

## VARIATION IN SPECIES RICHNESS AND SPECIES POOL SIZE ACROSS A pH GRADIENT IN FORESTS OF THE SOUTHERN BLUE RIDGE MOUNTAINS

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**Abstract:** PÄRTEL (*Ecology* 83: 2361–2366, 2002) and EWALD (*Folia Geobot.* 38: 357–366, 2003) suggest that the relationship between local species density and soil pH is determined by regional species pool size, which in turn reflects the relative abundance of soil types during the evolutionary history of the flora. Ewald observed that calcareous sites in Central Europe have higher species density and larger species pools than acidic sites, and argues that this is the consequence of a Pleistocene bottleneck for acidophiles.

The flora of the southern Blue Ridge Mountains USA has always been associated with primarily acidic soils. We used vegetation and soil data from 3328 100 m<sup>2</sup> southern Blue Ridge forest plots to examine the generality of the Pärtel-Ewald hypothesis. The Blue Ridge flora with less than 20% of species confined to sites above pH 4.7 contrasts dramatically with that of Europe. However, regional species pool size increases with pH. Genus- and family-level pools increase with pH, suggesting an ancient origin for this pattern. Mean species density is also strongly positively correlated with soil pH. Thus, both regional species pool size and plot species density of southern Blue Ridge forests fail to conform to predictions derived from the work of Pärtel and Ewald.

The increase in species pool with increase in pH exhibited by southern Blue Ridge forests appears to reflect broad species distributions and tolerance for high pH conditions among species that grow predominantly under acid conditions. We conclude that richness on higher pH sites is a consequence of generally more favorable conditions for plant growth and/or establishment. Ewald may be correct in asserting that the abundance of high pH specialists in Central Europe is an historical artifact, but our data contradict the assertion of Pärtel and Ewald that evolution of a flora in a primarily low pH environment will necessarily translate into a negative correlation between pH and species density in local vegetation.

**Keywords:** Acidophile, Calciphile, Pleistocene, Species density, Soil acidity, Species diversity, Species pool

### INTRODUCTION

EWALD (2003) and PÄRTEL (2002) propose that the pool of species suited to low versus high pH soils in a region should reflect the relative abundance of soil types during the evolutionary history of the flora. They further assert that the size of the regional species pool for a particular substrate should influence the number of co-occurring species in a community. Ewald, Pärtel and others have observed the abundance of high pH specialists in the flora of Central Europe and see in this an apparent contradiction to theory in that this is a region of predominantly acid soils. Ewald resolves the inconsistency by invoking Pleistocene persistence of the flora in regions to the south where high pH soils were dominant.

Although Ewald's case is appealing, it is speculative and based on a sample size of just one region. We set out to test its generality by examining the forests of the southern Blue Ridge Mountains region of the southeastern USA, a region dominated by temperate forests that

contrasts in the dominance of acidic parent material in both its contemporary distribution and in its regions of presumed Pleistocene persistence. The regions in the southeastern USA dominated by calcareous substrate are over a hundred kilometers to the west and northwest in Tennessee and Kentucky, and certainly outside the predominant route of Pleistocene migrations southward toward the Gulf of Mexico or southeastward to the Atlantic Coastal Plain. The occasional occurrences of islands of higher pH soils (i.e. > 6) in the southern Blue Ridge region are associated with primarily intrusive igneous rocks particularly rich in mafic minerals such as amphibolite. Carbonate and serpentine soils are so rare as to be effectively absent. Thus, the plants of the Blue Ridge could not possibly have experienced a recent evolutionary history of primarily calcareous soils or a Pleistocene acidophilic bottleneck of the sort proposed for Europe. As a test of Ewald's thesis, we examine whether the floristic patterns in Central Europe that he attributes to historical context also apply to the upland forests of the southern Blue Ridge Mountains physiographic province (THORNBURY 1965), or whether a different pattern occurs as a possible consequence of the long-time dominance of low pH soils during the evolutionary history of the regional flora. Specifically, we test whether the flora of the southern Blue Ridge Province has a larger regional species pool for relatively acidic habitats, given its history of predominantly acid soils; and whether species pool size explains richness patterns observed at the plot scale.

EWALD (2003) develops his case by first observing, along with PÄRTEL (2002) and others, that temperate (e.g. GRUBB 1987, PEET & CHRISTENSEN 1988) and arctic (e.g. GOUGH et al. 2000) plant communities of neutral soils tend to possess higher species densities than those of acid soils. However, Ewald and Pärtel both attribute the pattern to evolution of the floras in regions dominated by high pH soils. We test whether southern Blue Ridge forests (western North and South Carolina) conform to the general temperate zone pattern of high diversity on high pH sites (e.g., GRUBB 1987, PEET & CHRISTENSEN 1988), or the pattern of high richness on low pH sites predicted based on the evolutionary context experienced by the regional flora.

EWALD (2003) and PÄRTEL (2002) suggest that the species richness of high pH sites in the temperate and arctic regions may be due to a species pool effect (ZOBEL et al. 1998) deriving from a disparity in the number of calciphilous versus acidophilous species (throughout his paper Ewald uses pH as a surrogate for calcium). We examine the generality of this pattern by quantifying variation in species pool size across the pH gradient for southern Blue Ridge forests.

The pattern of increase in regional species pool size with increasing pH found in Central Europe remains if plants are treated at the genus or family level, thus suggesting that the pattern of variation in the species pool with pH has ancient origins. We test the generality of this observation by comparing trends in species, genus, and family pool size across the southern Blue Ridge pH gradient.

Finally, EWALD (2003) attributes the strong positive correlation between pH and species pool size in Central Europe to the large number of high-calcium specialists. He explains that markedly basiphilous and calciphilous plants constitute more than 50% of the Central European vascular flora. As part of our cross-continental comparison, we examine the degree to which southern Blue Ridge forest species are specialists of high versus low pH sites. We conclude by examining the likely generality of the species pool-based conceptual framework

developed by RICKLEFS (1987), PÄRTEL et al. (1996), ZOBEL et al. (1998), PÄRTEL (2002), and EWALD (2003) for explaining patterns in community diversity.

## MATERIALS AND METHODS

### Study area and field methods

We used vegetation plots from the Carolina Vegetation Survey (archived by the North Carolina Botanical Garden). We first examined all plots with soil chemistry information from throughout the Carolinas ranging from maritime forest to high mountains (7390 plots of 100 m<sup>2</sup>) and obtained results generally similar to those reported here. However, we chose to base this paper on plots from the upland forests of the southern Blue Ridge Mountains (western North and South Carolina; see NEWELL et al. 1999 for a map). Our data from that region generally cover the full range of known compositional variation and contain no known bias with respect to inclusion of vegetation or soil types. If there is a bias it is that stratification of potential sampling sites resulted in unusual sites such as those with high calcium or high pH having been included in the database with greater relative frequency than that in the actual landscape.

The southern Blue Ridge Mountains Province of North Carolina and adjacent South Carolina is a physiognomic region formed in Precambrian times by an massive overthrust of predominantly acidic igneous rock. It extends roughly 350 km along a southwest to northeast axis with a maximum width of roughly 130 km and a total area of around 22,000 km<sup>2</sup>. Elevations rise abruptly from around 300 m at the base of the Blue Ridge Escarpment to 2000 m atop the highest peaks. For more details on the environment of the region consult PITTILLO et al. (1998). The landscape of the southern Blue Ridge Province is ancient and its soils are largely derived from mica gneiss, similar felsic rocks, and acidic metasedimentary rock units. The combination of acidic substrate and millions of years of weathering is reflected in the predominance of infertile, acid soils. Extractable aluminum from the upper mineral soil (0–50 cm) generally exceeds 50% of the cation exchange capacity, and often exceeds 90%. Most soils have a pH of less than 5.0 in all horizons (BUOL 1973, GRAHAM & BUOL 1990). Exceptions occur predominately where igneous bedrock contains high levels of mafic minerals such as amphibolite that weather to produce rich, circumneutral soils. During the Pleistocene glacial advances the flora of this region was largely displaced southward toward the Gulf of Mexico or southeastward toward the Atlantic Coastal Plain (DELCOURT & DELCOURT 1987), though the contemporary distribution of endemic species suggests some persistence at low elevations along that portion of the Blue Ridge escarpment that defines the southern edge of the Province (ESTILL & CRUZAN 2001). The region from the southern edge of the Blue Ridge to the Gulf of Mexico and the Atlantic Coastal Plain is similarly dominated by acidic soils (BUOL 1973). The southern Blue Ridge region is well away from areas of periglacial deposition of aeolian sediment (over 500 km from the Mississippi river basin) and experienced none of the loess deposition that significantly enriched soil nutrients over large areas of Europe and North America during and immediately following the Pleistocene.

Vegetation plots of the Carolina Vegetation Survey were generally collected as regional projects. Within a project the landscape was typically stratified by environment and dominant vegetation, with plots evenly distributed across potential vegetation types. A total of 14 such

projects were used for the present analysis, effectively spanning the geographic extent of the Blue Ridge Province of the Carolinas. The dataset analyzed contained 3328 100 m<sup>2</sup> plots (10 × 10 m) scattered across the region. The plots contain 1050 vascular plant species representing 401 genera and 117 families (families follow the traditional family treatment employed in KARTESZ 1999). The entirety of the Blue Ridge Province of North Carolina contains roughly 1800 species (USDA, NRCS 2002), and this includes species of many habitats other than upland forests, such as fields, floodplains, shrublands, rock outcrops, and wetlands. Therefore, we feel our sample plots contain the great majority of the total species pool to be encountered in the southern Blue Ridge Province.

The methodological protocol employed in collecting Carolina Vegetation Survey plots is described in PEET et al. (1998). All plots used in this study were collected between 1990 and 2001. Vascular plant nomenclature was standardized to follow KARTESZ (1999). Plots used in this analysis are 100 m<sup>2</sup> in area, often arranged in clusters of 2–4, and all higher plant taxa were recorded. We chose to include in our analysis all 100 m<sup>2</sup> plots from the upland forests of the Blue Ridge Province where a soil sample had been collected within the plot and analyzed for both pH and Ca. Soil samples represent the top 10 cm of mineral soil (after removal of the litter layer). Available calcium was measured using Mehlich 3 extraction (MEHLICH 1984). All soil analyses were conducted by Brookside Laboratories, Inc., New Knoxville, Ohio. Although small-scale spatial variation in soil chemistry derived from *in situ* weathering of ancient igneous-rocks can be considerable (PALMER & DIXON 1990), soil chemistry estimated from a single soil sample in a 1000 m<sup>2</sup> plot has been shown to be a very strong predictor of vegetation composition (e.g., PEET & CHRISTENSEN 1980, REED et al. 1993, NEWELL & PEET 1998, NEWELL et al. 1999).

## Analysis

EWALD (2003) and PÄRTEL (2002) both discuss a calcium gradient but base their analyses on a pH gradient. We conducted our analyses separately with first pH and then extractable calcium. The results were effectively the same, so we report in detail only the results obtained for the pH gradient.

Forest soils of the southern Blue Ridge region tend to be highly acid, so many more of our plots occurred on acid soils than on basic soils (Fig. 1). We calculated mean species richness of vascular species per 100 m<sup>2</sup> plot for sets of 100 contiguous plots along the pH gradient. Twenty-eight plots were dropped at regular intervals along the plot sequence so as to assign equal numbers of plots to each gradient segment.

Regional species pool generally refers to the set of species in the region that can physically grow under specified environmental conditions (e.g. PÄRTEL et al. 1996, ZOBEL et al. 1998, WILSON & ANDERSON 2001, ZOBEL 2001). A common problem among many studies that examine species pools is that as the spatial scale from which the pool is drawn increases, so does the range of environmental conditions included. Only species that are able to occur under specified conditions should be viewed as occurring in the regional pool (ZOBEL et al. 1998, GRACE 2001, WILSON & ANDERSON 2001). Our approach involved deducing the regional pool from the occurrence of species in a large number of plots delimited by specific environmental conditions. To assess the regional species pool size for a segment of the pH

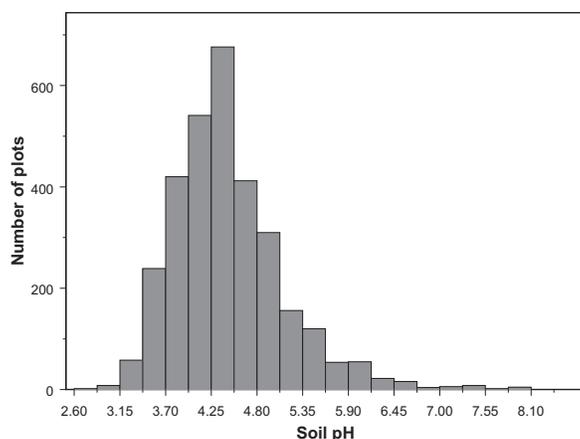


Fig. 1. Distribution along a pH gradient of 3328 vegetation plots in upland forests of the southern Appalachian Mountains of North Carolina and adjacent South Carolina.

gradient we counted the total number of unique species occurring in that segment. Plots on acidic soils tend to have fewer species, so if we used a constant number of plots for counting species occurrences we would accumulate more species along high pH segments than along low pH segments simply because there would be nearly twice as many species occurrences within which to acquire species. To compensate, we ordered all species occurrences within plots along the pH gradient. In total, our 3328 plots contained 101,400 species occurrences. We

then counted the number of unique species occurring per 10,000 species occurrences, omitting occurrences at regular intervals until we retained an even 100,000 occurrences. To assess genus and family pool size we similarly counted the number of unique genera and families occurring within a set of 10,000 species occurrences along the pH gradient.

Species specialization along the pH gradient was examined in several ways. We first calculated species median positions along the gradient and presented this information in the form of curves of the cumulative number of species medians with one curve starting at high pH and one at low pH. However, species medians give effectively no information on the spread of occurrences (niche breadth), so are not ideal for assessing species specialization. To examine specialization we created cumulative curves of species' first occurrences moving from low pH to high and from high pH to low (cumulative number of minimum and maximum species pH values, respectively). To avoid possible problems associated with chance outliers we also examined inner quartile distributions as well as inner 90% distributions. However, the patterns were similar and little new insight was gained by these intermediate strategies, so we present here only curves of cumulative occurrences and cumulative medians.

## RESULTS

Vegetation plots of the Carolina Vegetation Survey were collected in a stratified manner so as to cover all the variation in vegetation within the region. Consequently they should have a more even coverage across the pH gradient than would be expected in a random sample. Nonetheless, examination of the distribution of plots relative to pH shown in Fig. 1 reveals that they are concentrated on low pH sites. The median pH of the 3328 plots in the dataset is 4.3.

Mean species richness of plots in upland forests of the southern Blue Ridge (and also the southeastern United States in general, as revealed by examination of the full Carolina Vegetation Survey database) is strongly positively correlated with soil pH (Fig. 2). These

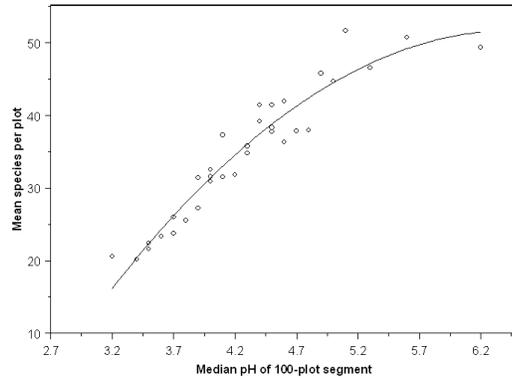


Fig. 2. Average number of species in 100 plots of 100 m<sup>2</sup> area drawn from throughout the upland forests of the southern Appalachian Mountains of North Carolina and adjacent South Carolina. Plots were combined into 33 pH segments of 100 plots each.

forests show essentially the same pattern as reported for Europe, and more generally for the temperate zone (e.g. GRUBB 1987, PEET & CHRISTENSEN 1988, GOUGH et al. 2000, PÄRTEL 2002, EWALD 2003). These results show that the positive correlation observed in temperate forests between pH and species richness is not restricted to glaciated landscapes or floras with a history of association with high pH soils. In particular, the prediction of PÄRTEL (2002) and EWALD (2003) that species density (i.e. richness per unit area)

should be maximal on low pH sites where the flora has evolved in a low pH context is not supported by our results.

Regional species pool size, as assessed by total species in 10,000 species occurrences, increases steadily along the pH gradient (Fig. 3a), a result consistent with the general pattern observed for Europe by Ewald. Again, this pattern is contrary to the predictions of PÄRTEL (2002) and EWALD (2003) that regional species pool size should mirror the relative abundance of conditions that the flora has experienced over its evolutionary history.

The pattern of increase in species pool with pH is repeated at the genus (Fig. 3b) and family (Fig. 3c) levels, suggesting that the increase in regional pool with increase in pH is not a result of recent speciation, but is ancient in origin. This result and interpretation is consistent with that of Ewald for Central Europe.

Given the predominance of acid soils in the southern Blue Ridge, we expected to find more acid specialists than is the case in the European flora. We examined this question by examining the distribution of species ranges and species medians along the pH gradient. Half of all species have their median pH of occurrence below 4.6 (Fig. 4), suggesting at least a tolerance of acid conditions. However, this result should be interpreted cautiously owing to the large number of plots on low pH sites (median plot pH is 4.3).

The distribution of species minimum and maximum occurrences on the pH gradient clarifies the degree to which species are pH specialists. The number of specialists at a given pH can be calculated as the distance between the accumulation curve and its maximum value of 1050 species. The curves of cumulative species encountered moving from low to high pH and high to low cross at pH 4.7. This is the point where there are equal numbers of species confined to one side or the other of this soil pH value. However, in each case we see that the specialists so defined constitute less than 20% of the flora. Further examination of Fig. 4 reveals that there are almost no specialists confined to sites above pH 5.7 or below 4.1. We acknowledge that the high concentration of our plots at low pH values might have influenced

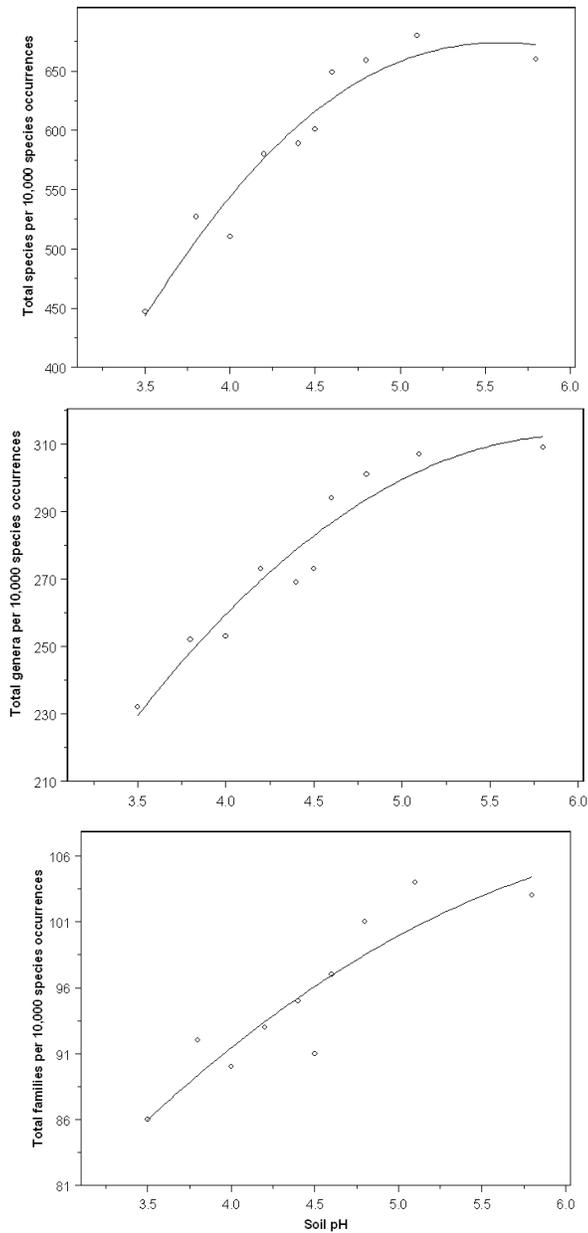


Fig. 3. (a) Species pool for a pH range calculated as the total number of species occurring in a set of 10,000 species occurrences drawn from 3328 plots of 100 m<sup>2</sup> distributed throughout the upland forests of the southern Appalachian mountains of North Carolina and adjacent South Carolina. (b) Genus pool calculated as above. (c) Family pool as calculated as above.

the results of this analysis, but inclusion of more plots at high pH would only have served to broaden perceived species niche breadths and thus to have shown even less specialization than we observed.

The southern Blue Ridge flora with less than 20% of the flora confined to sites above pH 4.7 contrasts dramatically with the European flora where over 50% of the flora has an Ellenberg R value of 7–9. An R-value of 7 indicates a plant of moderately acid to moderately basic conditions, entirely absent from strongly acid soils. If we define strongly acid as 5.5, only about 5% of the flora of the southern Blue Ridge could be assumed to have an Ellenberg R of 7–9, and if we are more conservative and define strongly acid as pH 5 we still have less than 20% with R-values of 7–9. This is not a landscape of obligate high pH species.

Inevitably there are some outliers in absolute minimum and maximum values that distort species ranges. A more conservative test is to look at species median positions. EWALD (2003) reports that 55% of all species in the central European vascular flora “prefer” to grow on calcareous or at least very base-rich soil. If we use median pH as an indicator of “preference”, then we observe that less than 15%

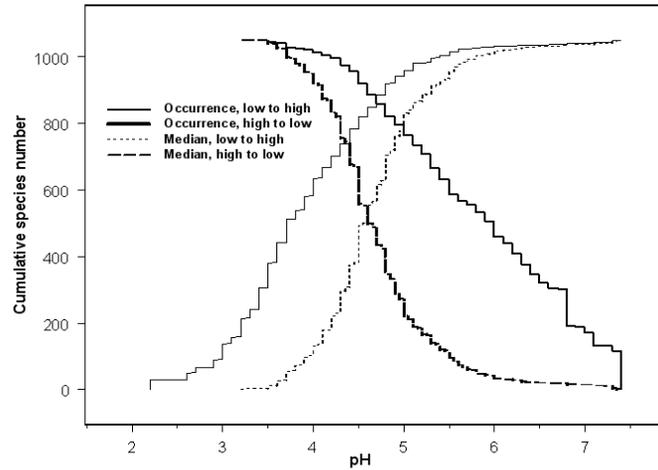


Fig. 4. Cumulative species occurrences and cumulative species median positions encountered in 3300 100 m<sup>2</sup> plots when moving across the pH gradient from low to high, and from high to low, in upland forests of the southern Appalachian Mountains of North Carolina and adjacent South Carolina.

of the flora of the southern Blue Ridge “prefers” to grow above pH 5.5. We conclude that the flora of the southern Blue Ridge Mountains is far poorer in high pH specialists than is the European flora.

## DISCUSSION

### Assessment of species response to environment

Ultimately, assessment of species response to environment must depend on field observations of species behavior. Indicator value systems such as those developed by Ellenberg (ELLENBERG et al. 1991) allow prediction of environment from vegetation data, if adequate calibration has been employed. Ewald used Ellenberg values for his analysis of central European vegetation. For our analysis of the southern Blue Ridge forests we lacked Ellenberg values and instead used records of species distribution linked with measurements of soil chemistry. There are potential problems with use of the Ellenberg values. As ZOBEL et al. (1998) point out, Ellenberg values indicate optimum and not amplitude, so direct observations that include both range and central tendency should be of greater utility for comparisons. In addition, direct comparisons with other regions lacking Ellenberg values are not possible. Finally, the validity of the Ellenberg values must be taken on faith or carefully tested. Recent evaluations of Ellenberg values have cast some doubt on their meaning, precision and accurateness (e.g. SCHAFFERS & SÝKORA 2000, WAMELINK et al. 2002). In particular, WAMELINK et al. (2002) observe that Ellenberg indicator values for acidity appear to be biased towards the values that experts expect for the various phytosociological classes. We recommend that future studies of potentially broad vegetation patterns, wherever possible, be based on direct observation of the environment so as to facilitate comparison with other studies.

### **The imprint of biotic history on the species pool**

Regions of possible periglacial persistence of the Blue Ridge flora are all predominantly acidic. A bottleneck of the type proposed by Ewald for Europe would not have been possible for the Southern Appalachian region. Our southern Blue Ridge data differ strikingly from those of Central Europe in that there are rather few specialists of high pH sites. Here, at least, there seems to be a contrast between the regions attributable to the contrasting histories of the two biotas. However, species pool size is strongly positively correlated with pH in southern Blue Ridge forests, suggesting that this pattern is not a consequence of a Pleistocene bottleneck and that some other explanation should be sought. The answer is to be found in the breadth of distribution of species. Roughly half of the species in the regional pool occur on sites with pH over 6.0, despite the relatively small number of plots at the high pH end of the gradient. In short, the increase in species pool with increase in pH exhibited by the vegetation of the southern Blue Ridge Mountains appears to reflect broad species distributions and tolerance for high pH conditions among species that grow predominantly under acid conditions. However, it should be noted that the southern Blue Ridge largely lacks sites with extremely high pH and high nutrient stress such as found on carbonate and serpentine sites of Europe, which could explain the contrast between our results and those of others such as GIGON (1987). The few examples of such sites in the southern Blue Ridge (e.g. MANSBERG & WENTWORTH 1984) tend to have substantial numbers of specialists, but the sites are so rare as to have little impact on the overall data structure and their physiognomy was such that they generally did not qualify as forests (> 60% canopy cover) for inclusion in the dataset.

### **Control of community diversity**

PÄRTEL et al. (1996) propose a general conceptual theory of species pool size and community diversity. They suggest that the size of the regional species pool is determined by evolutionary and historical processes, the size of the actual species pool (the pool of species to be found in the immediate vicinity of a site and thus not dispersal limited) is largely determined by the regional species pool, and the species density of a community is largely determined by the actual pool. PÄRTEL (2002) went on to assert that the effect of evolutionary history on local-scale diversity patterns is pervasive and global in distribution. Specifically, he asserted positive relationships to occur between species density and pH where the pool of species suited for high pH soil is larger than the pool of species suited for low pH soil, and that negative relationships occur between species density and pH where the pool of species suited for low pH soil is larger than the pool of species suited for high pH soil. EWALD (2003) proposed an explanation as to why Central Europe appears to be an exception to this general pattern.

The Pärtel-Ewald theory does not fit our southern Blue Ridge Mountain data. The Blue Ridge has a long history of vegetation dominated by acid soils, and the flora has a preponderance of acid-tolerant species, half the species having a median occurrence at pH 4.6 or lower. But this is, nonetheless, a region where the regional species pool increases with pH, and mean species density is twice as high on high pH sites as on low pH sites.

The explanation for the mismatch of theory and the southern Blue Ridge data appears to be that there are many species with broad tolerance that can occur on high pH sites. A large

proportion of the plants found on acid sites is also found widely on higher pH sites, whereas the reverse is not true. The prevailing skew toward high pH in species distributions is indicated in Fig. 4 by the greater area between the high-to-low occurrence and median lines than between the low-to-high occurrence and median lines. In general high pH sites are less stressful for plants (at least high pH in the sense of the Blue Ridge region where pH rarely exceeds 6.5 and carbonates and serpentines are effectively absent). We observe that several recent studies have shown that more base-rich sites are more generally invasible (e.g. STOHLGREN et al. 1999, DAVIS et al. 2000, BROWN & PEET 2003), presumably owing to greater resource availability on high-base sites. We conclude that richness on higher pH sites is a consequence of the generally more favorable conditions and that this can serve to at least partially counter-balance differences in regional floristic history and evolution. EWALD (2003) may well be correct in asserting that the abundance of high pH specialists in Central Europe is an historical artifact, but our data suggest that it is premature to attribute the high species density of high pH sites to this same historical artifact, either in the southern Blue Ridge or in Central Europe.

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