

Scale dependence of the local-regional diversity relationship: empirical evidence from a woody plant community

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The local-regional diversity relationship of woody plant species along an altitudinal gradient of Mt. Holomontas, Greece was studied. It was found that this relationship depends on scale, and more precisely on the difference in scale between what is considered local and what is considered regional scale of observation. When the local scale covers a large part of the region, then local diversity depends on regional diversity. When the difference in scale is large, then local diversity is independent of regional diversity. These findings highlight the limitations of the local-regional diversity relationship for inferring community saturation due to species interaction.

Key words: community saturation, local-regional diversity relationship, scale.

INTRODUCTION

Identifying the factors that control local community species richness is a central issue in community ecology (Morin, 1999). So far, several factors are known to play a role in the process. These factors can be distinguished according to the scale they operate. For example, species interactions operate at the fine (local) scale, while immigration from adjacent areas operates at the coarse (regional) scale. Ecologists have been trying to identify the relative importance of fine-scale factors versus coarse-scale factors by studying the local-regional diversity relationship. A linear relationship between regional species richness and local species richness is supposed to indicate that the local community is a random sample of the regional species pool, and that the local community is not saturated due to species interactions, thus indicating the supremacy of coarse scale factors. According to this approach in such a community, invading species will have a high probability of establishment. A curvilinear relationship reveals that as regional richness increases, local species richness attains a plateau above which it does not rise despite continued increases in regional richness. The latter type of

local regional diversity relationship is supposed to indicate a saturated community, where new species will have a low probability of establishment, and thus advocates the supremacy of fine-scale factors (Cornell & Lawton, 1992).

This method has received a lot of criticism both on empirical and theoretical grounds. Several practical difficulties, such as pseudo-replication, non-independence of regional species pools, and selection of the appropriate regression techniques, arise when trying to estimate the local-regional diversity relationship (Griffiths, 1999; Srivastava, 1999). Furthermore, studies on communities known to be significantly affected by species interactions, counter-intuitively produce linear relationships seeming to suggest non-saturated communities (Valone & Hoffman, 2002). Loreau (2000) has shown that the relationship does not indicate community saturation due to species interactions, but reflects whether the contribution of beta diversity (spatial turnover of species) to total diversity remains constant as regional diversity changes.

In this paper we estimate the local-regional diversity relationship of the woody plant species community along an elevation gradient, in order to estimate the scale dependence of the relationship.

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MATERIALS AND METHODS

The study took place on Mount Holomontas at a site located approximately 65 km southeast of Thessaloniki in Northern Greece. It is a forest managed by the Forestry Service. The area has not been burned or grazed for the previous 60 years at least. The climate is characterized as Continental-Mediterranean. The area is densely vegetated, and the dominant woody species are *Quercus coccifera*, *Q. pubescens*, *Q. ilex*, *Arbutus andrachne* and *Erica arborea*.

We sampled on two slopes (800 to 850 m above the sea level), one with eastern and the other with western aspect. Site A was located at 23° 26' 38" E, 40° 23' 06" N and site B at 23° 30' 35" E, 40° 23' 53" N. On each slope, we defined four square sampling areas, each covering 4096 m². Within these sampling areas, we superimposed a grid with a grain size of 4 m² and we recorded the woody plant species composition of each cell.

There were two problems to resolve in order to estimate a local-regional diversity relationship. These problems were a) definition of the regional species pool and b) pseudo-replication (Srivastava, 1999).

The definition of the regional species pool in practice is a difficult issue. In theory, the species pool consists of all species that could potentially colonize the study area if competitive exclusion was unimportant (Zobel, 1997). Even if we could identify the species pool for a given region, it is difficult to identify regions with independent species pools and identical habitats (Fox *et al.*, 2000). Therefore, consistent with Gering & Crist (2002), we defined the regional diversity as all the species recorded in a region, and we defined regions in a way that they represent identical habitats but contain non-independent species pools. Our definition of small areas (e.g. 16 m²) as regions may seem controversial, but in the context of the "local-regional" relationship (Cornell & Lawton, 1992; Srivastava, 1999), our aim was to stress the primacy of the *relative* difference in scale as opposed to the absolute scale of what might be considered local and regional.

On each region we superimposed a grid of cells with a size equal to that of the local scale we wanted to study. In order to resolve the issue of pseudo-replication, i.e. to obtain one estimate of local diversity for each value of regional diversity, we calculated the average species richness from all the cells in the region.

We examined the scale dependency of the local-

regional diversity relationship. Scale was defined by two characteristics, grain and extent. Grain refers to the minimum cell size and extent to the total area covered by the region. In order to examine the effect of grain, we kept the regional area constant, and altered the local area size. In other words, we considered the regional scale to be 4096 m², and we considered five scales as local, namely 1024, 256, 64, 16 and 4 m². In order to examine the effect of extent, we kept the local area size constant, and varied the regional area. For the latter approach, we assumed local scale always to be 4 m², and we considered four regional scales, namely 16, 64, 256 and 1024 m². Because the number of points increases rapidly, we only used one sampling area to build Fig. 2, but we used data from all sampling areas for fitting the lines.

Our different regional samples were not independent from each other, thus the statistical results of linear regression are not applicable. However, the least squares procedure may still be used to find the best fitting line, rather than relying on visual inspection.

RESULTS

In Fig. 1 we explore the effect of grain size; we keep the regional area constant at 4096 m², and estimate the average local species richness for local areas of size 1024, 256, 64, 16 and 4 m², respectively. For small differences in scale, local diversity is dependent on regional diversity. For example, when the grain equals 25% of the extent, the local diversity of the most diverse region is by 55% higher than that of the least diverse region. As the difference in scale between local and regional increases, the local diversity becomes independent of the regional diversity. For example, when the grain equals 0.1% of the extent, the local diversity of the most diverse region is by 1% lower than that of the least diverse region.

In Fig. 2 we explore the effect of extent; thus we keep local area constant at 4 m², while we estimate the regional diversity for regions of area 1024, 256, 64 and 16 m², respectively. Here again, we see that if the difference in scale between regional and local is small, local diversity is dependent on regional diversity, but as the scale difference increases the two variables become independent from each other.

In Table 1 we present the results of linear regression for the local-regional diversity relationship. These results verify the observations in Figs 1 and 2: as the difference in scale between local and regional

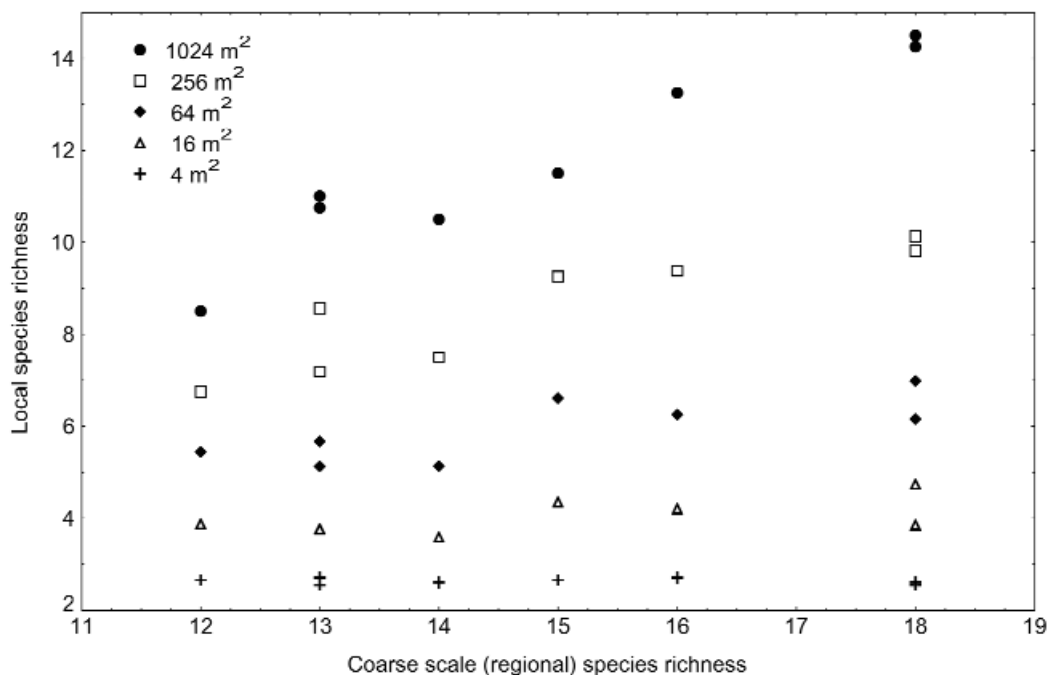


FIG. 1. Effect of grain size on the relationship between average local species richness and coarse scale (regional) species pool. The regional species pool always refers to the species observed at the coarsest sampling scheme (area 4096 m²). Local species richness refers to the average species richness observed for grids with cell size equal to 1024, 256, 64, 16 and 4 m².

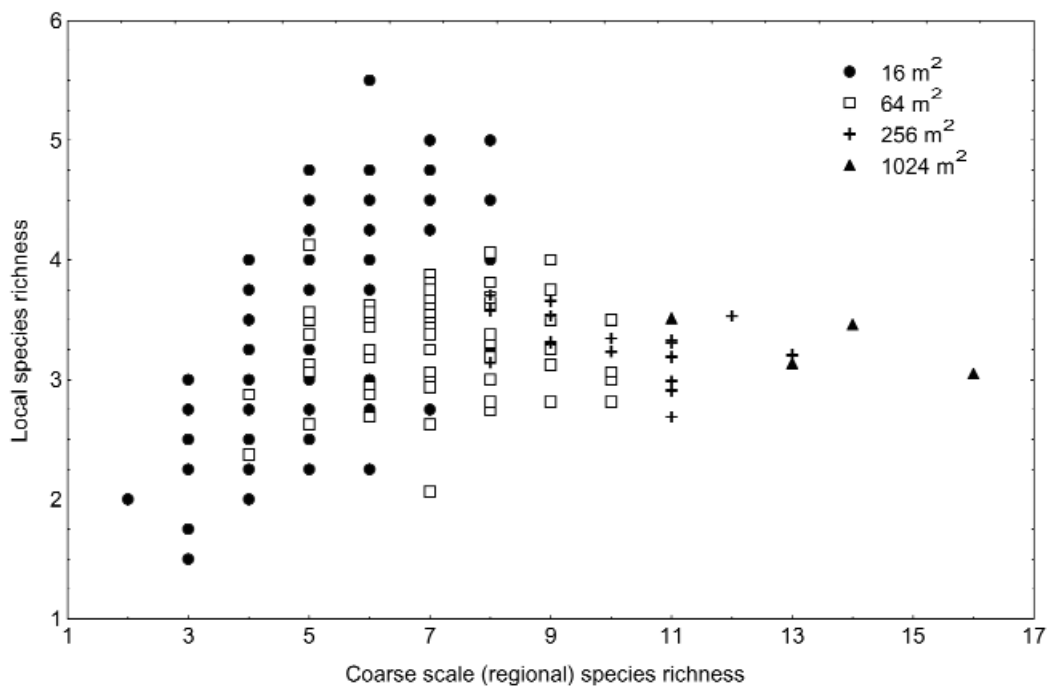


FIG. 2. Effect of spatial extent on the relationship between average local species richness and the coarse scale (regional) species pool. In this graph the local species richness always refers to the average species richness observed for grids with cell size equal to 4 m². The regional species richness has been estimated for different sampling areas equal to 1024, 256, 64 and 16 m².

TABLE 1. Linear regression analysis for the local-regional diversity relationship. On the same data set we performed the analysis defining different scales as local and regional. The correlation coefficient (R^2) is offered only as an indication of the goodness of fit, because the different regional samples are not independent

| Regional scale (m ²) | Local scale (m ²) | Slope | Intercept | R^2 |
|----------------------------------|-------------------------------|---------|-----------|--------|
| 4096 | 1024 | 0.8619 | 1.0390 | 0.9190 |
| 4096 | 256 | 0.5019 | 1.1044 | 0.8119 |
| 4096 | 64 | 0.2323 | 2.4640 | 0.5981 |
| 4096 | 16 | 0.1010 | 2.5187 | 0.3673 |
| 4096 | 4 | -0.0075 | 2.7392 | 0.0737 |
| 1024 | 4 | -0.0225 | 4.9587 | 0.4521 |
| 256 | 4 | -0.0805 | 4.0795 | 0.1927 |
| 64 | 4 | 0.0477 | 2.9630 | 0.0242 |
| 16 | 4 | 0.3515 | 1.6480 | 0.3582 |

increases the slope of the relationship tends to zero, and in some cases it even becomes negative.

DISCUSSION

Ecologists are still trying to resolve what determines local species richness. By its very nature, this subject is complex and multidimensional. Several factors are already known to play a role. Trying to isolate the influence of each factor and assess its relative importance in natural communities is usually impractical. The local-regional diversity relationship showed a lot of promise in estimating the relative importance of local factors, e.g. species interactions, versus regional factors, e.g. immigration from the regional species pool, (Cornell & Lawton, 1992; Cornell & Karlson, 1997). However, the utility of this approach, and how it has been applied, have received considerable criticism (Griffiths, 1999; Srivastava, 1999; Loreau, 2000; Valone & Hoffman, 2002). One aspect that has received particular attention is the effect that the scale of observation has on the relationship.

Srivastava (1999) was concerned with the effect of different sample sizes used to build a single local-regional diversity relationship. She suggested a method based on the species area relationship to control for these differences. This is not applicable in our case, since our sampling design already controls for area.

A major problem inherent in the construction of a local-regional diversity relationship is identifying the replicates needed to build the relationship. This method compares the species richness of a given habitat's community for independent regional species pools. If the regional species pools are independent from each other, that corresponds to samples which are separated by large geographical distances, and

usually (for example consider S. Africa vs. the Mediterranean) by different environmental conditions and different habitats, and in essence different communities. If, on the other hand, we study the same habitat, i.e. choose sites close together then, the species pool will not be independent. Furthermore, Rosenzweig's (1995) thought-provoking argument claims that habitats are not an inherent, objective, abiotic property of the region, but they are coevolved responses of organisms. Under this approach, different regional species pools will usually create different habitats. Our trade-off was to opt for the same type of habitat in the same region, i.e. with non-independent regional species pools.

Caley & Schluter (1997) explored the effect of grain size on the local-regional diversity relationship for several taxa at large spatial extent. They used two grain sizes, with local area being either 1% or 10% of the regional area. Their results indicated that in all cases the relationship was linear, but for smaller local areas the slope of the regression was lower, as we found in our data. However, their study covered considerably larger areas than our study, and the change in grain size implied the inclusion of more habitats and that is how the authors explained the observed difference in slope. This explanation does not apply in our case since we sampled in a single habitat. Furthermore, the changes in our scale of observation were not large enough to be associated with changes in environmental heterogeneity, important to organisms of the size studied.

Gering & Crist (2002) investigated the scale dependency of the local-regional diversity relationship for beetles across five hierarchical levels. Their results indicated that the local-regional diversity relationship differs from one scale to another. At coarser local

scales the slope of the relationship is steeper, compared with finer scales. A similar trend is observed in our data as well.

Karlson & Cornell (2002) studied the influence of sample size on local-regional diversity relationship. They found that very small samples did not show any dependence on regional diversity, contrary to larger scale samples that were dependent on species pool. In our study, we also observed that for large differences in scale, local diversity becomes independent of regional diversity. This is most important, because it changes the estimate of whether the local community is saturated or not. These results seem to indicate that the same community can be considered both saturated and non-saturated depending on the scale of observation. Karlson & Cornell (2002) attribute this apparent contradiction to sample size, suggesting that the small sample size represents a spatial threshold for the detection of regional enrichment. In our case, it is not the small sample size that is preventing the detection of regional influences, but the difference in scale between what is considered local and what is considered regional. Even the finest scale diversity is dependent on regional diversity if the region covers an area four times larger than the local area (i.e. when regional scale is 16 m² and local scale 4 m²). And this is a major drawback of the method since there is no strict method for defining what is local and what is regional.

Koleff & Gaston (2002) studied the avifauna of southeast Scotland and found that local species richness was positively correlated with regional species richness, when the latter was calculated for small scales, but no relationship was observed as region size increased. In their study, the area corresponding to local community was kept constant. Our findings are in agreement with theirs.

Our study supports Loreau's (2000) arguments. He has shown that the local-regional diversity relationship reflects the relative contribution of beta diversity, and thus the shape of the relationship is not necessarily related to the saturation of a community with species due to local scale biotic interactions. In accordance with his prediction, as grain size decreases space becomes a limiting resource leading to species "saturation" irrespectively of species interactions, or other fine scale factors. Also, in accordance with his prediction, when the local scale covers a large part of the region, local diversity incorporates most of the regional diversity, and thus it is dependent on the latter irrespectively of species interactions.

In conclusion, our study, in accordance with Koleff & Gaston (2002) and Loreau (2000), emphasizes the importance of scale (what is defined as local community and as region) in studies of local-regional diversity relationship, and the fact that different studies of the same community at different scales may support different models for the relationship. This study, also, confirms that the local-regional diversity relationship does not necessarily infer that a local community is saturated due to species interactions, because the relationship between species-richness at various scales is increasingly independent the larger the difference in scales is. Here, pattern does not infer process, and should be used in conjunction with other information, as Cornell & Lawton (1992) advise. However, the local-regional diversity relationship is not uninformative; it offers us an insight into the contribution of beta diversity to the regional diversity.

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REFERENCES

- Caley MJ, Schluter D, 1997. The relationship between local and regional diversity. *Ecology*, 78: 70-80.
- Cornell HV, Karlson RH, 1997. Local and regional processes as controls for species richness. In: Tilman D, Kareiva P, eds. *Spatial ecology*. Princeton University Press, Princeton.
- Cornell HV, Lawton JH, 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of animal ecology*, 61: 1-12.
- Fox JW, Mcgrady-Steed J, Petchey OL, 2000. Testing for local species saturation with non-independent regional species pools. *Ecology letters*, 3: 198-206.
- Gering JC, Crist TO, 2002. The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. *Ecology letters*, 5: 433-444.
- Griffiths D, 1999. On investigating local-regional species richness relationships. *Journal of animal ecology*, 68: 1051-1055.
- Karlson RH, Cornell HV, 2002. Species richness of coral assemblages: detecting regional influences at local spatial scales. *Ecology*, 83: 452-463.
- Koleff P, Gaston KJ, 2002. The relationship between local and regional species richness and spatial turnover.

- Global ecology and biogeography*, 11: 363-375.
- Loreau M, 2000. Are communities saturated? On the relationship between alpha, beta and gamma diversity. *Ecology letters*, 3: 73-76.
- Morin P, 1999. *Community ecology*. Blackwell Science, Maiden, Massachusetts.
- Rosenzweig ML, 1995. *Species diversity in space and time*. Cambridge University Press, New York.
- Srivastava DS, 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of animal ecology*, 68: 1-16.
- Valone TJ, Hoffman CD, 2002. Effects of regional pool size on local diversity in small-scale annual plant communities. *Ecology letters*, 5: 477-480.
- Zobel M, 1997. The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? *Trends in ecology & evolution*, 12: 266-269.