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The relationship between local and regional species richness: comparing biotas with different evolutionary histories

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The fact that the local richness of communities is not strictly dependent on local conditions but is also affected by regional richness was recently stressed (Cornell and Lawton 1992, Cornell 1993, Schluter and Ricklefs 1993). According to Cornell and Lawton (1992) local species richness (LSR) and regional species richness (RSR) are interrelated in various ways. Graphically, two endpoints along a continuum can be distinguished: proportional sampling (linear relationship between the two variables, Type I curve) and ceiling (local species richness increases with regional species richness but reaches an asymptote, Type II curve). Proportional sampling reveals unsaturated communities in which species interactions are not sufficient to limit local species richness. Cornell and Lawton (1992) considered how the relationship between LSR and RSR could be affected if species' characteristics of the regional pool change over evolutionary time. For instance they argued that the LSR/RSR ratio increases if species added, by immigration or speciation, to the regional pool are better dispersers and decreases if they are superior competitors. The same arguments hold if regional pools from areas which have undergone different evolutionary histories are compared. The major aim of this note will be to illustrate the effect that the mixing of biotas with different evolutionary histories has on the assessment of the relationship between LSR and RSR. Hypothetical as well as real examples are included, and methodological and conceptual issues will be briefly addressed.

History may obscure the LSR-RSR relationship

Up to now, community saturation studies have only integrated two spatial scales: local and regional. A region is delimited in such a way that propagules of all species are available to all of its localities over ecological time scales. Within the region, localities are the areas where ecological processes (species interaction, disturbance) predominate. Province, as defined by Rosenzweig (1995: 264), is hereby introduced as a third spatial scale. By definition, two different provinces have very few or no species in common and they are assumed to harbor independently evolved biotas. This "three spatial scale" framework taken into consideration, two catetories of community saturation studies can now be distinguished. The first category includes works in which regions are drawn from the same province and species similarity between regions is high. An example is provided by the work of Ricklefs (1987) on bird communities in West Indian islands. The second category includes works in which regions are drawn from different provinces. Lawton et al. (1993), for example, compared insect herbivore species richness on bracken between UK, USA, South Africa and New Guinea. These two kinds of studies are generally considered as equivalent with regard to community saturation testing. It is thus implicitly assumed that there is no historical effect on the LSR-RSR relationship; or in other words the LSR-RSR relationship does not differ between provinces. However, we emphasize that the mixing of regions which are highly dissimilar in species composition may introduce substantial noise in the data by increasing the likelihood that biological features affecting the LSR-RSR relationship (such as dispersal ability) are not distributed equally between regional biotas. As for a hypothetical example of how not taking into account the historical factor may obscure the results, let us consider the relationship between LSR and RSR assessed with regions belonging to three different provinces (Fig. 1). If we assume that there is no historical effect then there is only one LSR-RSR relationship.
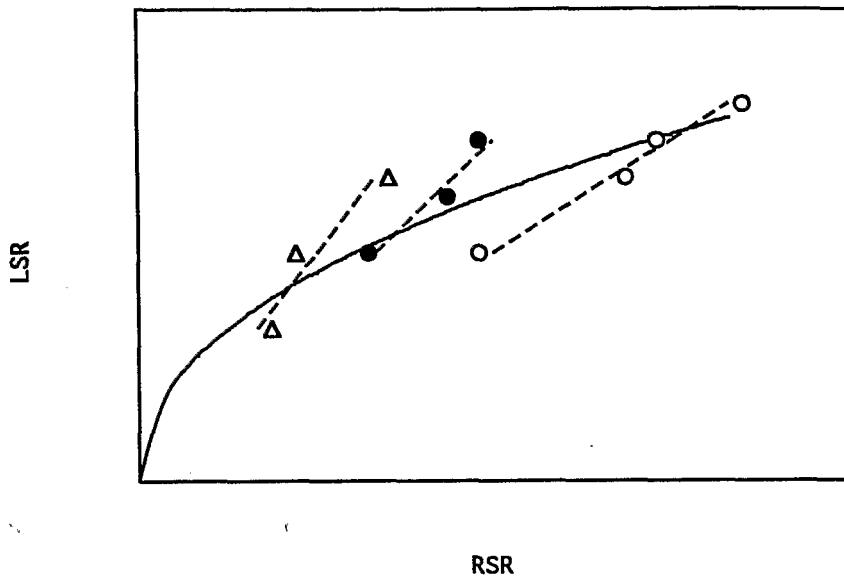
Fig. 1. Relationship between local species richness (LSR) and regional species richness (RSR) for three provincial biotas. Two models are fitted to these data. The first assumes that there is no historical effect: one curve describes the relationship between LSR and RSR (a Type II curve in this case; solid line). The second model considers that there is a historical effect: three different curves (Type I curves in this case; broken lines) are fitted, one for each province.

In our hypothetical example the best fit is provided by a curvilinear relationship. Conversely if we assume that there is a historical effect then three different LSR-RSR curves must be fitted, one per province. In this case, the best fit is provided by three Type I curves. Accepting the existence of a historical effect leads to the conclusion that the communities are unsaturated whereas rejecting this existence leads to the opposite conclusion. Deciding if there is a statistically significant historical effect becomes, therefore, crucial and is the aim of the next section.

Testing for a historical effect

We will assume that curves displaying non-proportional sampling are roughly fitted by a second order polynomial. For convenience these curves are called Type II curves even if an asymptote is not reached. Another valid approach is to use a log-log transformation of the data so that non-proportional sampling appears with a slope significantly less than unity (see, for instance, Griffiths 1997). However, we will only focus on the polynomial approach because it allows us to test simultaneously for saturation and historical effect in an easier way than by a log-log transformation. To test for a historical effect we used a regression procedure which included one predicted variable: LSR (local species richness); two explanatory variables: RSR (regional species richness), RSR^2; and two interaction terms: $PROV \times RSR$ and $PROV \times RSR^2$; where PROV is a dummy variable coding the province. Since the curves were constrained to pass through the origin, the constant term is excluded from the model. For the same

reason, PROV is not considered as an explanatory variable. We then applied a stepwise selection. This method permitted us to distinguish between four cases according to the variables included in the regression model (Table 1): 1) the same Type I curve is fitted within each province; 2) the same Type II curve is fitted within each province; 3) different Type I curves are fitted within each province; 4) different Type II curves are fitted within each province or there is a mixing of Type I and Type II curves. Obviously if there are not enough data to assess the LSR-RSR relationship independently within each province, there can be no way of testing for historical effect and thereby no reliable conclusion can be made about the occurrence of saturation in the communities studied.

An example of a historical effect

We will now further illustrate these points with a concrete case. The LSR-RSR relationship has been assessed for river fish communities of two intertropical areas: Côte d'Ivoire in West Africa (Sahelo-Soudanian region), and French Guiana in South America (Guianan-Amazonian region). A complete separation of the two continents was achieved between 106 and 84 million years ago (Goldblatt 1993) and they have no freshwater fish species in common. Experimental fishing was carried out using sets of gill nets 15 to 25 m long and 2 or 2.5 m deep with various mesh sizes (from 10 to 40 mm in Africa, 10 to 70 mm in Guiana). Sampling took place in pools more than 1 m deep, 15 m wide, and 500 m long, with low current velocity (lower than

Table 1. Intraprovincial LSR-RSR relationships implied by various regression models.

RSR	RSR^2	RSR × PROV	RSR^2 × PROV	Conclusions
Yes	No	No	No	NH, all Type I
Yes/No	Yes	No	No	NH, all Type II
Yes/No	No	Yes	No	H, all Type I
Yes/No	Yes/No	Yes/No	Yes	H, all Type II
Yes/No	Yes	Yes	Yes/No	or Type I + Type II

Note: The explained variable is LSR (local species richness) and a stepwise selection of variables is used (RSR: regional species richness, PROV: dummy variable coding the province). "Yes" means that the presence (absence if a "No" occurs) of the variable in the regression model is a necessary condition to validate the corresponding conclusion. "Yes/No" means that the absence or presence of the variable has no effect on the conclusion. "NH" means that there is no historical effect, "H" means that there is an historical effect. Type I and Type II refer to the shape of the intraprovincial LSR-RSR relationships.

0.2 m/s). Regional species richness (RSR) is the number of species known to occur in a river and local species richness (LSR) is the number of species sampled by locality within this river. Data from 47 localities distributed among 10 West African rivers come from Hugueny and Paugy (1995). Data for four Guianan rivers (Karouabo, Malmanoury, Sinnamary and Approuague) and 22 localities were provided by Boujard et al. (1990), Tito de Morais et al. (1995) and B. de Mérona, D. Ponton and S. Mérigoux (unpubl.). In the Approuague river, Boujard et al. (1990) computed species richness in each locality per mesh size but not for the entire gang of nets. Consequently, we estimated the local species richness by the midpoint between possible maximum value (the sum of the species richness observed per mesh size) and possible minimum value (the highest species richness observed per mesh size). The resulting value conforms with the value of the Sinnamary river which has an RSR similar to the Approuague river.

Without distinction between the two provinces it is tempting to claim that community saturation has been demonstrated because a Type II curve, described by a second order polynomial, gives a good and significant fit (the second order term has a significant contribution, $p < 0.00001$). When the above stepwise regression procedure is applied, only RSR and PROV × RSR are included in the model ($p < 0.00001$ in both cases). According to Table 1, the LSR-RSR relationship differs between provinces, i.e. each province displayed its own Type I curve (Fig. 2). As previously demonstrated (Hugueny and Paugy 1995), Ivoirian rivers are clearly unsaturated. Guianan rivers are probably unsaturated too, but data are less reliable due to a lower number of rivers studied. If we accept that a Type I curve is a good model for Guianan rivers, its slope is smaller (0.18) than the slope obtained with Ivoirian rivers (0.27). A comparative study (Tito de Morais and Hugueny unpubl.) carried out on small stream fish communities of the Sinnamary river (Guiana) and those of an Upper Niger tributary (West Africa) suggests that the low LSR/RSR ratio may be a general feature of the Guianan ichthyofauna compared to the West African one. This study was based on rotenone samples effected

in habitats covering similar environmental gradients between the two rivers. The LSR/RSR ratio was found higher in the Niger river than in the Sinnamary river after removing the effect of local habitat structure. As a whole, the data analyzed in this note suggest that the different evolutionary histories undergone by the two ichthyofaunas compared lead to different LSR-RSR relationships. However, the effect of some confounding factors, such as sampling bias or habitats imperfectly matched between provinces, cannot be completely ruled out and our data must be considered merely as a possible case of historical effect waiting for other supporting evidence. One major process that can produce such a historical effect is that some biological features affecting the LSR-RSR relationship are not distributed equally between the West African and the Guianan ichthyofaunas. Body size distributions are different between the two ichtyofaunas: small species (less than 20 cm in body length) constitute a higher proportion ($\chi^2 = 9.24$, 1 df, $p < 0.005$) of the fauna in the Synnamary river than in Côte d'Ivoire (75%, $n = 126$, versus 58%, $n = 154$). In freshwater fishes, body length is related to characteristics that probably enhance dispersal ability, for instance optimum swimming speed increases with body size (Videler 1993), and large fishes migrate more than small fishes (Roff 1988). Our results seem to be consistent with the suggestion made by Cornell and Lawton (1992) that the LSR/RSR ratio increases with average dispersal ability of species. Whatever the underlying processes, our example provides the first evidence of a provincial effect on the LSR-RSR relationship.

Conclusion

The LSR-RSR relationship can differ between provinces, as illustrated by river fish communities of Côte d'Ivoire and Guiana. As a result, sampling local richness in different provinces without simultaneously sampling regions within provinces can lead to incorrect interpretation of the LSR-RSR relationship. Mixing different provincial biotas increases the likelihood that biological features affecting the LSR-RSR relationship
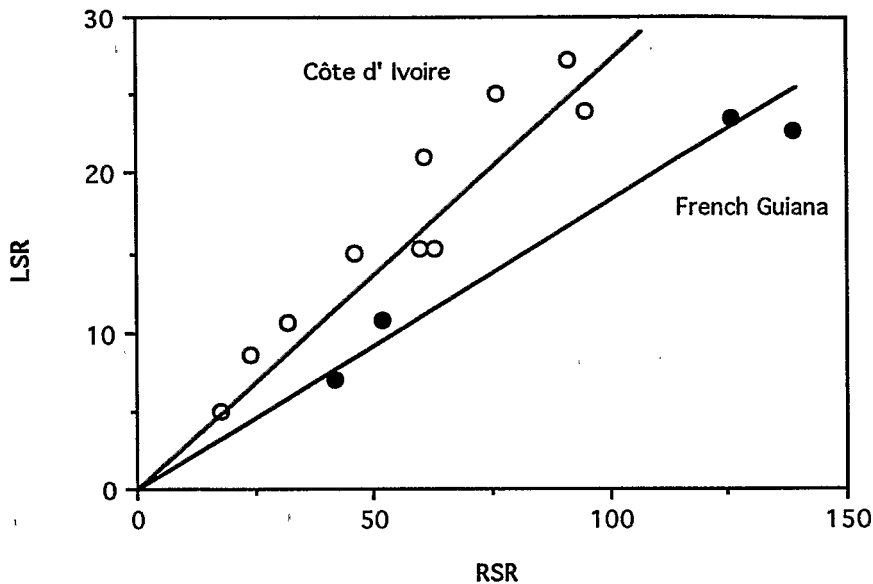
Fig. 2. Relationship between local species richness (LSR) and the number of fish species in the catchment area (RSR). Mean local species richness is plotted for each river. Regression lines are constrained to pass through the origin and fitted separately for Ivoirian and Guianan rivers using the 69 local species richness estimates.

will not be distributed equally between the different biotas, due to different evolutionary histories. Theoretically the same problem could be encountered when comparing regions within provinces. However, the high species similarity expected between regions located in the same province (as defined in this note) impairs this possibility.

Within the 17 community saturation studies reviewed by Cornell and Karlson (in press) we identified at least four studies (Hawkins and Compton 1992, Lawton et al. 1993, Caley and Schluter 1997, Griffiths 1997) that have employed data drawn from regions located on different continents or within the same continent but along a large latitudinal gradient. It is very likely that, in these studies, biotas with different evolutionary histories have been mixed. Other studies may be influenced by history, such as those based on host-parasite systems in which a host species is assimilated to a region (Cornell 1985, Aho 1990, Hawkins and Compton 1992, Aho and Bush 1993, Dawah et al. 1995, Kennedy and Guégan 1995). Parasite species frequently display a high host specificity leading to parasite species pools that overlap slightly among host species. In this case, according to our definition, host species are different provinces with regard to parasite biotas. Unfortunately, except for Caley and Schluter's (1997) study, none of the above-mentioned investigations provided the data necessary for assessing the importance of history in shaping the LSR-RSR relationship. Using data from 8 taxa and 2 continents (Australia and North America), Caley and Schluter (1997) showed that the slope of the curve relating local to regional species richness was the same for the two continents. This result suggests that the effect of history can be neglected. In contrast, a re-analysis of Caley and Schluter's data (Hugueny un-

publ.) reveals that the slope of the LSR-RSR relationship decreases with latitude, a result that may be explained in part by a historical effect. Empirical evidence supporting the view that the LSR-RSR relationship is partly shaped by history is therefore still scarce but we believe that this reflects more the paucity of suitable data than the low occurrence of historical effects.

The exploration of the relationship between local and regional species richness is probably not the most effective way of testing community saturation if biotas with different evolutionary histories are mixed. Nevertheless these studies may reveal interesting macroecological patterns and processes. As a concluding footnote, we want to comment briefly on this point in terms of speculative guidelines only because of the present paucity of empirical data. We agree with Ricklefs (1987) who suggested that rate of speciation may have a profound impact on the structure of local communities as well as on regional pattern of diversities. We hypothesize that between-province differences in speciation rate may affect intraprovincial LSR-RSR relationships if at least two processes are coupled: patch occupancy dynamics and selective speciation. Theoretical models of patch occupancy dynamics have shown that the LSR-RSR relationship is affected by intrinsic features of the species composing the regional pool (Caswell and Cohen 1993). Selective speciation is the process by which some properties of species increase the likelihood of a speciation event (Fowler and Mac-Mahon 1982). If we assume that there is a biological feature affecting both patch occupancy dynamics and speciation rate then it follows that the LSR-RSR relationship is affected by speciation rate. As an example, dispersal ability is assumed to increase the LSR/RSR ratio (Cornell and Lawton 1992, Caswell and Cohen

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1993) and to decrease speciation rate (Jackson 1974, Hansen 1978, Reaka 1980). Given this framework, it is expected that speciation-prone provincial biotas are composed of species with low dipersal ability and, ceteris paribus, that they display a lower LSR/RSR ratio than provincial biotas which have undergone a lower number of speciation events. Undoubtedly, more inter-provincial comparisons of the interplay between local and regional controls on richness are needed for assessing the validity of these speculations. A multi-scale understanding of community structure may greatly benefit from these comparisons.

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