opposition (Helmus et al. 2007). For example, a regional assemblage could have clustered trait values if

there is an optimum trait value (and thus, stabilizing selection) in cold conditions. However, competition could prevent the most similar species in the regional assemblage from co-occurring, leading to local communities with greater trait dispersion than the regional assemblage. Our method allows us to quantify the extent to which regional and local filters act in concert or in opposition and the ramifications of opposite effects, which can mask the amount of total observed variation (e.g., Helmus et al. 2007).

The relative importance of regional and local processes are hypothesized to differ between tropical and temperate environments. Building on the writings of Wallace and Darwin (Mittelbach et al. 2007), Dobzhansky (1950), Fischer (1960), and MacArthur (1969, 1972) all suggested that in high latitude environments, the requirement to survive and reproduce in “harsh” conditions dominates community structure. Alternatively, in tropical, “benign,” environments, local processes such as competition are predicted to determine community structure. The hypothesis predicts that, in temperate areas, regional filters will account for more variation in trait dispersion than local filters, while in the tropics, the opposite will occur.

We evaluated the relative importance of regional and local filters in determining the body size dispersion of treefrog (Hylidae) communities in the continental Americas. We partitioned variation in body-size dispersion (BSD) among regional and local filters for the Americas as a whole, and separately for tropical and temperate areas. Overall, we found that regional filters explained more variation in BSD than did local filters. Also, regional filters decreased BSD, while local filters increased it. However, this pattern was driven solely by strong, significant antagonistic effects in temperate, but not tropical, regions. Within the temperate zone 76–90% of the variation in community trait dispersion was masked by clustering at the regional scale and overdispersion at the local. Alternately, tropical community assembly appeared to be stochastic with respect to body size.

METHODS

Partitioning the variation in community trait structure

Measuring trait dispersion in species assemblages.—Numerous methods to quantify the trait dispersion of a species assemblage have been presented, including range, mean Euclidean distance in trait space among species pairs, variance (or standard deviation), standard deviation of nearest neighbor distances, and kurtosis (Kraft et al. 2008, Prinzing et al. 2008, Cornwell and Ackerly 2009, Ingram and Shurin 2009, Moen and Wiens 2009). For our analysis, two critical characteristics of any index are (1) its upper limit is not set by the value at the next highest hierarchical level and (2) it is sensitive to filters that decrease dispersion (such as habitat filtering) or increase it (such as competition). Thus, measures such as trait range or convex hull

volume (Villéger et al. 2008, Ingram and Shurin 2009, Moen and Wiens 2009) are inappropriate because, for example, the trait range in a local community cannot be greater than the range in the regional assemblage. Similarly, the standard deviation of nearest neighbor distances can reflect competitive interactions but it does not capture effects of processes that may cause clustering. Here, we use mean Euclidean distance among species pairs in an assemblage because it can increase or decrease as one moves between hierarchical levels and we expect it to increase or decrease under processes such as competition or habitat filtering, respectively. Also, it allows for a common index that can easily be applied to one or many traits simultaneously. Since we deal with one trait, log(body size), it represents the mean of the logarithm of body size ratio among species in a community.

A disadvantage of mean pairwise Euclidean distance as a measure of trait dispersion is that the same value can arise multiple ways. For example, an assemblage of species with moderately similar body sizes could have the same body size dispersion as an assemblage of species where the majority of species are almost identical, but there is a single, outlying species with an extreme body size. However, these two scenarios would differ in their standard deviations of nearest neighbor distances in trait space. Therefore, to determine if such patterns were likely to bias our results, we evaluate the correlation between the standard deviation of nearest neighbor distances and mean pairwise Euclidean distance in local communities with richness greater than two. We found no significant correlation (Pearson’s $r = 0.27$, $P > 0.15$) between these indices, indicating that the distribution of species within local communities with respect to their nearest neighbors does not vary in a manner likely to influence our results. Additionally, for comparison, we also quantify trait dispersion using the coefficient of variation of body sizes in an assemblage.

Quantifying variation in trait dispersion.—Considering the three scales of species assemblages discussed above (continental, regional, local), the trait dispersion of local community j in region i (L_{ij}) can be expressed as a linear model:

$$L_{ij} = C + (R_i - C) + (\bar{L}_i - R_i) + (L_{ij} - \bar{L}_i) \quad (1)$$

where C is the trait dispersion of the continental species pool, R_i is the trait dispersion of the regional species assemblage (all species whose geographic ranges overlap the region’s boundaries), and \bar{L}_i is the mean trait dispersion of the n_i communities in R_i , calculated as

$$\bar{L}_i = \frac{1}{n_i} \sum_{j=1}^{n_i} L_{ij} \quad (2)$$

Eq. 1 can be expressed as the deviation of a local community’s trait dispersion from the trait dispersion of the continental species pool:

$$(L_{ij} - C) = (R_i - C) + (\bar{L}_i - R_i) + (L_{ij} - \bar{L}_i). \quad (3)$$

Assuming m regions and an equal number (n) of communities in each region, squaring and summing across all communities gives

$$\begin{aligned} \sum_{i=1}^m \sum_{j=1}^n (L_{ij} - C)^2 &= n \sum_{i=1}^m (R_i - C)^2 + n \sum_{i=1}^m (\bar{L}_i - R_i)^2 \\ &+ 2n \sum_{i=1}^m (R_i - C)(\bar{L}_i - R_i) \\ &+ \sum_{i=1}^m \sum_{j=1}^n (L_{ij} - \bar{L}_i)^2. \end{aligned} \quad (4)$$

This equation differs from the standard nested-ANOVA equation because of the existence of the covariance-like term on the right side of the equation; in a nested ANOVA, it would equal zero (Sokal and Rohlf 1995). However, in our formulation, regional and continental trait dispersion are not the mean of the samples at the next lower hierarchical level. Therefore, this term does not necessarily sum to zero, though empirically it could take this value. Eq. 4 summarizes the total variation in trait dispersion of local communities, relative to the continental species pool.

Partitioning the variation.—The variation in Eq. 4 explained by regional and local filters can be determined using the general formula for r^2 in regression analysis (from Quinn and Keough 2002):

$$r^2 = 1 - \frac{SS_{\text{residual}}}{SS_{\text{total}}} = \frac{SS_{\text{regression}}}{SS_{\text{total}}} \quad (5)$$

where SS is sums of squares. This formula can be written for our purposes as

$$r^2 = 1 - \frac{\sum_{i=1}^m \sum_{j=1}^n (L_{ij} - \bar{L}_i)^2}{SS_{\text{total}}} = \frac{SS_{\text{filters}}}{SS_{\text{total}}}. \quad (6)$$

However, our goal is not simply to determine the overall explained variation, but to partition it among regional and local filters. The explained variation (SS_{filters}) can be divided into three components, corresponding to the initial three terms on the right side of Eq. 4: a main regional effect (SS_R), a main local effect (SS_L), and a multiplicative effect (SS_{LR}):

$$SS_R = n \sum_{i=1}^m (R_i - C)^2 \quad (7)$$

$$SS_L = n \sum_{i=1}^m (\bar{L}_i - R_i)^2 \quad (8)$$

$$SS_{LR} = 2n \sum_{i=1}^m (R_i - C)(\bar{L}_i - R_i). \quad (9)$$

SS_{LR} can be either positive or negative. When regional and local filters operate in the same direction (e.g.,

regions are clustered relative to the continent pool, and local communities are clustered relative to regions), SS_{LR} will be positive and will have a synergistic effect on the total variation in community trait dispersion, increasing it beyond the additive local and regional effects. However, when local and regional filters oppose each other (e.g., regions are clustered, local communities are over-dispersed), then SS_{LR} will be negative. This antagonistic effect will obscure the total variation in the system by reducing the realized total sums of squares (RSS_{tot}), measured by the left side of Eq. 4:

$$RSS_{\text{tot}} = \sum_{i=1}^m \sum_{j=1}^n (L_{ij} - C)^2. \quad (10)$$

Thus, we propose an alternative measure of the total sums of squares, the absolute total sums of squares ($AbSS_{\text{tot}}$) that captures the total variation in the system regardless of whether synergistic or antagonistic effects are present:

$$\begin{aligned} AbSS_{\text{tot}} &= n \sum_{i=1}^m (R_i - C)^2 + n \sum_{i=1}^m (\bar{L}_i - R_i)^2 \\ &+ \left| 2n \sum_{i=1}^m (R_i - C)(\bar{L}_i - R_i) \right| \\ &+ \sum_{i=1}^m \sum_{j=1}^n (L_{ij} - \bar{L}_i)^2. \end{aligned} \quad (11)$$

When SS_{LR} is positive, then $RSS_{\text{tot}} = AbSS_{\text{tot}}$ and when SS_{LR} is negative then $RSS_{\text{tot}} < AbSS_{\text{tot}}$. To determine the proportion of variation explained by main regional and local effects and the multiplicative effect we simply divide SS_R , SS_L , and SS_{LR} by $AbSS_{\text{tot}}$. We can also determine the proportion of variation that is obscured by antagonistic effects (r_{ant}^2) as

$$r_{\text{ant}}^2 = 1 - \frac{RSS_{\text{tot}}}{AbSS_{\text{tot}}}. \quad (12)$$

One further characteristic of SS_{LR} requires clarification. As a multiplicative effect, it is clearly akin to the familiar interaction terms from ANOVA, and it is tempting to interpret it as such. However, it is not a true interaction (nor is it a covariance) because it can be nonzero even if $R_i - C$ and $\bar{L}_i - R_i$ do not covary. Such a situation could arise, for example, if both were nonzero but the former was constant across all regions while the latter was not. Thus, SS_{LR} should not be considered an interaction, but rather as a multiplicative effect that, when negative, measures the tendency of regional and local filtering to have effects that counteract each other, and are therefore not apparent in the realized total variation in trait dispersion.

Significance testing.—In studies of trait and phylogenetic structure, null models have been used to determine if the observed patterns could have arisen by chance (i.e., from random sampling of the species pool; Strong et al. 1979, Ricklefs and Travis 1980, Webb 2000, Webb

et al. 2002, Cavender-Bares et al. 2004, 2006, Kembel 2009). When multiple communities are included, these tests also help ensure that observed patterns are not due to species richness differences among assemblages (Stevens 2006). We defined filters broadly as any factor that changes the trait dispersion of a species assemblage; this definition could include factors that limit the number of species in a community (though, alternatively, the number of species could be a result of filters acting on traits). However, by constructing a null model, it allows for the determination of whether the amount of explained variation at a particular scale is greater than expected based simply on species richness differences among regions and communities.

The null hypothesis that the observed variation explained by a filter does not differ from random, given the observed species richness, can be tested by randomly drawing species from the relative species pool. For our analysis, three separate random draws were needed. First, to determine the random expectation for regional filtering, a set of null regional assemblages with the same numbers of species as observed assemblages were drawn at random from the continental species pool. SS_R for the null assemblages (SS_{Rnull}) was then calculated. To determine the random expectation for local filtering, a restricted random draw was used where null local communities of the appropriate species richness were drawn from the observed regional assemblage and SS_{Lnull} was calculated. This approach isolated the effect of local filters from regional ones and is analogous to the restricted randomization suggested for permutation tests in nested ANOVA (Anderson 2001). To test the multiplicative term, we used a third randomization that is unconstrained by the observed regional assemblages and is based on unconstrained permutations for interaction terms in two-way ANOVA (Anderson 2001). For this test, random regional assemblages were drawn from the continental pool, null local communities were drawn from the random null assemblages and SS_{LRnull} was calculated. This set of random draws was also used to test the total variation explained.

For significance testing, we sampled the relevant (continental or regional) species pool 1000 times. We maintained the observed species richness in our random samples. Several authors have shown that null models that do not account for species frequencies across communities can be subject to high Type I error rates (Gotelli 2000, Kembel and Hubbell 2006, Kembel 2009). To account for this, we weighted the probability of a species being selected by its range size (e.g., Blackburn and Gaston 2001). For random regional assemblages we used species' range sizes within the continental Americas. For local draws, we used the area of species' ranges within the relevant ecoregion as weights.

Hylid frogs in the continental Americas

We used the above method to quantify the variation explained by regional and local filters in the body size

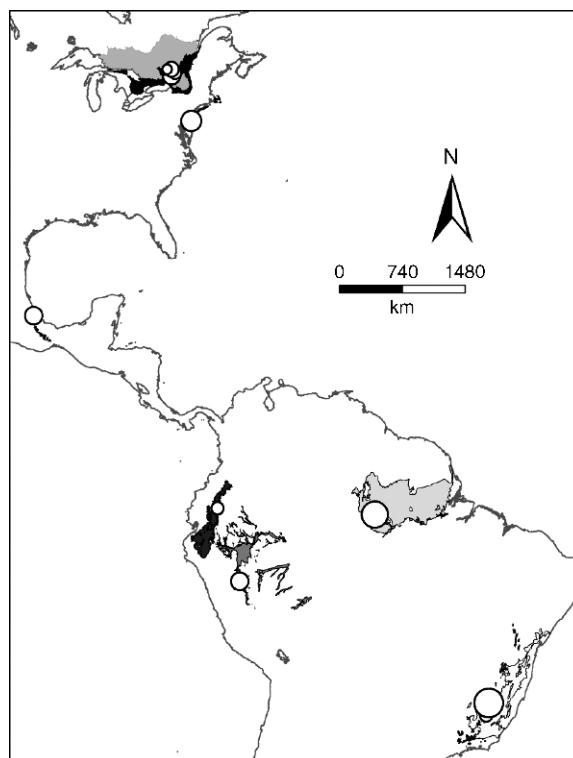


FIG. 2. Location of local communities collected from the literature. Ecoregions are shown in shades of gray to allow differentiation of adjacent regions. Local communities are shown by the white circles. Larger circles indicate that more local communities were sampled at those (or geographically indistinguishably similar, given the figure's resolution) coordinates.

dispersion (BSD) of treefrog (Hylidae) assemblages in the continental Americas. At the local scale, body size dispersion in these frogs can potentially be influenced by competition for prey (prey size is correlated with body size; Moen and Wiens 2009). At the regional scale, clade age (time for divergence) may act as an evolutionary filter, possibly resulting in regional assemblages with more similar body sizes in recently invaded regions (Moen and Wiens 2009).

Data.—We compiled information on local community composition for 55 local communities from the published literature, nested within nine World Wildlife Fund ecoregions (Fig. 2; Olson et al. 2001). Details on these communities are given in Appendix A. To be included in our study, published studies had to provide the following information: adult species composition of individual ponds or stream segments (and surrounding habitat), latitude and longitude, and survey area. For several ponds, only pond volume was given; we converted this to surface area by assuming a depth of 0.89 m (the mean depth of other water bodies in the analysis). Species richness of local communities ranged from two to eleven.

TABLE 1. Proportion of variation in body size dispersion explained by regional and local filters using mean Euclidean distance.

Effect	All regions			Temperate			Tropical		
	Mean	2.5%	97.5%	Mean	2.5%	97.5%	Mean	2.5%	97.5%
Main regional	0.324	0.288	0.371	0.360	0.334	0.413	0.140	0.098	0.207
Main local	0.264	0.169	0.422	0.175*	0.134	0.195	0.262	0.134	0.437
Multiplicative	-0.211	-0.311	-0.100	-0.450	-0.471	-0.412	0.204	0.033	0.319
Suppressed	0.422†	0.200	0.620	0.898*	0.794	0.942	0.002‡	0.000	0.000
Total explained	0.800*	0.714	0.897	0.984*	0.951	1.000	0.609	0.394	0.844

Notes: Given are the proportions explained by main regional and local effects, the multiplicative local \times regional effect, the proportion of variation suppressed by opposing local and regional effects, and the total explained variation, i.e., r^2 (Eq. 6). Shown are means and 2.5% and 97.5% quantiles of 1000 subsamples of three communities from each region. Data include 55 communities distributed among nine regions: six tropical and three temperate.

* $P < 0.05$; † $P < 0.10$; based on null models.

‡ Mean is outside 2.5% and 97.5% quantiles because there was strong right skew. Median is 0.000.

We considered a regional assemblage to be all hylid species whose ranges overlapped the relevant WWF ecoregion. We used the Natureserve range maps for the 492 species compiled by Algar et al. (2009; maps available online).⁴ As Natureserve did not include range maps for the genus *Dendropsophus*, we used ArcMAP 9.0 (ESRI 2004) to geo-reference online range maps (maps available online).⁵ Overall, our analysis included 580 species.

Following Moen and Wiens (2009), we quantified body size as the maximum snout-vent length (SVL) for a species, regardless of sex. For the majority of South and Central American species we used the body sizes given by Moen and Wiens (2009). Body sizes not included in Moen and Wiens' list were obtained from taxonomic references, field guides and original species descriptions (Appendix B). Body size was log-transformed prior to all analyses. Unfortunately, sufficient data were not available to evaluate how intraspecific variation may influence our analysis. In the *Discussion*, we address the implications of intraspecific variation on the patterns we uncover. However, we note that Moen et al. (2009) found that variation in body size among species was greater than within species for male tropical hylids.

Although local communities and ecoregions varied in area, body size dispersion of regional assemblages was not correlated with ecoregion area (Pearson's $r = 0.30$, $df = 7$, $P > 0.4$). The correlation between local body size dispersion and local survey area was low, but on the boundary of significance (Pearson's $r = 0.26$, $df = 53$, $P = 0.055$). However, local communities within an ecoregion are not independent as they share regional influences and are geographically proximate. Applying Dutilleul's modified t test (Dutilleul 1993) to account for spatial autocorrelation resulted in a nonsignificant correlation between area and local body size dispersion ($r = 0.26$, $df_{\text{eff}} = 21.17$, $P > 0.2$). Thus area has no detectable relation with body size dispersion and thus is unlikely to confound our results.

Partitioning the variation in community trait dispersion requires multiple local communities to be sampled within each region. The number of local communities sampled within the ecoregions we considered ranged from three to thirteen. However, our method requires a balanced design. While an unbalanced design could be utilized, it would weight those regions where more communities had been sampled more heavily, which may be undesirable if the number of communities sampled does not reflect ecological properties of regions, such as area. A balanced design is simple to obtain by randomly choosing an equal number of communities from each region; in our case, we used the minimum number: three. To quantify the variability in the results associated with this sampling procedure, we repeated it and the subsequent analyses 1000 times. We partitioned the variation among local and regional filters as described above.

Tropical vs. temperate regions.—To compare the role of regional and local filters within tropical and temperate areas, we divided our nine regions (and the local communities they contained) into a tropical set (six regions with geographical centers between 23.4° N and 23.4° S, containing 34 communities) and a temperate set (three regions with geographical centers above 23.4° N, containing 21 communities). Treating tropical and temperate regions separately, we repeated the variation partitioning analysis following the same procedure already described.

RESULTS

Variation partitioning

On average, regional and local filters explained 80% of the variation in hylid BSD (Table 1) using mean Euclidean distance. Mean main effects of regional filters explained slightly more variation in BSD than did mean main effects of local filters (33% vs. 26%) but there was substantial overlap in the subsampled values indicating that regional and local filters had similar effects on community trait dispersion (Table 1). We found a substantial antagonistic effect between local and regional filters: local communities were generally over-dis-

⁴ (<http://www.iucnredlist.org/technical-documents/spatial-data>)

⁵ (<http://www.iucnredlist.org/initiatives/amphibians>)

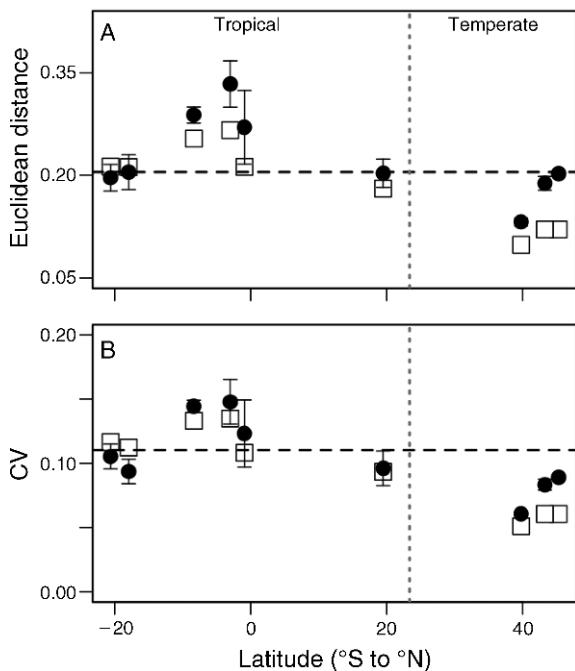


FIG. 3. The relationship between body size dispersion (BSD) in the continental species pool (black dashed line), regional BSD (open squares), and local BSD (solid circles) at different latitudes. BSD was calculated using (A) mean Euclidean distance between species pairs and (B) the coefficient of variation of body size. For local communities, means are shown with standard errors when not obscured by points. The number of local communities per region ranged from 3 to 13. Some points have been slightly shifted latitudinally (~1°) to improve visual clarity. The vertical dotted gray line delineates the tropical and temperate zones. Regional BSD ranges from clustered (below the continental line) in the temperate zone to generally over-dispersed (above the continental line) in the tropics. On average, local communities are over-dispersed relative to regions.

persed, relative to their respective regional assemblages, while regional communities ranged from clustered to over-dispersed with respect to the continental species pool (Fig. 3). Thus, over a portion of the data, local and regional filters had synergistic effects, but their overall magnitude was less than the antagonistic effect in the remainder of the data. This antagonistic effect account-

ed for an average of 21% of the total variation and had substantial implications for the realized variation in the system: 42% of the total variation was masked by the opposing effects of regional and local filters (Table 1). Results were similar when regions with at least five communities were included, with regional and local filters having antagonistic effects, though the relative importance of regional filters increased slightly. 75% of the total variation explained was explained by main and multiplicative effects. Regional filters explained 40% of the variation, local filters 21%, while 25% of the total variation was suppressed. Local filters were of less relative importance because two of the three regions that were excluded due having fewer than five sampled communities were tropical, and regional effects had less importance in tropical environments.

Results using the coefficient of variation (CV) to quantify body size dispersion were similar to those using mean Euclidean distance with one exception. Partitioning variation in CV resulted in more variation explained by regional filters than by local ones (mean = 42% and 14% respectively; Table 2). However, we note that the 2.5% and 97.5% quantiles for these estimates overlap with those based on mean Euclidean distance. The mean total variation explained was almost identical to that for mean Euclidean distance, while the proportion of variation suppressed was slightly higher for CV, but still overlapped with estimates based on Euclidean distance.

Using mean Euclidean distance, significance testing that controls for species richness differences revealed that neither of the main effects (regional and local) were significantly greater than expected based on random sampling from the continental or regional species pools ($P > 0.14$). The multiplicative term was also not statistically significant ($P > 0.08$). However, both the proportion of variation masked by the antagonistic effect and the total variation explained were greater than expected based on chance alone ($P < 0.04$). The disparity between a lack of significance of main and multiplicative effects and significant overall variation explained suggests that filtering independent of species richness was not especially strong at either local or regional scales. However, overall, the magnitude of their

TABLE 2. Proportion of variation in body size dispersion explained by regional and local filters using the coefficient of variation.

Effect	All regions			Temperate			Tropical		
	Mean	2.5%	97.5%	Mean	2.5%	97.5%	Mean	2.5%	97.5%
Main regional	0.427	0.366	0.501	0.519	0.489	0.591	0.168	0.125	0.218
Main local	0.141	0.085	0.251	0.090†	0.066	0.102	0.203	0.086	0.407
Multiplicative	-0.236	-0.320	-0.135	-0.381	-0.409	-0.314	0.073	-0.015	0.278
Suppressed	0.471	0.264	0.639	0.762*	0.628	0.817	0.048‡	0.000	0.302
Total explained	0.803*	0.729	0.897	0.990*	0.962	1.000	0.492	0.332	0.772

Notes: Given are the proportions explained by main regional and local effects, the multiplicative local × regional effect, the proportion of variation suppressed by opposing local and regional effects, and the total explained variation, i.e., r^2 (Eq. 6). Shown are means and 2.5% and 97.5% quantiles of 1000 subsamples of three communities from each region. Data are the same as for Table 1.

* $P < 0.05$; † $P < 0.1$; based on null models.

‡ Mean is outside 2.5 and 97.5% quantiles because there was strong right skew. Median is 0.000.

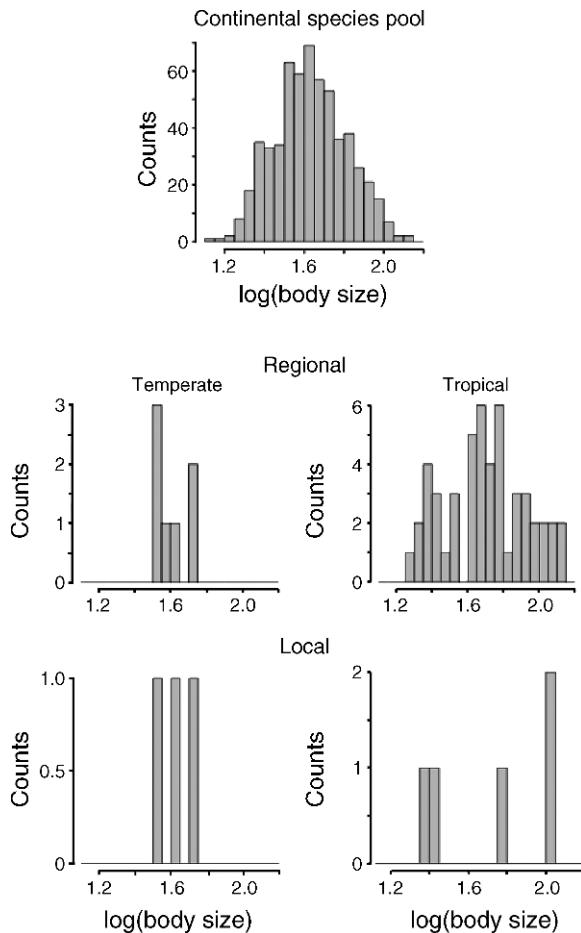


FIG. 4. Raw body size distributions in the continental species pool and representative regional assemblages and local communities nested within them. One temperate (Atlantic Coastal Pine Barren, northeastern United States) and one tropical (Uatama-Trombetas Moist Forest, eastern Brazil) regional assemblage are shown, as well as a single local community from each. Note that the y -axis scales differ. Note also the narrow distribution of the regional temperate assemblage relative to the continental pool and the overdispersion in local communities relative to regions.

combined effects was large and the joint strength of filtering at both levels was stronger than expected due to chance, as was the degree to which local and regional acted in opposition. Significance testing on CV produced similar results (Table 2).

Tropical-temperate comparisons

The relative importance of regional and local filters differed between tropical and temperate regions. Within the tropics, using mean Euclidean distance, local filters explained more variation in community trait dispersion than regional filters (26% vs. 14%; Table 1) though neither of these results differed from the random expectation that incorporated species richness ($P > 0.8$ in both). Alternatively, in the temperate zone, regional

filters were of greater importance than local ones (36% vs. 18%; Table 1). However, the magnitude of regional filtering did not differ from the random expectation ($P > 0.4$), but the magnitude of local filter was greater than expected ($P < 0.03$). Two other differences between tropical and temperate zones are evident. First, the total variation explained was much higher in the temperate zone (98% vs. 61%). The remarkably high total variation explained in the temperate zone can be attributed to the strong regional filtering that leaves little opportunity for variation among local communities. Second, in tropical areas, regional and local filters acted in concert, both increasing BSD above the global mean (Table 1, Figs. 3 and 4). However, in temperate areas, an antagonistic effect was present, with local and regional effects acting in opposition (Table 1, Figs. 3 and 4). The antagonistic temperate effect was, overall, stronger than the synergistic tropical effect, which explains the masked variation we detected when all areas were considered together. This result suggests that filters influencing community structure may appear weaker in temperate zones than in tropical ones, due to the masking effect of filters acting in opposition at different scales.

Results were broadly similar using CV when comparing tropical and temperate regions, though, as with the total dataset, it tended to place more weight on regional, rather than local, filters (Table 2). However, in tropical regions, local filters still explained more variation than regional filters, though the difference was small, while in temperate areas regional filters explained more variation than local filters (Table 2). Furthermore, local and regional filters were still found to be synergistic in the tropics and antagonistic in temperate regions. However, less temperate variation was suppressed using CV (76%). Also, using CV, the magnitude of variation explained by local filters in temperate regions was marginally nonsignificant ($P = 0.075$; Table 2). However, the proportion of variation suppressed was significant ($P < 0.04$), indicating that while the magnitude of the local effect was not quite significant at $\alpha = 0.05$, the combination of magnitude and direction (over-dispersion) was unlikely to have occurred by chance.

DISCUSSION

Ecological community structure likely arises from a combination of processes operating at local and regional scales (He et al. 2005, Ricklefs 2006, 2007, Harrison and Cornell 2008). Research into this question has predominantly focused on species richness and the evaluation of local-regional richness regressions (Ricklefs 2007, Harrison and Cornell 2008), an approach that is littered with potential pitfalls (Cornell and Lawton 1992, Srivastava 1999, Loreau 2000, He et al. 2005). In addition to these drawbacks, the local-regional regression approach is also limited to asking whether local communities are saturated (local control) or not (regional control). While the relative importance of processes at these two scales can, perhaps, be loosely inferred from the degree of

departure from a positive linear relationship, there is no formal method to do so. Here, we introduced a novel approach that focuses on community trait structure, rather than species richness. Our method quantifies the variation in community trait dispersion that is explained by local and regional scale filters, as well as antagonistic (or synergistic) effects of the two scales. In doing so, it treats regional and local control of community structure as two ends of a continuum, rather than as mutually exclusive alternatives.

Overall, 80% of the variation in community trait dispersion could be explained by regional and local filters. The remaining 20% could arise from a number of sources, such as local stochasticity or perhaps local environmental gradients (e.g., Weiher et al. 1998, Bryant et al. 2008, Cornwell and Ackerly 2009). Overall, regional filters had greater effects on trait dispersion than local filters, though the degree of difference depended on how trait dispersion was measured. However, clearly both local and regional scale filters influence trait dispersion. This result was not due simply to the reduction in species richness as one moves from continental to regional to local scales, as the proportion of total variation explained was greater than expected based on random sampling from the continental and regional species pool. However, our restricted randomizations showed that, treated separately, neither regional nor local effects were greater than predicted by null sampling. These seemingly contradictory results indicate that while the neither regional or local effects were significantly strong, there is a low probability of jointly observing regional and local effects as strong as we did. Thus, while species richness differences between local and regional assemblages undoubtedly influence variation in body size dispersion, there is evidence that filters influence body size independently of species richness. Furthermore, it could be argued that processes or factors that exclude entire species, and thus limit species richness, are merely whole-phenotype filters. Thus, it is possible that the differences in species richness among regions and communities are a result, rather than a cause, of patterns in trait dispersion. Our current analysis cannot tease apart these alternatives and further research is needed to address these questions.

Ecologists and evolutionary biologists have long proposed that the processes structuring communities differ between temperate and tropical regions (e.g., Dobzhansky 1950, MacArthur 1969). Our results reveal a fundamental difference between the tropics and temperate zones in how variation in trait dispersion is partitioned at regional and local scales. In the tropics, local and regional filters predominantly acted in concert, but in temperate regions, regional filters limited trait dispersion, while local filters tended to enhance it. Several studies have alluded to such an effect by finding that plant species assemblages can change from over-dispersed to clustered as spatial scale increases (Cavender-Bares et al. 2006, Swenson et al.

2007). More directly, in a large sample of sunfish (Centrarchidae) communities, Helmus et al. (2007) showed that filters also acted in opposition: environmental factors induced clustering among lakes, but phylogenetic repulsion acted within lakes, with the net result that communities appeared to be randomly structured (see also Cavender-Bares et al. 2009 and a related discussion by Cornwell and Ackerly 2009). Our analysis was able not only to detect such effects, but also to quantify their relative importance for community structure. For temperate hylids, their importance was striking: the antagonist effect of local and regional filters masked between 76% and 90% of the total variation in temperate community BSD. Such strong effects rendered the trait dispersion of local communities similar to the overall species pool (Fig. 3) and were influential enough to leave a statistically significant signature in the complete dataset, despite the lack of suppressive effects in tropical regions. Whether the magnitude of the masked variation is a general property across taxa and high latitude regions, or unique to the New World hylids can be answered only by future work; we suspect that further comparisons among taxa and continents will reveal new insights into how processes interact across scales.

Temperate and tropical zones also differed in the relative importance of regional and local filtering and in whether their effects differed from the null expectation. In tropical regions, local filters explained more variation than regional filters; in temperate zones, regional filters were of greater importance. At high latitudes, “harsh” conditions, such as cold temperatures, have been proposed as the dominant selective force determining community structure, while at low latitudes, interspecific interactions, such as competition, have been hypothesized to dominate (Dobzhansky 1950, Fischer 1960, MacArthur 1972, Mittelbach et al. 2007). Assuming that abiotic filtering due to harsh environmental conditions is primarily a regional scale process, our results are consistent with the hypothesis that regional processes are stronger in temperate areas, though we cannot differentiate effects on body size from those on species richness at the regional scale. However, our results also suggest that local processes may not have diminished effects in the harsher, temperate, conditions. Although local filters accounted for more variation in the tropics, neither total variation explained nor variation at regional or local scales differed from the species richness-based null expectation. Alternately, in temperate zones, although regional filtering was not statistically significant, local filtering, suppressed variation, and the total variation explained were all greater than expected by chance, or very nearly so. While seemingly strong temperate regional filtering may be due to species richness, which is low at high latitudes in hylids (Wiens et al. 2006, Algar et al. 2009), random sampling cannot account for the over-dispersion of temperate local communities relative to the regional pool.

Over-dispersion of traits within communities suggests a possible role for competition in determining community structure (Weiher et al. 1998, Kraft et al. 2008, Cornwell and Ackerly 2009). Facilitation is also a possible mechanism, but it is difficult to hypothesize how disparately sized hylid species may benefit each other. If over-dispersion is an honest indicator of competition, then our results suggest that it has detectable effects on trait dispersion in temperate communities. Prinzing et al. (2008) showed that when phylogenetic lineage diversity is reduced within plant communities, species interactions result in greater trait variation. Regional phylogenetic clustering increases with latitude (specifically, with decreasing temperature) in hylids (Algar et al. 2009), a pattern that has been linked to the conservation of cold tolerance across the phylogeny (Smith et al. 2005, Algar et al. 2009). Regardless of whether regional filters act directly on body size, or through some correlated trait, our findings suggest that low BSD of regional assemblages in temperate regions may result in competitive interactions that leave a detectable signature on local community structure.

The lack of a statistically significant effect of local filters on body size dispersion in tropical communities suggests a fundamental difference in the dominant assembly processes within tropical and temperate communities. Unlike in temperate regions, competition mediated by interspecific differences in body size did not have a detectable effect on tropical hylid community structure. These results are consistent with the findings of Moen et al. (2009), who showed that body-size-mediated competition did not protect tropical hylid communities from invasion in evolutionary time by species with body sizes similar to those already present in the community. The lack of signal in body size dispersion in tropical communities could indicate that tropical community assembly is predominantly stochastic (Kembel 2009). However, alternative processes could also produce similar patterns. For example, it could be that in tropical regions, individuals partition a high-dimensional resource space, giving the appearance of random assembly, where the numerous, unmeasured, differences among individuals both within and between species give the appearance of stochasticity (Clark et al. 2007, 2010). One untested possibility is that in temperate areas, community assembly is dominated by differences among species, while in tropical regions, assembly is predominantly a function of variation among individuals, which allows for resource partitioning but does not produce differences in species means (Clark 2010). Improved data on intraspecific variation in traits along latitudinal gradients, specifically whether intraspecific variation is higher in tropical regions, could be used to test this hypothesis.

A key concern of ecologists is what constitutes local and regional scales (e.g., Ricklefs 2008, Brooker et al. 2009). Since partitioning variation in community trait

dispersion depends upon identifying species assemblages at different scales, this is a critical component of our method. We have considered local communities as inhabiting individual breeding areas and regional assemblages as those species occurring within ecoregions. An extension of our approach would be to examine the rate at which explained variation changes as spatial grain increases or decreases, which would allow for the identification of critical scales of assemblage organization, i.e., the scale which results in the greatest change in the proportion of variation explained.

Here, we introduced a new approach to evaluate the extent to which regional and local factors and processes influence community structure. Our approach treats local and regional influences as a continuum and thus allows for community structure to arise from a combination of processes acting at multiple scales. It also extends the capabilities of studies of community trait dispersion which, until now, have primarily focused on whether trait dispersion is nonrandom. Using our methods, it is now not only possible to ask whether filtering occurs, but to determine how much and at what scale. Additional studies on a wider range of taxa, traits, and spatial scales will further refine the method we have presented. They will also evaluate the generality of the patterns we have found for New World hylids, including the approximately equal influence of local and regional filters on community structure and differences in filtering among tropical and temperate zones, especially the strong antagonistic effects of regional and local filters within temperate, but not tropical, areas.

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APPENDIX A

Summary statistics for 55 Hylidae communities collected from the literature (*Ecological Archives* E092-076-A1).

APPENDIX B

Maximum snout–vent length (SVL), regardless of sex, of hylid species (*Ecological Archives* E092-076-A2).