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REPORTS

LOCAL PLANT DIVERSITY PATTERNS AND EVOLUTIONARY HISTORY AT THE REGIONAL SCALE

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Abstract. The effect of evolutionary history on local-scale diversity patterns has often been suggested, but not shown. I explored whether widely described local-scale relationships between plant species richness and soil pH are related to evolutionary history. I expected positive relationships to occur between richness and pH if the pool of species that is suited for high pH soil is larger than the pool of species that is suited for low pH soil. In contrast, I expected negative relationships to occur between richness and pH if the pool of species that is suited for low pH soil is larger than the pool of species that is suited for high pH soil. I call this the species pool concept, because the direction of the relationship between richness and pH depends on whether the species pool has evolutionary origin on soils of high or low pH. I used 85 published studies from all over the world and found that positive relationships between richness and pH were significantly more probable in floristic regions where evolutionary centers were on high pH soils, and negative relationships between richness and pH were more probable in regions where evolutionary centers were on low pH soils. Because soil pH increases with latitude, I also found that the relationship between richness and pH was positive at high latitudes and negative at low latitudes. Consequently, local relationships between plant diversity and soil pH are clearly related to evolutionary history.

Key words: acidity; biogeography; diversity; soil pH; species pool; species richness; vascular plants.

INTRODUCTION

Evolutionary history is presumed to influence all ecological communities (McPeek and Miller 1996), but there are very few cases in which the effect of evolution on contemporary local-scale diversity patterns has been explicitly shown (see reviews by Austin 1999, Grace 1999, Huston 1999, Lawton 1999, Gaston 2000). Examples include relationships between local and regional richness (Cornell and Lawton 1992, Caley and Schluter 1997), studies relating species' traits to community composition (Eriksson and Jakobsson 1998, Tofts and Silvertown 2000), and comparisons of diversity in environmentally similar but evolutionarily different regions (Qian and Ricklefs 1999).

Species richness varies in scale from global to local (Huston 1994, Rosenzweig 1995), but there are no studies in which local-scale species richness patterns are considered at the global scale. If a local-scale richness pattern is consistent over regions with different evolutionary backgrounds, it is likely caused by local-scale processes, for example, biotic interactions. In contrast,

if local-scale richness patterns vary systematically between regions, then differences in patterns should be caused by differences in evolutionary history. Vascular plant species richness has long been related to soil pH (Whittaker 1972). Here I explored to what extent local patterns of relationships between richness and pH can be explained by evolutionary history at the regional scale. I use "richness" for vascular plant species richness, and "pH" for soil pH.

The relationship between richness and pH in Europe is often positive, perhaps because of higher evolutionary rates in fluctuating and highly disturbed semiarid environments, where precipitation is low compared to evaporation, and calcium carbonate has not leached out from soils, resulting in high pH soils (Grime 1979). Most soils in northern and central Europe have been rejuvenated with additions of base-rich sediments during the course of several glaciations (Watts 1988). Grubb (1986, 1987) hypothesized that higher richness on high pH soils in Europe may be explained by the so-called "appearance" hypothesis: calcareous substrates have been widely available during the Quaternary period in both time and space, and the abundance of such soils has resulted in the evolution of many species on high pH soils.

The suggestions made by both Grime and Grubb can be formulated as the species pool concept, which states that local richness is mainly defined by regional species pool size and less by local interactions (Taylor et al. 1990, Zobel 1992, Pärtel et al. 1996, 2000). The regional species pool is the potential set of species capable of inhabiting a plant community, formed by speciation and historical migration (Eriksson 1993, Zobel 1997). It is determined both by a species' presence in the regional flora and by the species' traits, which allow it to grow in particular habitat conditions (Keddy 1992). If the pool of species that is suited for high pH soils is larger than the pool of species that is suited for low pH soils, a positive relationship between richness and pH soils is expected at the local scale. In contrast, if the pool of species that is suited for low pH soils is larger than the pool of species that is suited for high pH soil, a negative relationship between richness and pH is expected.

The species pool effect on the relationship between richness and pH should be evident in a comparison of floristic regions. A floristic region is the largest independent sample unit that can be used to describe a richness pattern; an area in which most of its species have also evolved (Rosenzweig 1999). Floristic regions are defined by endemism both at species and higher taxonomic levels (Takhtajan 1986, Tallis 1991, Cox and Moore 1993). Species requirements most probably correspond to the conditions where they evolved. Centers of species origin are surely not located randomly in a floristic region. Although it is difficult to know the evolutionary history of all species in a floristic region, potential evolutionary centers are indicated by areas of higher than average species richness, and are called richness hot spots (Tallis 1991, Myers et al. 2000). According to the species pool concept, the relationship between richness and pH should be positive in those floristic regions where the evolutionary center is on high pH soils, and negative where the evolutionary center is on low pH soils.

Apart from the consideration of floristic regions, the species pool concept should also be evident if the local relationships between richness and pH are concordant with global-scale variation in pH. Soil pH is primarily determined by the parent material, e.g., soils over calcareous rock have high pH. No rock itself is markedly acidic, but climatic factors in the tropics further acidify soils: Plentiful rain at high temperature leaches out calcium carbonate (Kinzel 1983, Huston 1994). Although low evaporation at higher latitudes decreases pH again, this is a geologically recent postglacial event and cannot be considered in evolution. Thus, there should be a latitudinal variation in pH, which causes positive relationships between richness and pH at higher latitudes, and negative relationships between richness and pH at lower latitudes.

The species pool effect may be obscured by locally acting factors. The potentially obscuring factor I ex-

plored is physiological tolerance. The survival of all plant species is low at extreme pH values (pH < 3 and pH > 9, Glass 1989). This means that the relationship between richness and pH close to the lower extreme should be positive, and close to the high extreme should be negative, since the richness beyond the extreme value is a priori zero. This richness pattern may occur along all gradients with fixed limits (Colwell and Hurtt 1994, Colwell and Lees 2000). Acidity is related to many chemical and physical processes in the soil (Etherington 1982). If the local processes determine the relationship between richness and pH, this relationship should vary across the observed soil pH gradient, since the observed pH is related to numerous other soil parameters, e.g., fertility (Huston 1980).

My goals were to determine how the sign and strength of the correlations between vascular plant species richness and soil pH at the regional scale is affected by the species pool effect and the local limits of physiological tolerance. I tested the following hypotheses: (1) Positive correlations between richness and pH are more common in floristic regions that have evolutionary centers on high pH soils, and negative correlations are more common in floristic regions that have evolutionary centers on low pH soils. (2) The correlation between richness and pH varies with latitudinal variation in soil pH, and is positive at higher latitudes and negative at lower latitudes. (3) The correlation between richness and pH depends on physiological tolerance, and is positive at lower pH values and negative at higher pH values.

METHODS

I collected published studies of relationships between richness and pH by searching *Biological Abstracts* (1985–2000), *Current Contents* (1997–2000), JSTOR (back issues of main ecological journals; available online),[2] using the help of colleagues, and checking the references in other papers. Eighty-five studies satisfied the following criteria:

1) They described more-or-less natural and homogeneous plant communities. I excluded studies of cultivated agricultural systems, but included studies from less disturbed areas, such as natural grasslands grazed by domestic livestock. I excluded studies if different sample sizes from the same site gave opposite results. Descriptive studies were used, except in one case, in which soil pH was manipulated and richness had stabilized over several years (Tilman and Olff 1991).

2) Vascular plant species richness and soil pH was actually determined. In many cases I determined species richness from phytosociological tables. I also included studies in which only one forest layer (trees, climbers, or field layer) was consid-

[2] URL: ⟨www.jstor.org⟩
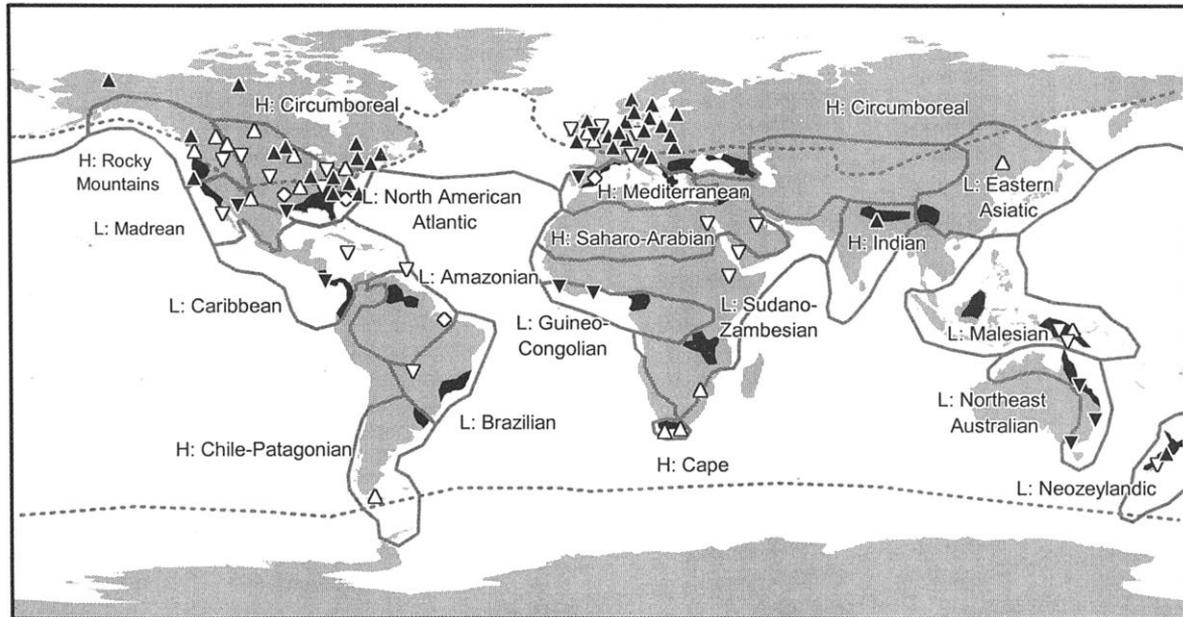
FIG. 1. Locations of 85 published studies of the relationship between vascular plant species richness and soil pH. An upward triangle indicates a positive relationship between richness and pH, a downward triangle indicates a negative relationship, and a diamond indicates no relationship. Solid symbols represents significant relationships at $P < 0.05$. Some locations are slightly shifted to make them visible. Floristic regions used in the study and the soil pH (H: high, L: low) in their evolutionary centers (black areas) are shown with solid lines and named. Borders of the direct influence of the last glaciation (permafrost or sea ice) are indicated with dashed lines.

ered. I did not separate pH measurements done in water or KCl solution since the difference is minor (0.4 to 0.8 pH units; Tyler 1997).

3) A correlation coefficient was used to describe the relationship between richness and pH, or I was able to calculate it. I used the correlation coefficient as a measure of the relationship between richness and pH because it was the statistic most often reported. The sign of the correlation indicated the direction of the relationship between richness and pH. In few cases, nonsignificant correlation coefficients were not reported in the literature, and the correlation was defined as zero in these analyses.

For each study I recorded the correlation coefficient between richness and pH, and its statistical significance. I also recorded mean observed pH (if given), location (longitude and latitude), and floristic region. Data are given in the Appendix.

In order to explore the effect of soil pH in evolutionary centers on the relationship between richness and pH, I examined floristic regions at the global scale (Takhtajan 1986). I defined the potential evolutionary centers for each floristic region using a world map of plant species richness per 10 000 km^2 (Barthlott et al. 1999), and found the mean soil pH for these hot spots from a global $0.5° \times 0.5°$ data set of soil pH properties (Batjes 1997). Floristic regions were classified into two groups according to soil pH in their evolutionary cen-

ters: low (pH < 5.5) and high (pH > 5.5), corresponding to the generally accepted boundary between acid and nonacid soils (Gough et al. 2000). I used a one-tail Fisher's exact test to determine whether studies reporting positive correlations were associated with high pH in their evolutionary centers, and whether studies reporting negative correlations were associated with low pH in their evolutionary centers.

To describe variation in soil pH associated with latitude, I calculated the mean pH for each degree of latitude (separately for north and south) using the data set of soil pH properties from 24 15° wide longitudes, and determined the Pearson correlation between latitude and soil pH. In the northern hemisphere, this was done only from 0° to 45° latitude in order to exclude areas that have been regularly glaciated (Tallis 1991). I used general linear models (GLM) to test whether the correlation coefficient between richness and pH varied with latitude, mean observed soil pH, and floristic region.

RESULTS

I found 33 studies from North America, 27 from Europe, seven from Africa, seven from Asia, six from South or Central America, and four from Australia and New Zealand (Fig. 1). There were studies from 18 floristic regions. Fifty-one studies had positive correlations between richness and pH, and 35 of these were significant ($P < 0.05$). Thirty studies had negative cor-
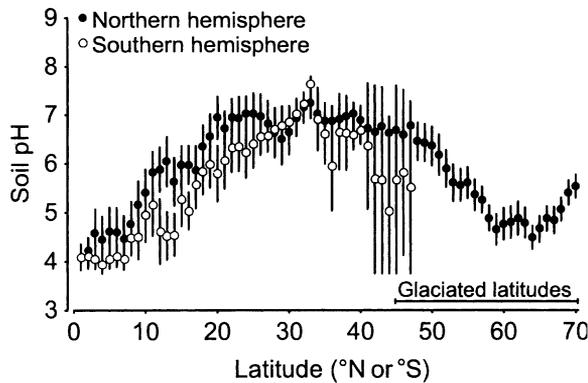
FIG. 2. Soil pH increased significantly with nonglaciated latitude. Mean ± 1 SE was calculated over 24 15° wide longitudes.

TABLE 1. General linear model (GLM) relating the correlation coefficient between richness and pH to latitude (°N or °S), observed soil pH, and floristic region.

Variable	Slope	df	F	P
Latitude	0.02	1, 60	5.6	0.021
Soil pH	−0.13	1, 60	8.2	0.005
Floristic region	⋯	17, 60	1.2	0.295

relations (ten of which were significant). No correlation was reported in four studies.

Positive correlations between richness and pH were found significantly more often in regions with evolutionary centers on high pH soils (38 positive and 9 negative correlations, Fisher's exact test, $P < 0.001$), similarly, negative correlations were found significantly more often in regions with evolutionary centers on low pH soils (13 positive and 21 negative correlations).

Soil mean pH increased from the equator to temperate regions (Fig. 2). The correlation between latitude and soil pH was highly significant both for the southern and non-glaciated northern hemispheres ($r = 0.71$ and $r = 0.83$, respectively, $P < 0.001$). The strongest increase in soil pH occurred from the equator to 20° latitude.

The GLM analysis indicated that the correlation between richness and pH increased significantly with latitude and decreased significantly with observed soil pH (Table 1, Fig. 3). Thus, both the effects of species pool (higher richness at pH that is characteristic for the closest non-glaciated latitude) and the local effect of physiological tolerance (higher richness at intermediate pH values and lower richness at pH extremes) were supported. In this model, the relationship between richness and pH did not differ significantly between floristic regions.

Thus, both contingency table and GLM analyses support the hypothesis that the sign and strength of the relationship between richness and pH is associated with differences in species pool sizes at high and low pH levels. Difference among floristic regions, however, simply reflects the latitudinal variation.

DISCUSSION

In accordance with the species pool concept, positive relationships between richness and pH were more likely in floristic regions where evolutionary centers were on high pH soils, and negative relationships between rich-

ness and pH were more probable in floristic regions where evolutionary centers were on low pH soils. Further, the relationship between richness and pH varied significantly with latitudinal variation in soil pH (Table 1, Fig. 3a). Once the effect of latitude was accounted for in the GLM, floristic regions did not explain any further variation in the relationship between richness and pH, suggesting that variability among floristic regions mainly reflected latitudinal variation in soil pH.

The effect of different species pools for different pH levels was shown in a "natural experiment" in Australia, where native plant species diversity was negatively correlated with soil pH, but the richness of alien species (mostly of Eurasian origin) was positively correlated with soil pH (Morgan 1998). This is in agreement with the distribution of low pH soils in the evo-
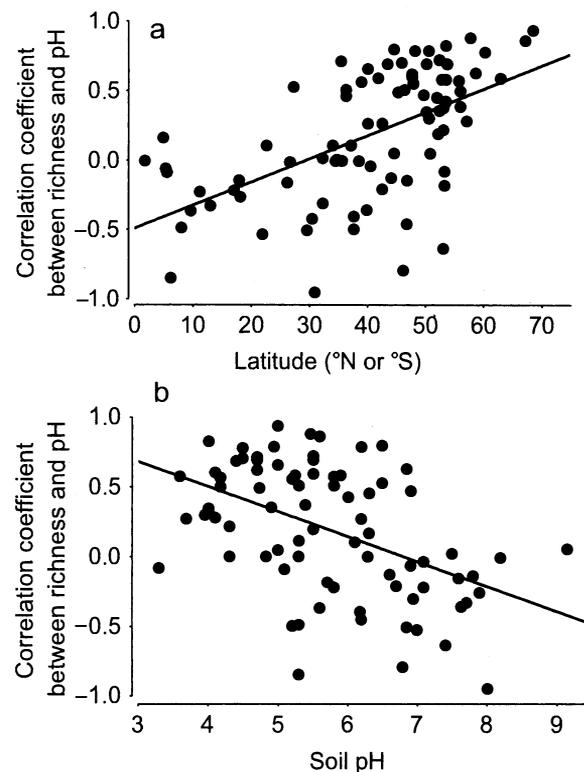
FIG. 3. (a) Correlation coefficient between vascular plant species richness and soil pH increased significantly with latitude (correlation coefficient = −0.5 + 0.02 × latitude) and (b) decreased significantly with observed soil pH (correlation coefficient = 1.2 − 0.13 × observed pH).

lutionary centers in Australia and high pH soils in the evolutionary centers in the Circumboreal region. The species pool effect on the relationships between richness and pH is also confirmed by a regional-scale study that described the realized niches for soil acidity of 2355 European plant species (Ellenberg et al. 1991). Sixty-four percent of species required high pH, which corresponded well to the high pH soils in the regional evolutionary center in Caucasus and southeast Europe. Similar data sets from other floristic regions would help enormously in studying the role of evolutionary processes behind local patterns.

Physiological tolerance had a significant local effect on the relationship between richness and pH: at low observed pH there were more positive relationships and at high pH more negative relationships (Table 1, Fig. 3b). However, this physiological limit did not obscure the species pool effect, and both regional and local factors remained significant in the GLM (Table 1). The effects of physiological tolerance and species pool may work in opposite directions, if the studied site is located in an evolutionary center. In the case of high pH soils, the species pool concept predicts positive relationships between richness and pH, but the physiological tolerance predicts negative relationships between richness and pH. In contrast, for low pH soils, the species pool concept predicts negative relationships between richness and pH, but the physiological tolerance predicts positive relationships between richness and pH. Both effects may also work in the same direction in cases in which the evolutionary center is at one end of the pH gradient, and the studied plant community is found at another end, outside the evolutionary center. An example of this is the relatively acid paludified or leached communities at glaciated areas in northern Eurasia and America, which are associated with high pH evolutionary centers in the Eurasian steppes (Fig. 1).

Predictable variation in the relationship between richness and pH suggests strategies for biodiversity conservation. The importance of protecting richness hot spots has been stressed (see Myers et al. 2000). If detailed information about diversity patterns is missing, one should protect habitats that support large species pools, such as high pH habitats in temperate regions in the northern hemisphere (e.g., natural steppe and prairie, calcareous grasslands, forests, and fens). This, however, cannot occur at the expense of protecting regionally unique habitats and species. Biodiversity conservation in North America and Europe is further complicated by acid pollution (Likens et al. 1996). Studies of acid rain have focused on trees and crops, and the direct effects of acidity on plants. The concentration of acid precipitation may be low enough that plants are not harmed, but in the long run this pollution may increase soil acidity, making large areas suitable for a considerably smaller pool of species than formerly, as shown in Europe (Bobbink et al. 1998, Gunnarsson et al. 2000). This result in dominance of acid tolerant species and disappearance of many rare species, which mostly require high pH (pH > 5; Roem and Berendse 2000).

In summary, the local relationships between richness and pH can be explained by the evolutionary history at the regional scale. Although locally occurring physiological tolerance of species was also significant, it did not obscure the species pool effect. Thus, local patterns in vegetation may be defined on much larger scale in both time and space.

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APPENDIX

A table providing the 85 published studies of vascular plant species richness and soil pH (including correlation coeffecients, mean observed pH, floristc region, longitude, latitude, and reference) used in this study is available in ESA's Electronic Data Archive: *Ecological Archives* E083-046-A1.

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