REPORT

The alpha–beta–regional relationship: providing new insights into local–regional patterns of species richness and scale dependence of diversity components

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Abstract

Ecologists frequently regress local species richness on regional species richness to draw inferences about the processes that structure local communities. A more promising approach is to quantify the contributions of alpha and beta diversity to regional diversity (the ABR approach) using additive partitioning. We applied this approach to four local–regional relationships based on data from 583 arboreal beetle species collected in a hierarchically nested sampling design. All four local–regional relationships exhibited proportional sampling, yet the ABR approach indicated that each was produced by a different combination of alpha and beta richness. Using the results of the ABR analysis, we also analysed the scale dependence of alpha and beta using a hierarchical linear model. Alpha diversity contributed less than expected to regional diversity at the finest spatial scale and more than expected at the broadest spatial scale. A switch in relative dominance from beta to alpha diversity with increasing spatial scale suggested scale transitions in ecological processes. Analysing the scale dependence of diversity components using the ABR approach furthers our understanding about the additivity of species diversity in biological communities.

Keywords

Additive partition, beetle, diversity components, ecoregion, local–regional richness, scale dependence, species diversity.

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INTRODUCTION

Ecologists study the relationship between local and regional richness to understand the relative strengths of local and regional processes in determining community structure (Cornell 1985; Ricklefs 1987). At least 30 studies have addressed local–regional (LR) relationships (reviewed by Srivastava 1999), indicating their importance to understanding how diversity is generated and maintained in biotic communities. Most of the studies attempted to distinguish between linear and curvilinear relationships in bivariate plots of LR richness. The shape of the relationship was then interpreted as evidence for which processes – local or regional – are more important in structuring the local community. A curvilinear (i.e. saturating) relationship between local and regional richness indicates that local richness becomes independent of the regional species pool and is regulated by strong interactive processes such as competition, predation, and niche pre-emption (Cornell 1993). A linear relationship (i.e. proportional sampling) suggests that local species richness depends upon the regional species pool, and that regional processes such as evolutionary history (Hugueny 1997), colonization–extinction dynamics, and speciation are relatively more important in structuring the local community (Ricklefs & Schluter 1993).

One shortcoming of this approach is that inferences about processes are based on the premise that saturating relationships are generated by interactive processes and linear relationships are generated by non-interactive processes. This is not always the case, however, because linear relationships can arise from interactive scenarios (Loreau 2000). Cornell & Lawton (1992), for example, have identified models in which interactive communities generate linear relationships between local and regional richness. These models show that saturating patterns can be obscured

by modest levels of habitat disturbance and that results from empirical studies should be interpreted with caution (Caswell & Cohen 1993). The notion that "patterns do not infer processes" should be seriously considered when drawing conclusions based on the shape of LR relationships. Additionally, determining the shape and statistical strength of the LR relationship (Griffiths 1999; Srivastava 1999) has been difficult. Over one-third of the data sets reviewed by Srivastava (1999) were spatially or temporally pseudoreplicated. Spatial pseudoreplication was more common, and occurred when local richness in a region was plotted as a cluster of values rather than a single mean value. The shape and strength of the LR relationship is further affected by the statistical approach (e.g. polynomial vs. logarithmic regression, constrained vs. unconstrained regression; Griffiths 1999) and by preferences for null models, such that a LR pattern may be interpreted as evidence for saturation by one ecologist and evidence for linearity by another ecologist (Srivastava 1999).

The patterns produced by the LR relationship have been important in developing our initial understanding of local and regional processes. But for LR relationships to be of further use to ecologists, we need to overcome the precedent of weak inference by finding an approach that will provide further insight about LR relationships and encourage ecologists to investigate the processes that structure communities. One possible approach is to examine the way in which regional diversity is partitioned into alpha and beta components (Loreau 2000). From a biological standpoint, alpha diversity – also referred to as within-habitat diversity (MacArthur 1965) – is the component of total (gamma) diversity that can be attributed to the average number of species found within homogeneous sampling units (i.e. habitats). Beta diversity – also referred to as between-habitat diversity (MacArthur 1965) – is the component of total diversity that can be attributed to differences in species composition among the homogeneous units in the landscape (Whittaker 1960; 1977). Ecological factors such as dispersal, habitat isolation, and habitat heterogeneity, among others, can affect values of alpha and beta diversity in a given landscape.

Although alpha and beta diversity have a strong conceptual meaning for ecologists, they have lacked until recently the mathematical properties to make them useful in empirical or experimental settings. Whittaker (1960) originally developed a multiplicative formula to explain how alpha and beta contributed to regional (gamma) diversity (i.e. regional = alpha × beta). The disadvantage of this relationship is that diversity components are not weighted equally when they are applied to more than one spatial scale. The additive relationship between regional diversity and its alpha and beta components (i.e. regional = alpha + beta) modified Whittaker's (1960) original formula, however.

The additive formula was originally proposed by Allan (1975), but has only recently has been evaluated (Lande 1996) and applied to ecological phenomena (Wagner et al. 2000; Gering et al. in press). The utility of the additive formula in the study of LR relationships is depicted in Fig. 1: after performing the regression analysis on the LR relationship, it is possible to decompose the area under the LR regression line into alpha and beta components so that regional diversity is being regressed against its diversity components instead of local diversity. Because of the additive relationship between regional diversity and its components, the area under the LR regression line must be explained entirely by the alpha and beta components. As
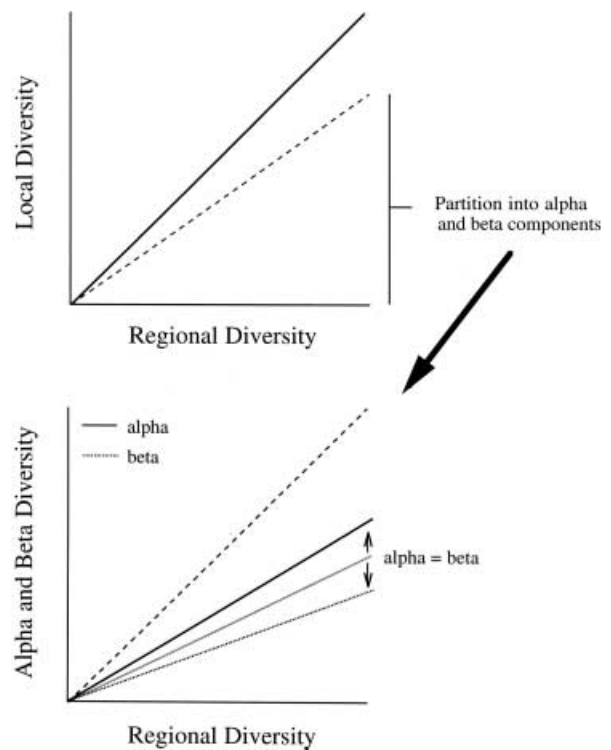

Figure 1 Schematic illustration of the relationship between local and regional diversity and the partitioning of regional diversity into its alpha and beta components. The upper graph shows a case of proportional sampling where the area under the local–regional regression line (dashed) is partitioned into alpha and beta components according to additive partitioning. Regional diversity is then replotted against alpha and beta components of diversity (the black arrow indicates this process). The dashed line in the lower graph represents the points on the graph where the sum of alpha and beta diversity equal the regional diversity, whereas the light grey line represents the points at which alpha and beta each account for half of the regional diversity. It is also possible for alpha and beta to account for differing amounts of the regional diversity (small arrows); we have drawn a case in which alpha diversity accounts for more of the regional diversity than does beta diversity.

shown in the lower panel of Fig. 1, it is therefore possible to establish a plane at which alpha and beta diversity contribute equally to regional diversity. Obviously, the additive relationship also makes it possible to determine if the alpha and beta components contribute unequally to the regional diversity (i.e. if one accounts for more area under the line).

Our first objective, then, is to empirically demonstrate and discuss the use of the alpha–beta–regional (ABR) relationship in the context of LR relationships. We do this by first analysing four LR relationships in the typical manner (i.e. with regression to determine the shape and strength of the statistical relationship) and then proceeding with the analysis of the ABR relationship for the same four LR relationships. In the process of comparing these approaches, we also explain how the ABR approach overcomes issues of spatial pseudoreplication that are common in studies of local and regional richness.

Our second objective is to investigate how the contributions of alpha and beta to regional diversity change as a function of spatial scale. The four LR relationships mentioned above are also hierarchical and scale-specific, which means that each was calculated from values of local and regional richness on different spatial scales. After analysing them with the ABR approach, we examined how alpha and beta changed across the range of spatial scales. Documenting the scale dependence (if it exists) of alpha and beta to regional diversity would be helpful in determining the processes that produce a LR pattern at a given spatial scale (Loreau 2000; Scheiner *et al.* 2000). There are presently few predictions about how alpha and beta diversity change across spatial scales (but see Huston 1999). Therefore, we developed hypotheses representing a broad range of possible scenarios (Fig. 2).

Scale independence in alpha and beta could occur only if the relationship of alpha and beta to regional diversity remained unchanged across spatial scales (Figs 2a,d). This scenario is analogous to a null model (i.e. no change in alpha and beta across scales), but is least likely to occur because processes that determine community structure change across spatial scales (Peterson & Parker 1998; Huston 1999) and subsequently affect the balance between alpha and beta (Loreau 2000). Alternatively, alpha and beta could exhibit constant scale dependence (Figs 2b,e), under which there would be a *constant* decrease (or increase) in the contribution of alpha or beta to regional diversity as the spatial scale is decreased (or increased). However, it is unclear whether these changes occur in a constant manner or in an *irregular* manner, so we also considered a situation where alpha and beta diversity would exhibit irregular scale dependence (Figs 2c,f). This could occur if abrupt transition zones were encountered across the range of spatial scales. Transition zones represent boundaries between scale domains, or ranges of spatial scales that are dominated by
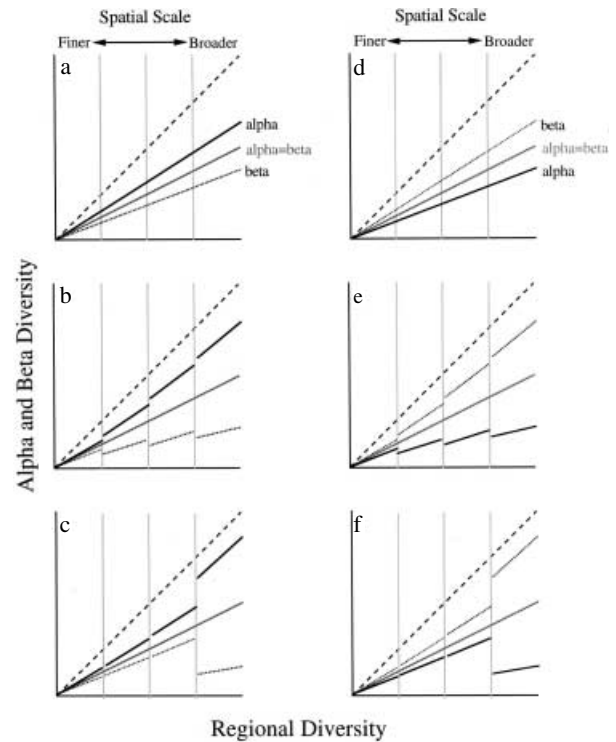

Figure 2 Potential relationships between alpha and beta diversity and regional diversity across four spatial scales. (a–c) Scenarios where alpha is the dominant contributor ("alpha-dominant" systems) to regional diversity. (d–f) Scenarios where beta is the dominant contributor ("beta-dominant" systems) to regional diversity. Scale independence (a, d) will occur when alpha and beta contribute in a consistent manner to regional richness across the range of spatial scales. Constant scale dependence (b, e) will occur if alpha and beta increase in a predictable manner across the range of scales, whereas irregular scale dependence (c, f) will be evident if alpha and beta contribute to regional richness in a nonlinear manner across the range of scales. As in Fig. 1, the dashed line in the graph represents the points on the graph where the sum of alpha and beta diversity equal the regional diversity, whereas the light grey line represents the plane at which alpha and beta each account for half of the regional diversity.

particular ecological processes (*sensu* Wiens 1989; see also King *et al.* 1991; Levin 1992). Finally, it is unclear whether alpha or beta diversity will contribute more to the regional diversity across the range of spatial scales, although Huston (1999) predicts that alpha diversity should contribute less to regional diversity as spatial scale decreases because direct interactions are more common at fine spatial scales (also see Srivastava 1999). In any case, we have included both scenarios in Fig. 2 (a–c are alpha-dominant scenarios, whereas d–f are beta-dominant scenarios). We tested these hypotheses using arboreal beetles collected by insecticide fogging from a hierarchically nested design that

encompassed four spatial scales – ecoregions, sites, forest stands, and trees – within deciduous forests of Ohio and Indiana.

MATERIALS AND METHODS

Study sites

Insect data for this study were collected from six sites in southern Ohio and south-eastern Indiana, USA: Hueston Woods State Park (HWSP; Preble Co., OH), Brookville Reservoir (BROK; Franklin Co., IN), Caesar Creek State Park (CACR; Warren Co., OH), Clear Creek Metro Park (CLCR; Fairfield Co., OH), Shawnee State Forest (SSFO; Scioto Co., OH) and Edge-of-Appalachia Nature Preserve (EOAP; Adams Co., OH) (Fig. 3). The first three sites are located in the beech–maple association of the eastern deciduous forest (Braun 1950) and the North-central Tillplain ecoregion (Bailey 1998). The forests are dominated by American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) and to a lesser extent by red oak (*Quercus rubra*), white oak (*Quercus alba*), elms (*Ulmus* spp.) and ashes (*Fraxinus* spp.) (Delcourt & Delcourt 2000). The ecoregion is dominated by agriculture and relatively flat due to glaciation and scouring of soft limestone and sandstone bedrock. The topography is characterized by ridges separated by shallow (10–15 m), sloping drainages. The last three sites are located in the mixed mesophytic association of the

eastern deciduous forest (Braun 1950) and the Western Allegheny Plateau ecoregion (Bailey 1998). The forest in this region is dominated by oaks and hickories (*Carya* spp.) in xeric areas and beeches, tulip poplars (*Liriodendron tulipifera*), and hemlock (*Tsuga* spp.) in mesic areas (Braun 1950; Delcourt & Delcourt 2000). The ecoregion is unglaciated, has variable soils, and a topography characterized by steep ridges and long, narrow drainages.

Sampling design

We sampled using a hierarchically nested sampling design. As described above, three sites were nested within two ecoregions. Within each site, we selected four 1-ha stands representing two mesic areas and two xeric areas and we sampled all the individual trees > 10 cm d.b.h. within each of those stands. Based on the surveys, we selected four individual trees within each stand that were representative of the dominant tree genera. *Quercus*, *Acer*, *Fagus*, and *Carya* were common, whereas *Liriodendron*, *Celtis* and *Fraxinus* were encountered less frequently. Every xeric stand contained at least one *Quercus* individual and at least one *Acer* individual. Finally, each tree was sampled (see below) using 12 0.5-m² collecting funnels. Thus, our sampling design consisted of five hierarchical levels which allowed us to evaluate LR and ABR relationships on four spatial scales: ecoregions vs. sites, sites vs. stands, stands vs. trees, and trees vs. funnels.

Insect sampling

We obtained samples of the insect communities from each tree during two sampling periods in the summer of 2000: 22 May to 20 June and 2–25 August. We sampled twice during the summer because temporal change has a significant effect on beetle community composition (Gering & Crist 2000). Hence, there are two separate estimates of richness for each individual tree, for a total of 192 samples (96 trees × 2 sampling periods). We sampled each tree using the insecticide fogging technique, which is relatively unselective, not dependent on arthropod activity, and results in comparable samples (cf. Basset *et al.* 1997; Stork & Hammond 1997). At dawn on windless mornings, the crown of each tree was inundated for 3 min with 0.5 L of a 0.5% pyrethrin-based insecticide (Pyrenone 50, AgrEvo Products) emitted from a radio-controlled Curtis Dyna-Fogger. During the following 2 h, insects fell into the ground-based array of 12 0.5-m² collecting funnels. The funnels were located beneath each tree crown so that insects from neighbouring tree crowns were unlikely to be collected. Our sampling protocol was based on previous insecticide fogging studies (e.g. Stork 1987; Davies *et al.* 1997; Stork & Hammond 1997; Gering & Crist 2000).

Figure 3 A map of Ohio and surrounding states showing the location of sampling sites and the boundaries (dark solid lines) that separate the ecoregions used in the study. Abbreviations for sampling sites are as follows: 1 – Hueston Woods State Park, 2 – Brookville Reservoir, 3 – Caesar Creek State Park, 4 – Clear Creek Metro Park, 5 – Edge-of-Appalachia Nature Preserve, 6 – Shawnee State Forest.

Insect processing

All beetle specimens were sorted and identified to families and Recognizable Taxonomic Units (RTUs or morphospecies; Oliver & Beattie 1993, 1996). The "morphospecies" approach is frequently adopted by researchers working on canopy arthropod communities because collections are large and the taxonomic expertise required for species determinations is often unavailable (Erwin 1995). Species grouped by coarse morphological features closely correspond to expert taxonomic identification (Longino & Colwell 1997), although this may vary among taxa with morphologically similar species. To validate our morphospecies designations, we sent 126 morphospecies to a Coleopteran systematist (Daniel Young, University of Wisconsin-Madison), who identified 140 actual species. Thus, our estimates of species richness were conservative. Most of the "lumping" in our designations occurred in one weevil genus (Curculionidae: *Curculio*) and one darkling beetle genus (Tenebrionidae: *Platydema*).

Data analysis

LR relationships

LR relationships were evaluated on four spatial scales: ecoregion vs. site, site vs. stand, stand vs. tree, and tree vs. funnel. We plotted the total number of species in a regional sample against the total number of species in *each* local sample. When sites served as regions, for example, we had four estimates (corresponding to the four stands) of local richness within each region (i.e. site). This approach suffers from spatial pseudoreplication (Srivastava 1999), but we used it because we wanted to compare our results to those from other studies and draw contrasts between the LR relationship and the ABR relationship.

Our preliminary analyses suggested that dividing the data set into sampling periods and ecoregions had no effect on the LR relationships. We thus included both sampling periods (early and late) and both ecoregions in our analyses. At the broadest spatial scale in the ABR comparisons, for example, there are four points, each of which corresponds to the estimate of alpha richness for a given ecoregion in a given sampling period (2 ecoregions × 2 sampling periods). An advantage of combining both sampling periods and ecoregions was that it enabled us to conduct a regression analysis on the broadest spatial scale (ecoregions vs. sites). Furthermore, the seasonal change in the species composition and abundance of these beetle communities is very pronounced. For the data set used in this study, we calculated only a 22% similarity in community composition, indicating that the sampling periods exhibited a high degree of biological independence (Gering *et al.* in press). In previous studies on the same systems, the similarity in

community composition between sampling periods has been < 15% (Gering & Crist 2000).

We determined the strength of each scale-specific LR relationship using simple linear regression (SYSTAT 1992). There was little evidence of a saturating relationship at any spatial scale, so we did not attempt to fit curvilinear models to the data. Although regressions of local–regional relationships are typically constrained (i.e. forced through zero; Caley & Schluter 1997), we used an unconstrained approach to provide consistency with the hierarchical linear model (HLM; see below) used to test for scale dependence of alpha. Constrained regressions can also be misleading because they make incorrect assumptions about the position of the intercept. Thus, Griffiths (1999) suggests using constrained regression only when intercept values are positive. Our intercepts were negative and, further, our exploratory data analysis showed no qualitative differences in the outcomes of constrained and unconstrained approaches.

ABR relationships

To investigate the ABR relationships, we plotted the total number of species in the regional sample against the *mean* species richness among local samples within the region. When sites served as regions, for example, we had a single estimate of local richness that represented the mean richness of the four stands within that region. According to additive partitioning, regional diversity is the sum of alpha and beta diversity (i.e. regional = alpha + beta) so that beta is the complement of alpha (Allan 1975; Lande 1996). Although both alpha and beta diversity are shown on some graphs, only alpha diversity was used in analyses because it is more commonly reported in the ecological literature and eliminates the problem of spatial pseuodreplication because it is a mean value (Srivastava 1999). An important point about the calculations is that they are specific to an individual spatial scale. We were not interested in examining how each spatial scale accounted for the total (study wide) species diversity as in other studies using additive partitioning (e.g. Wagner *et al.* 2000; Gering *et al.* in press). Instead, we focused on the way in which regional diversity was partitioned into alpha and beta within a particular spatial scale.

With the exception of the mathematical partitioning described in the previous paragraph, the data analysis for the ABR relationships was identical to that of the LR relationships. That is, we grouped both sampling periods and used unconstrained simple linear regression to determine the strength of the four scale-specific ABR relationships. As with the LR relationships, there was no evidence of saturation in our exploratory data analysis, so we did not attempt to fit curvilinear regression models.

There are also some important differences between the LR relationship and the ABR relationship. Unlike the LR

relationship, the ABR relationship is based on the additive properties of alpha and beta. From a mathematical standpoint, alpha and beta each comprise a portion of the total regional diversity at a given scale. Therefore, we often refer to the "contribution of alpha diversity to regional diversity" or the "contribution of beta diversity to regional diversity" to be consistent with the way in which they are calculated and were originally envisioned by Whittaker (1977) and MacArthur (1965). This phrasing does not necessarily imply causation in the biological sense; it does not indicate that the local species pool determines the regional species pool. In fact, numerous studies have provided evidence to the contrary (cf. Srivastava 1999; Blackburn & Gaston 2001).

Scale dependence of alpha and beta diversity

Testing for scale dependence in alpha (and therefore beta) richness required a statistical approach for comparing the slopes and intercepts of separate regression lines. Most procedures designed for this purpose assume that the regression lines represent independent groups or treatments (e.g. in comparing dose–response curves). However, hierarchical data do not exhibit complete independence. Instead of traditional approaches, we used a hierarchical linear model (HLM; Byrk & Raudenbush 1992, Littell *et al.* 1996; Sullivan *et al.* 1999) to test whether alpha richness exhibited scale independence (Fig. 2a,d) or scale dependence (Fig. 2b,c,e,f). HLMs are particularly useful for hierarchical and nested data because they relieve the independence assumption by incorporating variance components into the analysis (Byrk & Raudenbush 1992). In the context of HLMs, variance components operate on the assumption that measurements within the same group (in our case, a particular spatial scale) are more similar to each other than they are to measurements within other groups (spatial scales). The error estimate in our HLM therefore takes into account the variance among spatial scales as well as variance occurring within a spatial scale. This is reasonable in our situation because samples taken at one spatial scale may be influenced by a different set of ecological processes than those taken at another spatial scale. To formalize this idea, HLMs assume that each of the groups has its own intercept and slope within the hierarchical structure of the data. Therefore, the main assumption of the HLM in this study is that the slope and intercept of each scale-specific regression line are independent from one another within the hierarchical framework.

HLMs are also referred to as random coefficient models because they assume that the regression coefficients of a group represent a random departure from a population regression model (i.e. all groups combined) that is estimated from the data (Littell *et al.* 1996). Statistically significant departures of scale-specific regression coefficients (slopes or intercepts) from the population coefficients indicate scale dependence of alpha, whereas the absence of significant departures from the population regression model indicate scale independence (i.e. the scale-specific coefficients are essentially sampled from the same line).

HLMs also estimate the covariance matrix (component) between slopes and intercepts. In essence, the covariance component estimates how the slopes and intercepts of the individual regression lines covary with one another. If covariance exists, it should be accounted for in the significance tests to avoid Type I errors. The strength and importance of covariance in the data can be determined by comparing the log likelihood from a model with a covariance component to the log likelihood from a model where the covariance component is equal to zero. The difference between the two values corresponds (asymptotically) to a chi-squared distribution with one degree of freedom (Littell *et al.* 1996). We conducted HLM using PC-SAS (SAS Institute 1996) and the PROC MIXED module (cf. Sullivan *et al.* 1999).

RESULTS

General community patterns

We captured a total of 15 907 individual beetles representing 583 beetle morphospecies. We caught more individuals in the early (8662) than late (7245) sampling period, and more species in the early (467) than late (347) sampling period. The decrease in species richness is a predictable component of the study system and is due to patterns of emergence and voltinism (Gering & Crist 2000). Curculionidae (snout-nosed weevils) and Chrysomelidae (leaf beetles) were the dominant families within each sampling period.

LR relationships

All four LR relationships were linear and positive, indicating that each exhibited a pattern of proportional sampling (Table 1). Additionally, the slope coefficients of each LR relationships departed significantly from zero. However, an important nonstatistical difference between the four LR relationships was that regional richness accounted for a variable amount of local richness (Table 1; slope column).

ABR relationships

Regression analyses of the ABR relationship for each spatial scale indicated that regional richness explained a high percentage of the variation in alpha richness ($R^2 > 0.90$; Fig. 4a) and that slope coefficients of each regression line departed significantly from zero on each spatial scale as they did in the LR regressions. More importantly, the ABR

Table 1 Regression statistics and significance tests for departure of slopes from zero (H_o: slope = 0) for local–regional (LR) relationships of beetle species richness across four spatial scales. Data were collected by insecticide fogging in summer 2000 from 96 trees in a hierarchically nested sampling design where the broadest scales were represented by two different ecoregions located in southern Ohio and south-eastern Indiana (see text for details). We conducted separate regression analyses for each spatial scale

Spatial scale	Comparison	Y-int.	Slope	R^2	d.f.	Model MS	F
Broadest	Site vs. Ecoregions	−26.5	0.655	0.817	10	11490.57	44.6†
	Stand vs. Site	−8.4	0.493	0.649	46	13676.74	85.2†
	Tree vs. Stand	−2.3	0.419	0.553	190	14808.43	234.9†
Finest	Funnel vs. Tree	−0.7	0.201	0.529	166	1842.51	186.3†

†$P < 0.0001$.

analysis revealed that regional richness is comprised of alpha and beta richness in varying percentages depending upon the LR relationship being considered (Table 2).
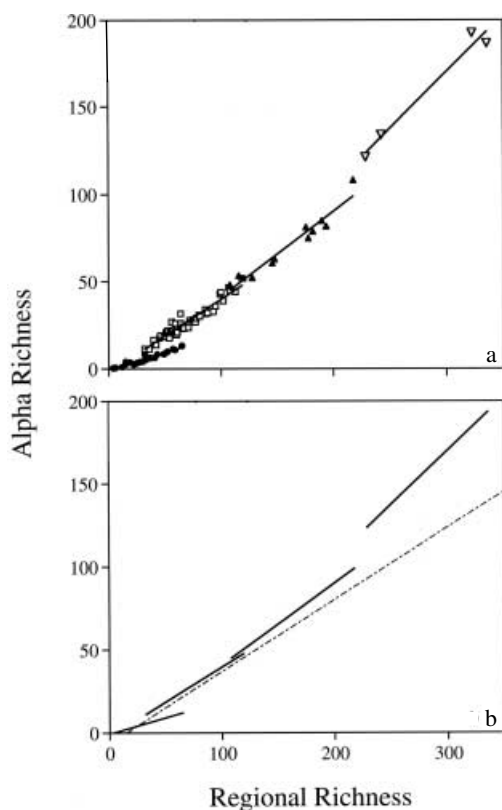

Figure 4 Regression plots of the relationship between alpha and regional richness for the four spatial scales in the study. In (a) the simple linear regression lines are shown over the points (see text and Table 1 for statistics). In (b) the points are removed and the graph shows the departure of remaining scale-specific regression lines (solid) from the null (i.e. population) regression line (irregular hash) as determined by the HLM (see text for details). The slope of the line at the finest spatial scale is significantly lower than the population regression line, whereas the slope of the line at the broadest spatial scale is significantly higher than the population regression line (see Table 2).

Scale dependence of alpha and beta

Tests for scale independence of alpha richness using HLMs identified a significant covariance component in the covariance matrix between intercepts and slopes. The covariance component of this model was negative, indicating an increase in slope coefficients and a corresponding decrease in intercept values for the regression lines. The log likelihood of the HLM with the covariance component (460.4) and that with a covariance component of zero (464.1) differed by 3.7, which was significant under a chi-squared distribution (d.f. = 1, $P < 0.05$). Thus, we used the more conservative HLM, which incorporated the covariance component into the analyses.

The HLM identified a population regression line with a y-intercept of − 6.468 and a slope of 0.433, which represented a significant departure from zero (d.f. = 3, t = 4.98, $P < 0.02$; Fig. 4b). The scale-specific deviations of intercepts and slopes from the population regression line showed varied results (Table 3, Fig. 4b). There were no significant departures of the scale-specific intercepts from the population intercept. However, the slopes of regression lines at the broadest spatial scale (ecoregion richness vs. site alpha richness) and the finest spatial scale (tree richness vs. funnel alpha richness) departed significantly from the slope of the population regression line. The slope coefficient of the line at the broadest spatial scale (0.611) was larger than the slope of the population regression line, whereas the slope coefficient of the line at the finest spatial scale (0.205) was smaller than the slope of the population regression line (Table 3, Fig. 4b).

DISCUSSION

The LR and ABR relationship

The first objective of this study was to demonstrate and discuss the use of the alpha–beta–regional (ABR) relationship in the context of LR relationships. This objective is best accomplished by first considering the regression results on the LR relationship. Our findings identified significant linear (i.e. non-saturating) patterns for each of the four LR

Table 2 Results from the analysis of alpha–beta–regional (ABR) relationships indicating the percentage into which regional richness was partitioned into alpha and beta components on four spatial scales. For comparison purposes, the qualitative results from the LR analysis are also presented in the table. The percentages of alpha and beta were determined by applying additive partitioning to the "regional" beetle species richness within an individual spatial scale (see text for details). Data were collected by insecticide fogging from May to August 2000 from 96 trees in a hierarchically nested sampling design where the broadest scales were represented by two different ecoregions located in southern Ohio and south-eastern Indiana (see text for details)

Spatial scale	Comparison	LR results	ABR results Alpha (%)	Beta (%)
Broadest	Site vs. Ecoregions	Linear	21	79
	Stand vs. Site	Linear	42	58
	Tree vs. Stand	Linear	49	51
Finest	Funnel vs. Tree	Linear	61	39

Table 3 Results from hierarchical linear models (HLMs) used to test for departures of scale-specific slopes and intercepts from the slope and intercept of a population regression line (i.e. null line) estimated from the data. The slope and the intercept of the population regression line were 0.443 and −6.47, respectively. There were 80 degrees of freedom for each comparison. Data were collected by insecticide fogging in summer 2000 from 96 trees in a hierarchically nested sampling design where the broadest scales were represented by two different ecoregions located in southern Ohio and south-eastern Indiana (see text for details)

Regression line	Y-int.	Slope	t (Y-int.)	t (slope)
Site vs. Ecoregions	−14.08	0.611	−1.76	2.04*
Stand vs. Site	−8.32	0.492	−0.46	0.67
Tree vs. Stand	−2.66	0.424	1.04	−0.11
Funnel vs. Tree	−0.82	0.205	1.55	−2.54*

*$P < 0.05$.

relationships, indicating that local species richness is dependent upon regional richness in a manner consistent with proportional sampling (Cornell 1993). Non-saturating relationships are common in studies of local and regional richness (Srivastava 1999), and are frequently interpreted as evidence for non-interactive communities (Cornell 1985; Caley & Schluter 1997). Models of non-interactive communities suggest that density-independent fluctuations, limited dispersal abilities (Strong *et al.* 1984), and open niche space combined with random colonization (Caswell & Cohen 1993) are processes that can produce proportional sampling. Cornell (1985, p. 1256) concluded that local communities of cynipine wasps on *Quercus* were regulated by, "…

distribution, host specificity, and dispersal ability." Beetles on temperate and tropical trees exhibit high degrees of host association (Mawdsley & Stork 1997; Wagner 1997; Gering & Crist 2000), which could produce patterns of proportional sampling by reducing interspecific interactions among beetle species on different host plants. But the other processes that produce unsaturated patterns – especially density-independent population fluctuations and random colonization – are also characteristic of insect populations (Price 1997). Obviously, we can not identify the process(es) that generate(s) proportional sampling without conducting further manipulative studies (Cornell 1993) or subdividing the data set into guilds or functional groups (e.g. Cornell 1985). Our only conclusion for each of the four LR relationships can be that local interactions were not strong enough to limit local richness (Cornell 1993). Hence, we are left with four LR relationships and little explanation for the processes that might be determining the patterns.

Furthermore, their superficial resemblance in pattern (all proportional sampling) may lead to the conclusion that the relationship between local and regional richness is caused by the same processes in each scenario. However, the analysis of the ABR relationship revealed that each pattern of proportional sampling was produced by a different combination of alpha and beta richness (Table 2). Alpha richness accounted for 21–61% of the regional richness, whereas beta richness accounted for 39–79% of the total richness. Since alpha and beta have a strong conceptual meaning for ecologists and are generally associated with particular ecological processes (e.g. dispersal increases alpha and decreases beta), it may be possible to use the ABR relationship to interpret the LR relationship better. For example, Loreau (2000) describes a scenario where the balance between dispersal and local competition in a mosaic of patches can shift the contributions of alpha and beta diversity in different areas. Perhaps comparing the empirical ABR relationships from a number of different areas with predictions based on modelling the dynamics of dispersal and competition will reveal if these processes are driving the LR patterns. Similarly, Loreau & Mouquet (1999) used elements of metapopulation models to show that the homogenizing force of regional dispersal can increase alpha values so that beta values become relatively unimportant in determining the regional diversity. As before, linking alpha and beta in empirical ABR relationships to predictions based on metapopulation models may allow us to more fully understand the processes that produce the LR pattern. The main advantage of the ABR relationship is that it decomposes the LR relationship and makes it possible to integrate – in a manner that surpasses inference – ecological ideas (e.g. metapopulations, source–sink models) to explain the LR patterns.

A second advantage of the ABR relationship is that it overcomes the issue of spatial pseudoreplication that is

common in studies of LR relationships. Srivastava (1999) suggested plotting a mean value of local richness for every value of regional richness to avoid spatial pseudoreplication. Fortunately, alpha richness is a mean value (Allan 1975; Lande 1996) that corresponds to the average number of species within sampling units on a given scale, so its use in regressions against regional richness is more statistically appropriate.

In summary, we have explained how the ABR relationship is based on additive partitioning and shown how it can be used to supplement the interpretation of the LR relationship by linking alpha and beta diversity to a literature base and modelling approaches that may be useful in further explaining LR patterns. We also noted that the ABR relationship overcomes spatial pseudoreplication by using alpha, a mean value. With the advent of additive partitioning (Allan 1975; Lande 1996; Wagner *et al.* 2000; Gering *et al.* in press), diversity components have become more tangible to ecologists and should experience an increase in applied use in forthcoming years. We believe that the ABR approach to investigating LR relationships represents an important extension of additive partitioning and could benefit ecologists in identifying the processes that determine community diversity and composition.

Scale dependence of alpha and beta

The second objective of this paper was to investigate how the contributions of alpha and beta to regional diversity change as a function of spatial scale. There are few predictions about how alpha and beta diversity change across spatial scales (but see Huston 1999). Scale independence of alpha and beta would be unlikely because ecological processes are scale dependent and have transitions which could in turn affect the balance between alpha and beta diversity on a given scale (Wiens 1989; Peterson & Parker 1998). Constant scale-dependence would also be unlikely unless there were gradual transitions in ecological processes that could generate constant and predictable changes in the contribution of alpha and beta to regional richness. Irregular scale dependence of alpha diversity is the most likely of the three possibilities and has already been alluded to by other authors. Wiens (1989), for example, conceptualized scale domains, or spatial scales over which ecological patterns and processes do not change or change monotonically. Scale domains are separated by abrupt scale transitions that occur when a set of ecological patterns and processes are replaced by another set of patterns and processes. It is at these transition points where non-monotonic changes are evident. Across the range of scales in a study, these transitions could result in a pattern similar to the irregular scale dependence in Fig. 2 (c,f). According to the population regression line [alpha richness = −6.47 + 0.443(regional richness)] estima-

ted by the HLM, alpha richness should have accounted for c. 44% of the regional richness across all spatial scales. However, we found that alpha richness accounted for a significantly larger portion (c. 60%) of the regional richness at the broadest scale while accounting for a significantly smaller portion (c. 20%) of the regional richness at the finest spatial scale. We consider this evidence for irregular scale dependence of alpha (and therefore beta) in this system (Fig. 4b) and conclude that the contribution of alpha and beta to regional richness can change significantly and in a nonlinear manner across spatial scales.

Moreover, the contribution of the diversity components can change to the extent that there is a switch in relative dominance across scales. This becomes apparent when alpha and beta are placed on the same graph (Fig. 5). The "alpha-dominant" and "beta-dominant" systems (Fig. 2) in our hypotheses were characterized by continual dominance of one component across the range of scales, although there was allowance for the extent to which the component was dominant (e.g. Figures 2b,d). However, our empirical data indicate a clear shift in dominance between alpha and beta components across the range of spatial scales (Fig. 5). This switch in dominance has been theorized by other authors. Loreau (2000), for instance, stated that alpha richness should decrease at fine spatial scales because the number of individuals is reduced and strong direct interactions could dominate the community, thereby increasing beta richness. The reverse is also true: the importance of alpha richness to overall regional richness should be more important at broader scales because local interactions are less important or undetectable (Huston 1999; Loreau 2000).

These explanations are realistic for our system because there is evidence that interspecific interactions (e.g. competition, facilitation, and resource sharing) among beetle species (and among other insect taxa) occur within tree crowns, which could decrease alpha diversity at the scale of the tree crown. For example, species of bark beetles (Curculionidae: Scolytinae) within spruce tree crowns avoid competition by using different parts of the tree (e.g. trunk vs. branches) based upon species-specific preferences for bark thickness. Exclusion experiments have also shown intense competitive interactions between cerambycids (long-horned beetles) and scolytids for gallery space, while resource sharing was evident in how gall dwellers (mites and flies) and leaf miners (weevils) partitioned leaf space on beech trees (Dajoz 2000). Shmida & Wilson (1985) also pointed out that niche relations are the strongest determinant of diversity at fine spatial scales (< 10 m^2). However, these interactions are probably not evident at broader spatial scales (e.g. sites within ecoregions), where processes such as dispersal and colonization–extinction dynamics structure the communities. In fact, dispersal of species into sites where
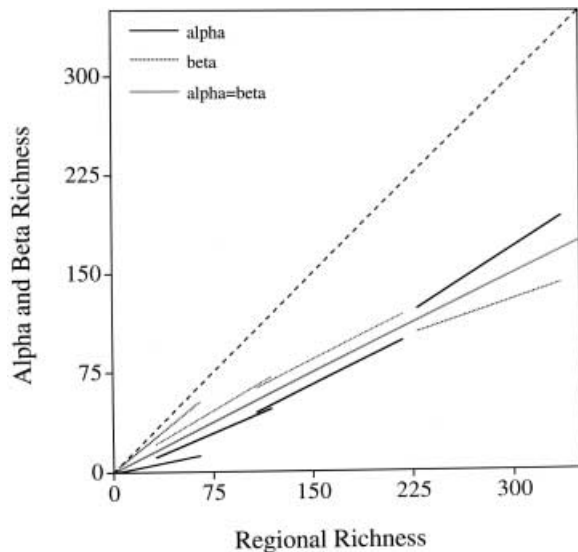
Figure 5 Graph showing the relative contributions of alpha (solid lines) and beta (stippled lines) richness to regional richness. As in the preceding figures, the hashed line represents the points on the graph where the sum of alpha and beta diversity equal the regional diversity, whereas the light grey line represents the plane at which alpha and beta each account for half of the regional diversity. Note the switch in dominance from beta to alpha at the broadest spatial scale.

they cannot be self-maintaining (i.e. the mass effect; Shmida & Wilson 1985) almost always results in increased alpha diversity (but see Shmida & Wilson 1985, p. 7) and is one mechanism, among others, that operates at broad spatial scales ($> 10^3$ m^2).

Although the scale-specific effects of the processes we described above could explain the switch in dominance between alpha and beta diversity across scales, we also acknowledge that sampling phenomena and/or statistical properties of the data set may also be causing the pattern we observed. For example, the slope of the regression line on the finest scale might be produced by differences in the geographical size of our region (similar to "pseudosatura-tion"; Srivastava 1999). Additionally, the spatial scales may have differed in the effectiveness in which they were sampled (i.e. the point reached on the species accumulation curve), such that sampling alone could lead to apparent differences in alpha and beta diversity across scales. Differences in the biogeographical history of the ecoregions may also contribute to the pattern we observed in the study (Hugueny 1997). Subsequent studies on scale dependence of diversity components should help reveal the prevalence and causes of the pattern we have documented in this study.

Finally, although the samples at the finest spatial scale (within funnels) do not represent real biological communities,

it is possible that the fine-scale interactions that occur within the tree crown only become apparent by examining data at the spatial scale of the funnel. In a general statement of this idea, Huston (1999) observed that local interactions may not be apparent unless researchers examine the scales on which the target taxa are likely to interact. Interspecific interactions among beetles probably occur within the spatial scale of a tree crown (c. 20–100 m^2) and not over broader scales (e.g. within stands or sites). Therefore, studies that restrict their analyses to broad scales (e.g. Caley & Schluter 1997) may be overlooking and underestimating important local interactions (Westoby 1998; Huston 1999; but see Caley & Schluter 1997), so future studies should use a broad range of spatial scales to be able to detect changes in the ABR relationship.

In summary, we have documented empirical evidence of irregular scale dependence in alpha richness (and therefore beta richness) using HLMs and found that diversity components could switch dominance over the range of spatial scales. There is considerable indirect evidence to suggest that this pattern may be related to changes in dominant ecological processes such as inter-specific interactions and colonization–extinction dynamics. However, the scale dependence of diversity components has not been well explored, so we cannot eliminate the possibility that sampling phenomena and/or statistical properties of hierarchical data could also generate the patterns we observed. Regardless, it is obvious that further studies of scale dependence of diversity components will strengthen our understanding about the additivity and scale dependence of species diversity in biological com-munities.

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