

ceiling on the species list of some particular type of 50 × 50 km local assemblage.

Cornell's formulation of plotting local vs. regional species richness (as in Fig. 1a) has very weak power when implemented for free-living organisms such as birds or trees, since at most there will be one data point (one level of regional species richness) per continent, unlike the situation for Cornell's gall wasps, where each host-plant species contributed a data point. Caley and Schluter's conclusions that local–regional slopes were uniform between taxa, and showed little evidence of curvilinearity, were founded on regressions using five data points for birds (Africa, Australia, Europe, North America, and South America), three for fish, three for mammals and four for reptiles. Regressions with this few data points have limited power to detect differences in slope, or curvilinearity.

An alternative formulation is to graph species richness for a given taxon against area (both log-scaled), with separate relationships for each continent or region (Fig. 1b and c). This formulation does not require arbitrary selection of two particular scales to represent "local" and "regional," with data from regions that are to be compared needing to be exactly matched for scale. Parallel lines (Fig. 1b) indicate local assemblages are not convergent in species richness between different regions, but rather are proportionate to regional richness. When lines are close at local scales but diverge at wider scales (Fig. 1c), this indicates convergence in local species richness despite divergent regional richness.

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## THE RELATIONSHIP BETWEEN LOCAL AND REGIONAL DIVERSITY: REPLY

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In Caley and Schluter (1997) we addressed the relationship between local and regional diversity, specifically the issue of saturation of local species diversity. Westoby (1998) takes issue with several aspects of our analysis of saturation: (1) that the sizes of our local assemblages are too large to detect saturation; (2) that we inappropriately combined different groups of organisms in our tests; and (3) that an alternative method for detecting saturation based on species–area regressions is superior to our method, which used regressions of local on regional diversity. We dispute each of these claims as follows.

#### Appropriate locality size

If local species saturation occurs, then perhaps a correct locality size exists at which this saturation would be evident. Saturation may then not be detected if tested using larger or smaller localities, although this cannot be assumed a priori. The correct locality size is unknown, but it may be small, as Westoby suggests. However, a variety of tests has already been conducted using small localities, and little evidence for saturation has been found (references in Caley and Schluter [1997]). Our analyses explored instead the upper size limits of what might be considered a locality.

Our use of large localities was also meant to solve three less-well-appreciated problems. First, locality sizes used to study local–regional diversity relationships have varied depending on the taxon investigated, making intertaxon comparisons difficult. Second, tests of saturation must guard against "pseudosaturation" arising from sampling constraints in small localities. Most species are rare, and the reduced numbers of individuals associated with sampling a small locality means that fewer rare species will be included. Since

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more-diverse assemblages have more rare species than less-diverse assemblages, this sampling constraint will affect them more, causing "local" diversities to apparently converge between regions whose total diversities differ greatly. Our simulations revealed that the minimum sample sizes needed to avoid this artifact are surprisingly large even under ideal conditions in which every individual is sampled independently. The spatial dynamics of populations will usually prevent independence, necessitating even larger samples. Our use of larger-than-typical localities minimized the impact of pseudosaturation on our estimates of local-regional diversity relationships. Third, many prior studies have compared local diversity between regions that vary in size in order to include a wider range of regional diversities. However, variation in region size can bias estimates of local-regional relationships. To minimize this bias and to allow intertaxon comparisons, we used a consistent sampling protocol and a fixed region size, which allowed very broad comparisons among taxa and continents but made necessary a larger, and therefore, coarser "locality." Our locality size is not ideal, as we stressed previously, but is informative and not otherwise inferior to smaller localities, which have their own limitations.

#### *Combining taxa*

We reported local-regional diversity relationships estimated from a wide range of taxa including amphibians ( $n = 2$  taxa), birds ( $n = 5$ ), butterflies ( $n = 1$ ), corals ( $n = 1$ ), dragonflies ( $n = 1$ ), eucalypts ( $n = 1$ ), freshwater fishes ( $n = 3$ ), mammals ( $n = 3$ ), reptiles ( $n = 4$ ), and trees ( $n = 2$ ) (Caley and Schluter 1997: *Appendix*). Increasing regional diversity was generally associated with a change in taxa, with mammals, reptiles, and freshwater fishes being the less diverse taxa and birds the most diverse. We agree with Westoby (1998) that "there is no reason to expect any ceiling on local species richness to be set at the same level in such different groups of organisms," but we find the uniformity of slopes and the absence of any detectable curvature to these relationships intriguing. An asymptote in our across-taxon local-regional relationships could have occurred if the relationships for birds had been linear but shallower than less diverse taxa, or had been concave down. Alternatively, separate asymptotes for each taxon may have been obscured by combining taxa. These two possible outcomes might indeed engender different interpretations than we presented. Neither result, however, was evident in our survey. No slope differences among taxa were detected and no curvature was detected within intrataxon relationships for birds (locality = 1% of region,  $P > 0.78$ ; locality = 10% of region,  $P > 0.19$ ), the only taxon with sufficient data for such a test.

#### *Tests of saturation*

Westoby (1985, 1993, 1998) presents the species-area plot as an alternative to the local-regional plot for testing saturation. Species-area plots are illuminating but not superior to local-regional plots, which depict the actual saturation curve, and thereby visually aid intuition.

A drawback of the species-area approach is that the curve for each region requires several points, but tests of saturation that include multiple values of species richness from the same region will suffer from pseudoreplication. That is, the sample size for a test of saturation is the number of regions sampled, not the number of localities sampled within each region. Westoby's examples (1998: Fig. 1b and c) and his other applications of this approach (Westoby 1985, 1993) include only two or three regions, and are therefore insufficient for a test of saturation. Species-area plots, although not limited to comparing two regions, do not escape the problem that the earth presents very few biogeographic regions to work with.

A second potential problem with Westoby's examples is that they show convergence in species diversity at a locality size approaching 1 ha. However, 1 ha in the most species-rich region is unlikely to contain enough individuals of many multicellular taxa to avoid the problems of pseudosaturation discussed above. Surveys of large-bodied taxa, such as most of those in our survey, require either corrections for pseudosaturation or much larger localities.

#### *Conclusions*

Perhaps there exists an appropriate locality size for each taxon at which saturation is evident, and where this saturation becomes blurred when surveys are conducted using smaller or larger localities. However, a growing number of local-regional comparisons at a range of scales along the locality-size spectrum, from a single oak tree (Cornell 1985a, b) to 25 000 km<sup>2</sup> areas on a map (Caley and Schluter 1997) suggests that local saturation is elusive. Many processes can result in the number of species coexisting within any locality of arbitrary size being determined to a considerable extent by inputs from the surrounding region, and therefore will be determined in part by the diversity of that region. Absence of saturation does not imply local processes have no impact on the character of local species assemblages—only that such processes place no hard limits on the numbers of species that may coexist locally. Our results and those of others suggest that regional effects are strong. Understanding the diversity of local assemblages requires that regional processes be considered.

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## HOW RISKY IS BIOLOGICAL CONTROL? COMMENT

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The authors of a paper “How risky is biological control?” (Simberloff and Stiling 1996) wrote about the risk of dispersal of biological control agents to areas that were not intended to be occupied, and to nontarget species. They claim that introduction of biological control agents is risky, and that such agents should be judged “guilty until proven innocent.” I think the legal metaphor chosen by Simberloff and Stiling is inappropriate, and I prefer to compare biological control to surgery rather than to law. First, as in biological control, surgery is one of several alternative courses of action to address a specific problem. There are risks

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associated with surgery and with alternatives to surgery, and these must be compared. Second, as in biological control, surgery has advanced in the past 130 years. It is no more appropriate to criticize modern biological control for disastrous introductions of the distant past (e.g., of the Indian mongoose, *Herpestes auropunctatus*) than to criticize modern surgery for deaths through lack of antiseptic methods used in the past, but many have learned from such errors.

I agree with Simberloff and Stiling that risk/benefit analysis is an important preliminary to biological control introductions. As an example of an introduction of biological control agents against nonindigenous pest insects, Simberloff and Stiling cited actions of the University of Florida’s mole cricket research program. In this comment I provide a risk/benefit analysis of introductions made by this program. Because I have been involved in the program for 12 years I am familiar with data (published only recently hence less readily available to Simberloff and Stiling) relevant to the questions posed by Simberloff and Stiling. They ask: “What is the likelihood that these [introduced] control agents would spread and, if they did, what is the probable effect on [a] native species [of mole cricket, *Gryllo-talpa major*]”? I ask, additionally, what are the likely environmental and economic effects of alternatives to introducing these biological control agents? My goal in this comment is twofold. First, I show how ecologists knowledgeable of a biological control system can conduct necessary risk/benefit analyses. Second, I show that in the specific case of mole cricket biological control the risks to *G. major* are trivial, but that the cost (to agriculture and horticulture) of not undertaking the program is very high and the harm from currently used chemical pesticides to nontarget organisms is widespread.

### *A broad perspective of biological control*

From January 1971 to late 1991 (a period of not quite 21 years), 271 immigrant insect species were newly reported as established in Florida (Frank and McCoy 1992). Few of these uninvited species have been studied. Among the immigrants were a few species, on average detected at about one per year, that either were known to be important pests elsewhere, or made their presence conspicuous as major pests (Frank and McCoy 1992). When these pests affected agriculture in the broadest sense, or infested buildings, or caused annoyance by biting, they became targets of control by repeated application of existing broad-spectrum pesticides. The natural trend is therefore for increasing use of pesticides, which is beneficial for commerce and creates jobs, but is costly to purchasers and detrimental to the environment. These invasive species may thus have far greater effects on ecosystems, both directly