A critical analysis of the ubiquity of linear local–regional richness relationships

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Despite theoretical criticisms, the ubiquity of linear relationships between local and regional species richness has long been used to justify it as a valid framework to conclude that local communities are not saturated with species. However, we reanalyzed published studies with a new unbiased method and found no prevalence of linear relationships and more than 40% of misclassifications, including textbook examples. We thus conclude that the prevailing argument in favor of associating a valid ecological interpretation to local–regional species richness plots, its ubiquity, is not sustained, and that ecologists could use for instance metacommunity theory to make inference on the strength of local and regional processes.

Identifying the relative importance of regional and local processes to local species diversity is a central issue to many questions in basic and applied ecology. One widely-used method is to plot local species richness against its regional richness to infer whether regional or local processes determine local diversity. However, this method increases the tendency to find regional prevalence as suggested by a recent simulation. We reanalyzed studies in the literature with an unbiased method and found no prevalence of either regional or local processes. In addition, almost 40% of the studies and 50% of the ecology textbook examples using the traditional method were misclassified. Our findings reinforce the need of alternative, novel tools identified by for instance metacommunity theory to go beyond the studies of local–regional relationships in the ecological literature that focus on the interdependence of regional and local processes.

Since the early development of ecology as a discipline, ecologists have been interested in explaining the processes driving local community richness (Elton 1946, Hutchinson 1959, MacArthur 1965, Ricklefs 1987). This interest started by focusing on local interactions among coexisting species and has been changing to a regional-based approach that considers biogeographical, evolutionary and historical processes as drivers of local richness (Ricklefs 1987, Huston 1999, Srivastava 1999, Harrison and Cornell 2008, Vellend 2010). Some proponents of the regional–historical viewpoint argue that the distribution of local communities in a given point is idiosyncratic and that a more predictive theory should consider the ecogeographic distribution of species throughout the region (Ricklefs 1987, 2004, 2008b). Whether processes acting at regional or local scales predominantly determine local community composition is still subject to much debate in the literature (Ricklefs 1987, Cornell and Lawton 1992, Shurin and Srivastava 2005, Harrison and Cornell 2008, Vellend 2010; but see Cottenie 2005), with important implications for ecological theory and conservation (Huston 1999, Srivastava 1999, Harrison and Cornell 2008, Vellend 2010).

To test the relative importance of regional and local processes, the traditional method consists of plotting local species richness (LSR) against its regional species richness (RSR) (Cornell and Lawton 1992, Srivastava 1999, Hillebrand and Blenckner 2002). When regional processes control LSR, this method predicts that communities will be unsaturated with species, since adding more species to the regional species pool will result in an increase in LSR. On the other hand, when local interactions limit local richness independent of the RSR, communities should be saturated with species and LSR will approach an upper asymptote (Fig. 1, Ricklefs 1987, Cornell and Lawton 1992, Srivastava 1999).

However, there has been several types of criticisms of LSR–RSR plots to assess the relative roles of regional versus local processes. The main criticism is that even in communities under strong local process control (e.g. competition), linear relationships between RSR and LSR can be found (Fox et al. 2013).
2000, Loreau 2000, Shurin et al. 2000, Hillebrand 2005, Fox and Srivastava 2006). For example, several studies have found that ‘unsaturated’ zooplankton communities are strongly controlled by local interactions (Shurin et al. 2000), which demonstrate the limited applicability in inferring processes from regressions between LSR–RSR (Shurin et al. 2000, Shurin and Srivastava 2005, Hillebrand and Blenchker 2002, Szava-Kovats et al. 2012). In addition, estimates of LSR and RSR are generally not independent (Loreau 2000), which also increases the predominance of linear relationships, especially in cases where local scale is too large compared to the regional scale (Hillebrand and Blenchker 2002, Shurin and Srivastava 2005). Other criticisms pointed out that the traditional method is sensitive to issues of pseudoreplication, the arbitrary choice of local and regional area, autocorrelation and body size of the organisms (Griffiths 1999, Srivastava 1999, Loreau 2000, Hillebrand and Blenchker 2002, He et al. 2005, Hillebrand 2005, Szava-Kovats et al. 2012).

The traditional method used to distinguish between unsaturated and saturated communities compares the best fit (generally the largest F-statistic) of linear and polynomial regression models (Ricklefs 1987, Cornell and Lawton 1992, Srivastava 1999). If the linear regression presents the best fit to the data, the community is considered unsaturated. However, if the polynomial regression presents the best fit, the community is considered saturated (Srivastava 1999), as shown in Fig. 1. It has been suggested that the linear and polynomial regressions used to distinguish between saturated and unsaturated communities may actually have insufficient power to differentiate both communities (Hillebrand and Blenchker 2002). In addition, the traditional method use a constrained operational space, which increases the correlation between the components to be compared (Szava-Kovats et al. 2012).

To circumvent the statistical artifacts of the traditional method, Szava-Kovats et al. (2012) proposed a method based on log-ratio models (Fig. 1), that uses an unconstrained operational space. This unconstrained behavior enables RSR and LSR to vary independently without correlation (Szava-Kovats et al. 2012). The authors argued that the log-ratio method has the following methodological improvements: 1) the elimination of autocorrelation and spurious correlation, 2) a null-hypothesis for species saturation, 3) the use of a single model to distinguish for linearity or non-linearity, and 4) the mitigation of the effect of arbitrary selection of local and regional area (Szava-Kovats et al. 2012). They compared their model with the traditional model by simulating datasets with different degrees of curvature and LSR:RSR ratio. The results indicated that the log-ratio method successfully reproduced slopes (non-linearity), while the traditional method did not detect non-linearity in the majority of simulations, suggesting that their new method is unbiased and less sensitive than the traditional method.

The advantages of the log-ratio method relative to the traditional method have at least two major implications to studies testing local–regional species richness relationships. First, since the statistical artifacts of the traditional method increase the tendency to linearity between LSR and RSR (Szava-Kovats et al. 2012), studies using this method will be biased towards the conclusion that regional (i.e. historical) processes are the main forces driving local community structure (Ricklefs 1987, 2008b, Cornell and Lawton 1992). Second, the possible misclassifications of studies with the traditional method can lead to incorrect conclusions about the importance of local and regional processes in the ecological literature. The purpose of this paper is not to provide an extensive review to those drawbacks (Cornell and Lawton 1992, Caley and Schluter 1997, Srivastava 1999, Hillebrand

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Figure 1. Theoretical curves obtained by regressing local versus regional species richness in the traditional method (A) and regressing ln (RSR) against ln (LSR/(RSR–LSR)) in the log-ratio method (B). In communities fitted by type 1 models (unsaturated), local richness is dependent of the regional richness and other local ecological factors are weak or absent. In communities fitted by type 2 models (saturated), local richness is independent of the regional richness, which means that local biotic interactions as well as other ecological factors limit local species richness. The transformations performed by the log-ratio method compared to the conventional x- (RSR) and y- (LSR) axes change the traditional interpretation of saturation (non-linear) and unsaturation (linear) relationships (B). However, Szava-Kovats et al. (2012) proposed an inverse transformation so that one can compare the result of the log-ratio method with the traditional method. The 1:1 line presents the boundary in which local richness equals regional richness. In the traditional method, values above and below this line present, respectively, non-operational and operational spaces. In the log-ratio method there is no operational space (see text for details about the operational space). Adapted from Griffiths (1997) and Szava-Kovats et al. (2012).
and Blenckner 2002, Shurin and Srivastava 2005), but instead we aimed to 1) re-evaluate previous conclusions (i.e. the dominance of unsaturated patterns in the literature) in light of a new, unbiased statistical method, 2) evaluate the potential implications of the statistical drawbacks that the traditional method has to ecology and to studies interested in local–regional species richness relationships, and 3) discuss the interpretative problems of regressing local versus regional richness to infer processes driving community structure.

Methods

We searched studies in the database of Web of Science (isiknowledge.com) and Google Scholar (scholar.google.com.br). We used the keywords 'local richness AND regional richness AND satur* BY', 'local richness AND regional richness AND unsatur*', 'local diversity AND regional diversity AND satur*', 'local diversity AND regional diversity AND unsatur*', In addition, we examined the references of the main reviews in the topic (Cornell and Lawton 1992, Caley and Schluter 1997, Srivastava 1999, Hillebrand and Blenckner 2002), as well as the articles that cited these four reviews in the Web of Science database. We found 47 studies (one unpublished) that analyzed 113 ecological communities (Supplementary material Appendix 1 Table A1). We consider as a metacommunity each data set (provided as figures) in which authors analyzed the relationship between local (LSR) and regional species richness (RSR) with the traditional method.

The inclusion criterion was that the studies should use the traditional method to test for species saturation, i.e. the regression of local species richness (LSR; dependent variable) against its regional species richness (RSR; explanatory variable) (Srivastava 1999). In addition, the plots of LSR–RSR (as in Fig. 1) should be provided. We also obtained predictor variables of the organisms and system of each study, such as upper taxa (i.e. Kingdom, Phylum or Superphylum, such as cnidarians, invertebrates, plants, protozoan or vertebrates), trophic position (autotrophs, detritivores, herbivores, predators, saprophages or suspension), thermoregulation (ectothermic/homothermic), adult dispersal type (motile or sessile), realm (aquatic or terrestrial), hemisphere (Northern, Southern or both), study design (experimental, observational, or compiled data set), and scale (small, medium, large, continental or worldwide). Scale was defined as: 1) ‘small’ if the studies were performed within the same biome and the distance among their replicates was smaller than 500 km; 2) ‘medium’ as the studies performed within the same biome, but with the distance among their replicates higher than 500 km; 3) ‘large’ as the studies performed in different biomes, but that was not as large as the continental scale; 4) ‘continental’ included studies that presented data in the whole continent; and the 5) ‘worldwide’ scale were studies that collected data in most continents. We obtained those variables because it has been hypothesized that some predictor variables could explain whether some communities are predominantly saturated or unsaturated (Cornell and Harrison 2013).

We used the R-language environment (R Development Core Team) and the package ‘digitize’ (Poisot 2010) to extract data sets from figures. We tested the reliability of data extraction by comparing our scatterplots with the extracted LSR and RSR values to the original figures. We then regressed the original values against the extracted ones and found R²-values higher than 0.98. We did not use studies that applied log–log regressions (n = 2), residual local richness versus regional richness (n = 4), or other methods (n = 4). In addition, we limited our re-analysis to those studies with more than five replicates (n = 2 studies with less than five replicates). Thus, we re-analyzed 113 communities (90.4%) from the 125 found.

We first analyzed the extracted data with the traditional method by regressing the local species richness (y-axis) against the regional species richness (x-axis). We then reanalyzed the same data set with the log-ratio method proposed by Szava-Kovats et al. (2012): first, the regional richness is partitioned in a component of α-diversity (LSR) and of β-diversity (RSR–LSR). Then, these components are transformed by the additive log-ratio model y = ln (LSR/(RSR–LSR)). The relationship between LSR and RSR is tested by regressing the y-axis ln (LSR/(RSR–LSR)) on ln (RSR) with an ordinary least square regression (Szava-Kovats et al. 2012). The transformations performed by the log-ratio method compared to the conventional x- (RSR) and y- (LSR) axes change the traditional interpretation of saturation (non-linear) and unsaturation (linear) relationships. However, Szava-Kovats et al. (2012) proposed an inverse transformation to compare the result of the log-ratio method with the traditional method: regression results with negative slopes in the log-ratio method will have a saturated trend in the traditional method, while regression results with non-significant slopes will have a linear trend in the traditional method (Fig. 1). Although the x and y axis are different between the two methods, it is still possible to re-transform the data in order to access the traditional interpretations of saturation and unsaturation (Szava-Kovats et al. 2012).

Considering that the traditional method has several drawbacks (Srivastava 1999, Hillebrand and Blenckner 2002, Hillebrand 2005, Szava-Kovats et al. 2012), we consider as ‘misclassified’ those metacommunities which were classified as either saturated or unsaturated in the traditional method, but had the opposite classification with the unbiased log-ratio method. We used generalized linear models (GLM) with binomial distribution to test if the misclassifications are associated to the predictor variables (system features and organism traits). We used GLMs to test if the predictor variables explain saturated or unsaturated patterns.

Results and discussion

Seventy percent of the studies found unsaturated communities, while 30% found saturated communities with the traditional method (χ² = 16.66, p < 0.0001). The bias toward linearity was pervasive for vertebrates (which 85% of the studies found unsaturated patterns) and plants (75%), for observational (78%) and continental-scale studies (87%), and for both aquatic (73%) and terrestrial realms (68%). Thus, as expected, most studies using the traditional method concluded that regional processes are the main drivers of local richness (Fig. 2, Supplementary
et al. 2012), such misclassification obtained in studies using the traditional method has potential negative effects on the current ecological literature, because those biased conclusions have been drawn in almost 40% of the studies (Supplementary material Appendix 1 Table A1, A2). Thus, much of the current ecological thinking concerning local–regional relationships may have been rooted in weak or biased evidence. For instance, Ricklefs (1987) claimed that ecologists should use a regional/historical perspective to resolve many issues in community ecology (see also Ricklefs 2004, 2008b). One of his arguments was that ‘local diversity bears a demonstrable dependence upon regional diversity’; he used the traditional method and found an unsaturated pattern for Caribbean bird communities. However, when we reanalyzed this data set a saturated pattern was found (Supplementary material Appendix 1). The consequences of the unsaturation bias are also evident in the information brought by four classical ecology textbooks (Ricklefs and Miller 1999, Ricklefs 2008a, Begon et al. 2006, Krebs 2008) and has been used in a recent important review of ecological theory (Vellend 2010; see also Cornell and Harrison 2013); 50% of the examples of LSR–RSR plots were misclassified. The statistical drawbacks were seldom considered in those textbooks and the general idea related to LSR–RSR relationships is that unsaturated patterns are the most pervasive in ecological communities. For instance, one of the ‘Key concepts’ in Krebs (2008) is ‘Local species richness tends to increase linearly with regional species richness, suggesting that local communities are never saturated with species’ (p. 457). The content of four of the most widespread ecology textbooks reinforces the need of new paradigms concerning the relative importance of local and regional processes in structuring communities.

Figure 2. Comparison of the results of local–regional richness plots of 47 studies (113 metacommunities) that used the traditional method with the results reanalyzed with the log-ratio method.

material Appendix 1 Table A2). The prevalence of unsaturated patterns in the current literature has added more focus on community ecology as a regional/historical science (Ricklefs 1987, 2004, 2008b, Cornell and Lawton 1992). However, we reanalyzed those studies with the log-ratio method and found no prevalence of either unsaturated (53.1% of the results) or saturated (46.9%) communities ($\chi^2 = 0.44$, $p = 0.501$) (Fig. 2). There was no prevalence of one specific pattern when we compared upper taxa, trophic position, thermoregulation, adult dispersal type, realm, hemisphere, study design and scale (Supplementary material Appendix 1 Table A2). These results challenge the apparent dominance of unsaturated communities in the literature (Ricklefs 1987, Cornell and Lawton 1992) and emphasize that local and regional processes are probably interacting to determine both local and regional diversity (Lewinsohn 1991, Lortie et al. 2004, Brooker et al. 2009, Burgess et al. 2010). This view has been voiced in recent studies showing that local processes affect broad-scale ecological patterns (Greve et al. 2012, Lessard et al. 2012). Furthermore, there has been no predictor variable (e.g. organism’s trophic position, realm) that potentially explain saturated or unsaturated patterns (but see explanations of Cornell and Harrison 2013 for a different point of view).

By comparing the results between the traditional and log-ratio methods we found that 38% of the communities that were considered either unsaturated or saturated by the traditional method were misclassified (Fig. 2, Supplementary material Appendix 1). Indeed, this misclassification was not related to any predictor variable, such as realm, organism trophic position, thermoregulation, hemisphere, study design, or scale. Besides the bias toward linearity (as shown in our study and simulations of Szava-Kovats et al. 2012), such misclassification obtained in studies using the traditional method has potential negative effects on the current ecological literature, because those biased conclusions have been drawn in almost 40% of the studies (Supplementary material Appendix 1 Table A1, A2). Thus, much of the current ecological thinking concerning local–regional relationships may have been rooted in weak or biased evidence. For instance, Ricklefs (1987) claimed that ecologists should use a regional/historical perspective to resolve many issues in community ecology (see also Ricklefs 2004, 2008b). One of his arguments was that ‘local diversity bears a demonstrable dependence upon regional diversity’; he used the traditional method and found an unsaturated pattern for Caribbean bird communities. However, when we reanalyzed this data set a saturated pattern was found (Supplementary material Appendix 1). The consequences of the unsaturation bias are also evident in the information brought by four classical ecology textbooks (Ricklefs and Miller 1999, Ricklefs 2008a, Begon et al. 2006, Krebs 2008) and has been used in a recent important review of ecological theory (Vellend 2010; see also Cornell and Harrison 2013); 50% of the examples of LSR–RSR plots were misclassified. The statistical drawbacks were seldom considered in those textbooks and the general idea related to LSR–RSR relationships is that unsaturated patterns are the most pervasive in ecological communities. For instance, one of the ‘Key concepts’ in Krebs (2008) is ‘Local species richness tends to increase linearly with regional species richness, suggesting that local communities are never saturated with species’ (p. 457). The content of four of the most widespread ecology textbooks reinforces the need of new paradigms concerning the relative importance of local and regional processes in structuring communities.
Conclusion and future directions

While the traditional LSR–RSR relationships have been instrumental in ecology theory to recognize the joint importance of local and regional processes (Harrison and Cornell 2008), Srivastava (1999) also stated that ‘it is evidently easy to reach the wrong conclusion about species saturation by analyzing local–regional richness plots’. Our review supports this assertion and the conclusions of several studies (He et al. 2005, Hillebrand 2005, Shurin and Srivastava 2005) that the results of the traditional method should be treated with caution. Moreover, we also removed another argument in favor of using local–regional richness plots: the apparent ubiquity of linear relationships, which at first glance would suggest that important processes are potentially responsible for these results. By reanalyzing 113 LSR–RSR plots from independent studies using an unbiased statistical method (log-ratio transformations), we conclude that almost 40% of the studies that used the traditional method reached wrong conclusions and that neither unsaturated nor saturated pattern are predominant in ecological communities. We argue that instead of a unidirectional effect of regional process cascading to local communities, both regional and local processes interactively influence each other (Burgess et al. 2010).

Based on our re-analysis and criticisms of previous studies (Loreau 2000, Shurin et al. 2000, He et al. 2005, Hillebrand 2005), it is not likely that studies of LSR–RSR relationships using the traditional method enable an unbiased test of relative importance of local and regional processes. Maybe more importantly, even when using a potential improved and unbiased method, the main concern about local–regional species richness plots makes the inference of ecological processes unwarranted (Shurin et al. 2000, Hillebrand and Blenckner 2002, He et al. 2005). We speculate that the mean reason for the lack of reliable conclusions from LRS–RSR relationships is actually caused by the not including relevant information on these local and regional processes into the analyses. We suggest that, instead of focusing solely in local–regional richness plots to infer processes from patterns, additional approaches should be used to really understand the drivers of local community structure. Metacommunity theory provides a much more powerful framework to disentangle both local and regional determinants of local diversity in both marine and terrestrial systems. – Oikos 122: 288–297.

Cottenie, K. 2005. Integrating environmental and spatial processes with observational data with actual information on local environmental and dispersal processes included in the analyses. While the statistical issues surrounding this methodology are still hotly debated (Gilbert and Bennett 2010), this test is flexible enough to add more specific information on environmental and dispersal variables and thus illustrates that metacommunity theory and its applications are a powerful approach to study and model local and regional dispersal processes (Logue et al. 2011).

Interestingly, recent theoretical developments on the evolutionary aspects of metacommunity theory (Jocqué et al. 2010) illustrated the potentially important reciprocal relationships between local and regional diversity. They thus proposed that conceptually the axes in LRS–RSR relationships can also be flipped around. Local processes (for instance, tradeoffs between ecological specialization and dispersal) could be an important driver of regional diversity patterns. To incorporate evolutionary aspects of regional processes into metacommunity theory is the next big step in this research program in community ecology. Peres-Neto et al. (2012, for instance, suggest one way to use evolutionary information when studying spatial and environmental processes. Their proposed methodology is obviously more data intensive and computationally demanding compared to LSR–RSR plots, but the inferences will be much richer and more detailed as well. While these ideas are currently actively developed, we hope that they will soon make their way into standard ecology textbooks, and replace the potential biased methods and concepts that are still part of the standard ecological curriculum.

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Supplementary material (available as Appendix oik-00305 at www.oikosoffice.lu.se/appendix). Appendix 1.