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LOCAL PLANT SPECIES RICHNESS INCREASES WITH REGIONAL HABITAT COMMONNESS ACROSS A GRADIENT OF FOREST PRODUCTIVITY

Brandon S. Schamp[1,2], **Lonnie W. Aarssen**[1] **& Harold Lee**[3]

1) Department of Biology, Queen's University, Kingston ON, K7L 3N6, Canada;
2) Corresponding author: fax +1 613 533 6617, e-mail aarssenl@biology.queensu.ca
3) Ontario Ministry of Natural Resources, Science and Information Section, 659 Exeter Rd., London ON, N6E 1L3, Canada

Abstract: We tested the prediction that forest habitat types with relatively high productivity are not only relatively low in species richness but are also regionally uncommon. This relationship was supported by an analysis of data from 146 forest communities in southern Ontario, Canada. Potential forest habitat productivity was determined based on a classification scheme developed for the Canadian Land Inventory (CLI) project. Vascular plant species richness approximated a unimodal distribution across forest productivity classes with the lowest mean species richness recorded for the two most productive classes. The contemporary regional commonness of forest habitat productivity classes were also displayed as a unimodal frequency distribution. Hence, mean species richness per CLI class was positively correlated with the regional area of land encompassing each of these productivity classes and this relationship was increasingly significant at increasingly larger spatial scales of regional CLI class land areas. These results are consistent with the species pool hypothesis, which postulates that species richness is relatively low in highly productive habitats because such habitats have been relatively uncommon in both space and time and hence, have had relatively little historical opportunity for the origination of adapted species.

Keywords: Forest productivity, Habitat commonness, Species diversity, Species pool hypothesis

INTRODUCTION

One of the most common patterns reported for vegetation at the regional scale is a decline in species richness toward the high end of habitat productivity gradients, often (but not always) associated with a unimodal relationship (GRACE 1999). Most often these patterns are interpreted in terms of effects involving increased competitive exclusion at higher productivity levels (GRIME 1979, HUSTON 1979, 1994, TILMAN 1982). An alternative explanation is offered by the "species pool" hypothesis (TAYLOR et al. 1990, AARSSEN 2001, AARSSEN & SCHAMP 2002, SCHAMP et al. 2002). According to this model, habitats of very low, or very high productivity have relatively few species because such habitats have a relatively small "species pool" to draw from. The species pools here are relatively small, it is argued, because extremely productive and unproductive habitats are relatively uncommon in both space and time and hence, the historical opportunity for origination of adapted species in these habitat types is expected to have been relatively low. Habitats defined by their relative productivity can thus be expected to have a unimodal frequency distribution with

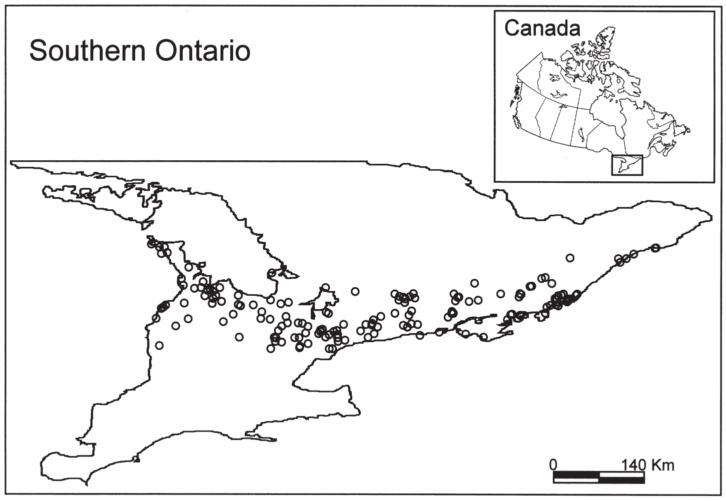

Fig. 1. Locations of study plots (n = 146) in mixed forests of southern Ontario, Canada. All study plots fall between 45°13′ and 43°48′ north.

low-to-intermediately productive habitats having been the most common geologically through time.

Evidence accumulated thus far supports the prediction of the species pool hypothesis that highly productive habitats are relatively rare (SCHAMP et al. 2002) and that frequency distributions of habitat commonness on productivity gradients tend towards unimodality (BROWN & SCHROEDER 1999, HANSEN et al. 2000). However, most data collected on this habitat commonness distribution have not been examined in light of the productivity-species richness relationship (but see SCHAMP et al. 2002). In the present study, we investigate this correspondence directly for forest communities in southern Ontario, Canada. We test three predictions derived from the species pool hypothesis: (i) species richness within southern Ontario forest communities will vary in a unimodal relationship with the potential productivities of these communities; (ii) the contemporary regional commonness of forest habitat productivity types will also be displayed as a unimodal frequency distribution; and (iii) (derived from i and ii) communities with higher species richness will be found in habitat productivity types that are regionally more common.

METHODS AND MATERIALS

Study region

The study was conducted within the Great Lakes – St. Lawrence Mixed Forest region that extends from east of Lake Huron in Ontario, Canada, to Québec and into the north eastern United States (Fig. 1). This forest region exists as an ecotone between the Northern Boreal Forest and the Southern Carolinian Deciduous Forest (BOLEN 1998). Primary canopy species in this region include sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), white ash (*Fraxinus americana*), red oak (*Quercus rubra*), eastern hemlock (*Tsuga canadensis*) and eastern white cedar (*Thuja occidentalis*) (GLEASON & CRONQUIST 1991, BOLEN 1998).

Site selection was restricted to a latitudinal band between 45° 13′ and 43° 48′ north in order to control for the effect that climatic processes associated with latitude have on both productivity and species richness (CURRIE & PAQUIN 1987). This range falls within Hills' site region 6E within the mixed forest region in southern Ontario (HILLS 1957). Hill's site regions were originally designated to identify regions of similar climate based on the successional trajectory of vegetation on similar substrates (HILLS 1957). Hills' site region 6E typically experiences mean annual temperatures between 4 and 7 degrees Celsius, has a mean length of growing season between 173 and 188 days, mean annual precipitation between 568 and 723 mm, and mean summer rainfall ranging from 201 to 305 mm (MACKEY et al. 1996). Such regional scales are where unimodal productivity-diversity relationships have been most commonly observed (GRACE 1999, WAIDE et al. 1999, MITTELBACH et al. 2001). Hill's site region 6E includes a wide variety of soil conditions ranging from dry, sandy soils with good drainage, to clay soils, and to deep organic soils (ONTARIO MINISTRY OF AGRICULTURE AND FOOD 1977). The inevitable range of productivities to be found on such a wide range of soil types makes Ontario mixed forests particularly suitable for this type of investigation.

Site selection

Study sites were chosen from those used in the Ecological Land Classification (ELC) project for Southern Ontario Forests (Ontario Ministry of Natural Resources; LEE et al. 1998). Forests included in the ELC project for southern Ontario are mature natural forests more than 50 years old, and represent the range of landforms, soils and topographies in the region.

Since both productivity and species richness can change with forest age (GOWER et al. 1996) and level of disturbance (HUSTON 1994), it was necessary to control for these two factors. Therefore, each chosen forest site possessed trees that were at least eighty years old and each site had to be relatively undisturbed over the last twenty years. Existing quantitative disturbance data were available from the ELC data base and enabled us to avoid forests that had been subject to extensive disturbance from factors such as logging, livestock grazing, fire and recreational use.

Survey plots

In each of the selected forest sites, a 10 m × 10 m vegetation plot was surveyed between 1996 and 2001 (LEE et al. 1998). This plot size was considered to be large enough to represent the forest community, while minimizing the effects of heterogeneity (HUSTON 1999). A total of 146 forest plots were included in the final data set (Fig. 1). For each plot, the total number of vascular plant species was recorded, and detailed soil data were collected. Soil characteristics in these forests including effective texture, moisture, and drainage were determined through field analysis of soil from a 1 × 1 × 1.2 metre soil pit dug near the centre of each plot according to ELC standards (LEE et al. 1998). Vascular plant species richness was determined from a detailed survey of the vegetation plot.

Relative productivity estimation

Data on relative habitat productivity for the study sites was based on the Canadian Land Inventory capability for forestry classification system (ENVIRONMENT CANADA 1965). This classification system was originally designed to provide a basis for resource and land use in Canada (Environment Canada 1965). Specifically, the classification for forestry capability is based on the productive potential of lands for the growth of native tree species. The capability for forestry classification is based on mean annual increment per acre expressed in cubic feet and is based on studies done within each region (Environment Canada 1965). All mineral and organic soils within a given region fall within 1 of 7 classes of productivity with class 1 soils yielding the highest mean annual increments (> 111 ft^3/acre/annum) and class 7 soils yielding the lowest (< 10 ft^3/acre/annum) (Department of Regional Economic Expansion 1970).

Since the Canadian Land Inventory (CLI) is based on research relating the potential productivity of different site regions in eastern Canada to physical soil characteristics, it was possible to use this classification scheme to estimate the potential productivity of our study sites. No forests were encountered in the region of study that fell into CLI class 7. Within Hills' site region 6E, class 7 land exists as bare rock lands or marshy areas of poorly decomposed peat, neither of which support forest growth (Department of Regional Economic Expansion 1970). Based on the soil data collected from each plot, each forest site was assigned to one of the six remaining CLI capability-for-forestry classes (classes 1–6) using the standards of the CLI.

Using maps and an associated geographic information system (GIS) data for CLI capability (scale 1:250,000), it was possible to estimate the regional area of land falling into each CLI class for site region 6E and for larger adjacent regional areas of Eastern Canada. This was accomplished using ArcView 3.2 GIS software.

Data analyses

Species richness was compared across CLI capability for forestry classes. Significant differences in mean richness between CLI classes were identified using a non-parametric Kruskal-Wallis test with Tukey-Kramer post-hoc comparisons. The distribution of regional area (habitat commonness) for the CLI classes was assessed at four progressively larger spatial scales, determined by adding available data from adjacent universal transverse mercator (UTM) zones. This allowed assessment of whether the distribution of habitat productivities changes with scale and whether patterns in species richness across CLI classes correspond to the regional areal coverage of these classes. Product-moment correlation analysis was used at each spatial scale to test the prediction from the species pool hypothesis that mean species richness per habitat productivity type (defined by CLI class) is correlated with the regional commonness of the habitat productivity type (i.e., areal extent of the CLI class).

RESULTS

Species richness is significantly different across CLI classes (Fig. 2a; Kruskal-Wallis $P = 0.0047$). Class 4 forest plots have significantly greater mean species richness than Class 1 and Class 2 forest plots (Tukey-Kramer; $P < 0.05$). Although not statistically significant for mean species richness (Tukey-Kramer; $P > 0.05$), a unimodal trend in maximum species

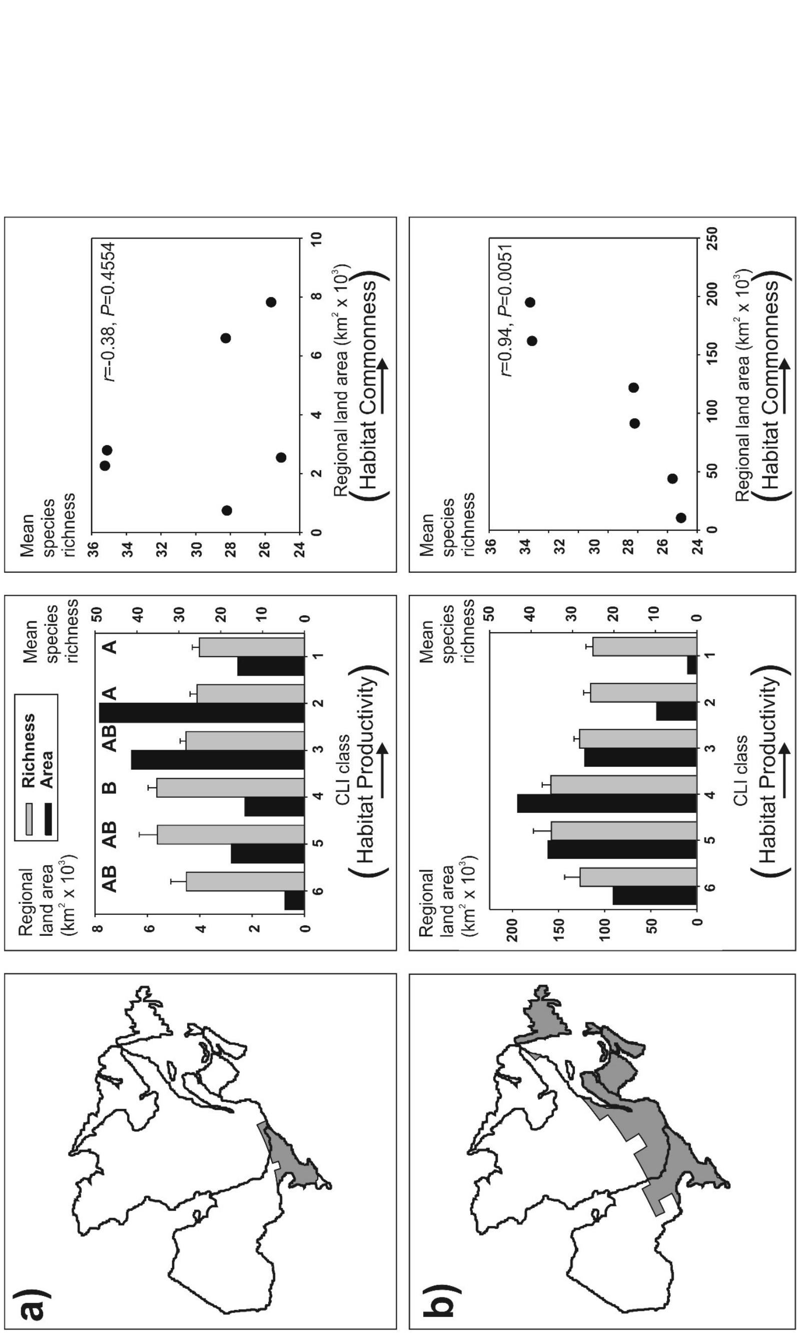

Fig. 2. Analyses of the coincidence of patterns of species richness within 10 × 10 m plots across habitat productivity types (CLI classes, representing a gradient of increasing potential productivity from class 6 to class 1) with the frequency distribution of regional land area for the corresponding habitat productivity types in eastern Canada. Bar graphs show mean (± s.e.) species richness per CLI class for the surveyed plots in southern Ontario shown in Fig. 1 (light bars) and the available regional land area of each CLI class (dark bars) at two spatial scales, (a) and (b) (determined by adding available data from adjacent UTM zones). Values for species richness that do not share the same letter code (A,B) are significantly different (Kruskal-Wallis, $P = 0.0047$; Tukey-Kramer post-hoc comparison, $P < 0.05$). At the smallest scale of regional land area of CLI classes, there is no correlation with mean species richness per CLI class from the southern Ontario forest plots (a). The latter however, is positively correlated with the regional commonness (land area) of CLI classes at the larger spatial scale across Eastern Canada (b).

richness across CLI classes is evident with peak maximum richness occurring at intermediate habitat productivity (Fig. 2a).

The relative areal extent of the six CLI classes of potential productivity is clearly unimodal, independent of the scale considered (Fig. 2). At the smallest spatial scale (Hills' site region 6E, Fig. 2a), the distribution does not correspond with that of species richness across the same CLI classes. Hence, there is no significant correlation ($P = 0.4554$) between mean species richness per CLI class and the area of land making up each of the six CLI classes within Hill's site region 6E (Fig. 2a). However, the distributions match well at each of the larger spatial scales across Eastern Canada, with significant ($P < 0.05$) positive correlations between mean species richness per CLI class within Hill's site region 6E and the regional area of land encompassing each of these classes. This positive correlation was most significant ($P = 0.0051$) for the largest spatial scale examined (Fig. 2b).

DISCUSSION

Recent reviews have identified that a right-skewed unimodal relationship, with a peak in species richness in habitats of relatively low productivity, while not ubiquitous, is the most common relationship observed at regional scales (GRACE 1999, WAIDE et al. 1999, MITTELBACH et al. 2001). Few studies, however, have examined this relationship for forest vegetation. The pattern of species richness recorded here across the six CLI classes of potential productivity in southern Ontario approximates a right-skewed unimodal pattern. The increase phase in the unimodal relationship, however, although apparent in our results for maximum richness, is not statistically significant for mean richness (Fig. 2a). This may be attributed to the inclusive categorical nature of the CLI classes, which limits the resolution for detecting statistically significant patterns over a relatively short range of habitat productivity. Nevertheless and more importantly, the obvious general decline in species richness toward habitats with the highest productivity (Fig. 2a) is consistent with the general trends reported in many previous studies, mostly involving herbaceous vegetation (GRACE 1999).

The species pool hypothesis predicts not only that species richness will display a unimodal relationship across habitat productivity types, but also that these habitat productivity types will, in turn, display a corresponding unimodal frequency distribution of regional commonness. This latter prediction is also clearly supported by our analysis of the CLI productivity classes (Fig. 2). Moreover, our analysis shows that unimodality is consistent over multiple spatial scales in this region (e.g. Fig 2a versus 2b). These results support a growing body of evidence indicating that highly productive habitat types are indeed relatively uncommon (BROWN & SCHROEDER 1999, HANSEN et al. 2000, SCHAMP et al. 2002).

This study is apparently the first to report a positive correlation between plot-level plant species richness in different habitat productivity types and the regional commonness of those habitat productivity types, as predicted by the species pool hypothesis (TAYLOR et al. 1990, AARSSEN 2001, AARSSEN & SCHAMP 2002, SCHAMP et al. 2002). This relationship was increasingly significant (i.e., with smaller P-values) at increasingly larger spatial scales of regional CLI class land areas (e.g. Fig. 2a versus 2b). Habitat types (defined here by relative potential productivity) that support the fewest species in southern Ontario (i.e., CLI class 1), while relatively common in Hill's site region 6E (Fig. 2a), are clearly the rarest in the eastern deciduous forests of Canada (Fig. 2b). It is presumably from neighbouring class 1 sites over this wider regional scale that the potential species pool is drawn from in effecting the species residency within the class 1 sites of Hill's site region 6E (Fig. 1). Accordingly, a forest community belonging to a relatively uncommon forest productivity type in eastern Canada, such as CLI class 1, may be expected to have relatively few resident (adapted) species, not only because of the potentially limited contemporary opportunity for immigration from other CLI class 1 forest communities within the region, but also because of the limited historical potential for origination of species that can successfully compete and recruit offspring within forest productivity types belonging to CLI class 1.

CONCLUSIONS

We recommend that future interpretations of patterns of species diversity along habitat productivity gradients take account of the regional commonness of habitat productivity types. While changing competition intensity (GRIME 1979) and/or changing habitat heterogeneity (TILMAN 1982) may be involved, neither need be invoked to explain the decline in species richness commonly observed in increasingly productive habitats if there is evidence to indicate that increasingly productive habitat types are also increasingly uncommon on a regional scale. The fact that larger spatial scales reveal an increasingly significant relationship (Fig. 2) highlights the difficulty in arbitrarily choosing a scale for this type of investigation. Moreover, the temporal scale of habitat commonness is at least equally as important as the spatial scale in terms of historical opportunity for origination of adapted species. Given the obvious practical difficulties in assessing the historical relative commonness of forest habitats belonging to different productivity classes, the present study was necessarily limited to the assessment of contemporary habitat commonness only. Several lines of evidence, however, suggest that the frequency distribution for regional commonness of forest productivity types has always been right-skewed unimodal, at least over recent evolutionary time scales (AARSSEN & SCHAMP 2002). Nevertheless, more direct evidence in support of this assumption awaits the attention of future research.

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