Trends of herbaceous species richness in relation to topography in the Ridge and Valley province of the southern Appalachians

by Anna Hess

Trends of herbaceous species richness were explored in 38 plots over four terrain types (cove, lower slope, upper slope, and ridge) in the Ridge and Valley province of the southern Appalachians. Herbaceous species richness per plot and species-area curves showed the same trends over the terrain types. Species richness was greatest in coves and decreased along the topographical gradient to reach the lowest value on ridges. Some habitat specialization was evident for individual herbaceous species but other species were found in both extremes, cove and ridge. Herbaceous percent cover, a measure of productivity, was the best predictor of herbaceous species richness per plot and analyses suggested that the greater productivity in coves was linked to more heterogenous soil resources which created more niches for herbaceous species. Tree species-area curves showed a similar trend along the topographical gradient but the similar number of tree species found in coves and ridges suggested that the tree species richness was not a cause of herbaceous species richness but was instead a result of the cause. The study suggests that productivity may be a cause of the extraordinary diversity found in the southern Appalachians.

Introduction:

The southern Appalachian mountains are a temperate region with an extraordinary diversity, especially among herbaceous plants (Davis, 1996). Many scientists have sought to explain peaks of diversity since traditional ecological thought predicts that each area will have only as many species as there are limiting resources. Tilman and Pacala (1993) concluded that greater diversity can be the result of more than one limiting resource, spatially heterogenous resource supply rates and physical factors, recruitment limitation, temporal heterogeneity of resources, localized mortality, or influence by higher trophic levels. This study explores the cause of the high herbaceous species richness in the southern Appalachians by focussing on the effects of topographical variation and its effects on heterogeneity.

The diversity in the southern Appalachians is greatest in the cove hardwood community which is found in coves and on moist slopes and is characterized by shared dominance in tree species and abundant herbaceous growth (Braun, 1950). Several hypotheses have been posited to explain the diversity in the cove hardwood community, including continuous occupation of the area by plants for 200 million years while nearby areas were glaciated (Wallace, 1993) and a more short term stability due to the moist environment which resists forest fires (Walker, 1978). However, since the diverse cove hardwood community is found primarily in coves, other factors linked to topography are also likely to have important effects on the composition of herbaceous plants in the cove hardwood forests. A study by Denslow (1995) in a tropical rainforest in Costa Rica found higher tree species richness on slopes than on ridges, which suggests that a topographical gradient in species richness may not merely result from the different tree communities found along the gradient in the southern Appalachians.

Whittaker (1956) showed that some herbs specialize to different parts of the mountain landscape on tall mountains. Specialization along the topographical gradient would create different herbaceous communities in the coves and ridges. However, no studies have explored the magnitude of change in elevation necessary to segregate herbaceous species along the topographical gradient. If any topographical habitat specialization occurs in the Ridge and Valley province of the Appalachian mountains where the ridges are relatively low, we would expect the greatest species richness on slopes where ridge and cove herbaceous communities overlap unless herbs are very tightly specialized to topographical positions.

Topography could also affect the herbaceous community indirectly through the trees. Several different tree communities are found in the southern Appalachians, but the ridge and valley province is predominantly made up of the oak-hickory community on ridges and dry slopes and the cove hardwood community in coves and on moist slopes (Braun, 1950). Since trees have been shown to influence the chemical composition of the soil on the microenvironment level (Finzi, 1996; Zinke, 1962; Boettcher and Kalisz (1990) showed that trees can affect the soil even in mixed species stands on steep slopes in the southern Appalachians), a more species rich tree canopy would be predicted to create a more heterogenous soil chemistry which could provide niches for more herbaceous species. Therefore, if heterogenous soil chemistry resulting from the influence of individual canopy trees is important, herbaceous species richness should be greatest in the cove hardwood community which has a large tree species richness.

Disturbance regime is another factor which differs along the topographical gradient. Since forest fires are usually repressed, individual tree mortality is the major natural disturbance event in southern Appalachian forests. Clinton et al. (1994) noted that the type of tree mortality differs in the two tree communities in the area - oak-hickory associations usually have standing dead snags while trees in the cove hardwood association fall and create treefall gaps. (Although the only study of tree mortality in the cove hardwood community was a study performed by Runkle (1982) in old growth, secondary forests are likely to have similar dynamics.) Treefall gaps provide habitat for early successional species which require more light than can be found under a closed forest canopy. Since the standing snags found on ridges do not provide this open canopy required for early successional species, treefall gaps would result in a greater species richness in coves.

Productivity may also vary along the topographical gradient. Boettcher and Kalisz (1990) noted that soil was most fertile under tulip-trees (*Liriodendron tulipifera*) which are found almost exclusively in coves, was intermediately fertile under other cove hardwoods, and was least fertile under hemlocks (*Tsuga canadensis*) on slopes. Furthermore, coves are a more moist environment than area exposed ridges, which may lead to greater productivity. The link between diversity and productivity has been debated (reviewed in Maranon and Garcia, 1997) but most scientists recognize a peak in diversity either at an intermediate productivity or at the greatest productivity, which predicts a maximum herbaceous species richness either on slopes or in coves.

This study seeks to distinguish between potential effects of topography on the herbaceous community by exploring trends in herbaceous species richness.

Study Area:

The study area consisted of the 2007 acres of forested land contained within Steele Creek Park in Sullivan County, Tennessee. The area is within the Ridge and Valley province of the southern Appalachian Mountains and the main ridges run from NE to SW. The area ranges in elevation from approximately 1300 to 2200 feet above sea level and is underlain by Athens shale. The soil consists of Hamblen, Whiteburg, and Prader silt loams and Dandridge soils which formed from calcareous shale (Howard, 1972).

Two forest communities are found in the area. Coves and lower or sheltered slopes contain the species rich cove hardwood community. Elsewhere in the park, the oak-chestnut community has been replaced by an oak-hickory community. Most of the park was clearcut in the 1940's, so the current forest is recovering second growth.

Methods:

Randomly generated coordinates were used to select 38 plots within the park, including 8 ridges, 7 lower slopes, 15 upper slopes, and 8 coves. Plots were surveyed during nine weeks between May 21 and August 6, 1999, with at least 1 cove, 1 ridge, and 3 slope plots surveyed during each week. Plot locations were approximated using a contour map, then by pacing an additional random distance (between 0 and 50 meters) in a random direction to prevent bias. Ridge plots were defined as those found on ridge crests which had an average slope of less than 20^{o}. Cove plots were found in the valley between two slopes and had an average slope of less than 20^{o}. All other plots were slope plots. A slope plot was estimated as being in the lower, middle, or upper third of the hillside and plots found in the middle third of the hillside were rejected to prevent overlap of the upper and lower slope terrain types.

Six 1 m^2, randomly located quadrats were surveyed in each plot to determine the herbaceous community. Quadrat locations were rejected if a rock, creek, or fallen log covered over half of the quadrat or if the quadrat overlapped the area in another quadrat. Each herbaceous species within the quadrat was identified and the percent cover of each species was approximated (as 1% or to the nearest 5%). Species richness for the plot was calculated as the total number of unique herbaceous species found over all quadrats. Grasses and sedges were excluded from the analysis, as were seven other genera (*Aster*, *Uvularia*, *Impatiens*, *Lactuca*, *Arabis*, *Sanicula*, and *Viola*), due to inability to identify individuals to species. The total herbaceous percent cover for each quadrat was calculated, as was the average herbaceous percent cover over all quadrats in a plot.

Degree of slope and depth of soil horizons were measured in each quadrat and an average of each value was calculated at each plot. Slope was measured as the number of meters from the end of a horizontally levelled meter stick to the ground. The degree of slope was calculated as the arctangent of the measured slope. A soil pit in the middle of the north side of the quadrat was used to measure the depth of the A and O horizons.

At each plot, the diameter at breast height (dbh) of each tree within an 11 m radius was measured. Trees with a dbh greater than or equal to 6 cm were identified to species. Recent treefall gaps were noted.

Species-area curves were constructed using a Linux program which randomly ordered the plots 1000 times and calculated species-area curves for each randomization. The 1000 values of unique species for each rank were used to create a mean value. 95% confidence intervals were reported for each rank by removing 2.5% of the highest and 2.5% of the lowest values for the rank and reporting the highest and lowest remaining values. Species-individual curves for trees were created in the same way, but with each rank being an individual tree rather than a plot.

Results:

Herbaceous species:

The herbaceous community was very species rich - 108 species were found in the 38 plots sampled. Specialization of these herbs along the topographical gradients was explored by graphing curves of the terrain types in which each species was found. Considering only the 22 species which were highly represented (defined as being found in at least 10 plots in the study), 12 species were found in all terrain types. However, 10 species which were highly represented in other terrain types were never found on ridges, suggesting that some specialization was occurring along the topographical gradients. Nevertheless, the species found in all terrain types suggests that herbs were not all segregated along the topographical gradients.

Herbaceous species richness per plot showed a trend of increasing richness from ridges down to coves (Figure 1). ANOVA showed a statistically significant effect of terrain type on herbaceous species richness ($p<0.0001$) and a Tukey/Kramer post-hoc showed that the richness was statistically significantly less in upper slopes and ridges than in coves and lower slopes ($p<0.05$). The same trend is evident in herbaceous species-area curves (Figure 2) and the 95% confidence intervals for all but lower slope and cove do not overlap.

Treefall gaps were not evenly distributed over the terrain types. Coves, lower slopes, upper slopes, and ridges contained 2, 5,1, and 0 treefall gaps, respectively, which made up 25, 33, 14, and 0 percent of the total number of plots surveyed. When sites which contained evidence of recent treefall gaps were removed, species-area curves maintained the same trend of the greatest herbaceous species richness in coves and the least on ridges (Figure 3). Furthermore, Figure 4 shows that the herbaceous species richness of plots containing recent treefall gaps does not seem to be different from the species richness of plots without gaps in the same terrain type. The lack of an effect of recent treefall gaps on trends of species-area curves and species richness is supported by the presence of only two species which could be termed gap specialists (i.e., were found in more than 1 plot and were found in only gap plots). Poke (*Phytolacca americana*) and Common Milkweed (*Asclepias syriaca*) were each found in two gap plots and in no non-gap plots.

Average herbaceous percent cover per plot was also linked to terrain type with the greatest average cover in cove plots and least in ridge plots. ANOVA showed a statistically significant effect of terrain on cover ($p<0.0001$; Figure 5). Furthermore, cover was positively linked to herbaceous species richness (Figure 6). An ANCOVA showed a statistically significant effect of cover on richness ($p=0.0272$) and no statistically significant interaction with terrain type ($p=0.529$), so cover had a similar effect on richness at each terrain type. When the ANCOVA removed variation in richness due to cover, there was no statistically significant effect of terrain on richness (p=0.0636).

Although herbaceous percent cover was a very good indicator of herbaceous species richness per plot, cover was not a good indicator of richness per quadrat (Table 1). Separate ANCOVAs were performed at each terrain type to test the effect of plot (since quadrats within the same plot were not independent of each other) and cover on each quadrat's herbaceous species richness as well as to test for an interaction between plot and cover. The analysis on the ridge showed a statistically significant interaction between plot and cover (p=0.0087), which means that cover had different effects on the richness in different plots and thus cover was not a good indicator of richness on ridges. In coves and upper slopes, cover had no statistically significant effect on cover (p=0.2339 and p=0.1737, respectively), suggesting that cover was not a good indicator of richness in coves or upper slopes. The analysis for lower slope quadrats was the only ANCOVA which showed a statistically significant effect of cover on richness (p=0.006) and the trend was the same as that on the plot scale, toward greater cover being linked to greater richness.

Dividing the total herbaceous species richness by the average herbaceous percent cover at a plot gives an approximation of the number of species found in 6% cover in the plot. (The ratio gives an approximation of the number of species in 6% cover since the average percent cover is the total cover over 6 quadrats divided by 6.) ANCOVA showed a statistically significant effect of terrain type on this ratio with the value for the ridge statistically significantly higher than the value at all other terrain types (Figure 7; p=0.0027; Tukey/Kramer post hoc, p<0.05).

There was a trend toward a deeper A horizon in cove plots and a shallower A horizon in ridge plots (Figure 8). ANOVA showed a statistically significant effect of terrain on the depth of the A horizon (p=0.0005). There was a statistically significant negative correlation between the depth of the A horizon and the depth of the O horizon (Figure 9; p=0.0013). However, an ANCOVA showed that depth of the A horizon did not have a statistically significant effect on herbaceous percent cover (p=0.8290) and that when the variation in cover due to the depth of the A horizon was removed, terrain was still a statistically significant predictor of herbaceous percent cover (p=0.0473). There was no statistically significant interaction between terrain type and depth of the A horizon (p=0.0791).

ANCOVA showed a statistically significant interaction between terrain and depth of the A horizon in relation to herbaceous species richness (p=0.0348), suggesting that depth of the A horizon had a different effect on richness at different terrain types. Therefore, depth of the A horizon was not a good indicator of herbaceous percent cover or herbaceous species richness.

Tree species:

Of the 34 tree species found in the 38 plots, 28 were found in coves and/or ridges. When species found in only one plot in the study were excluded, the cove and ridge communities had 14 species in common and each of the cove and ridge had 5 species not found in the other terrain type. Therefore, a larger percentage of the tree species than of the herb species were specialized to ridges.

Tree species-area curves (Figure 10) were plotted for each terrain type. Species-area curves did not appear to level off at any terrain type and the 95% confidence intervals overlapped for most terrain types. However, Condit *et al.* (1996) showed that species-individual curves were more useful in assessing and comparing diversity than species-area curves because richness tends to increase more predictably with increasing numbers of stems than with increasing area. Therefore, species-individual curves were also considered.

Density of trees was lowest in cove plots and greatest in ridge plots, so the species-individual curves (Figure 11) contained 102 and 290 trees for the cove and ridge curves, respectively. The 95% confidence intervals for cove and ridge curves did not overlap and since the ridge curve leveled off, although the cove curve did not, we can conclude that the cove tree community is more species rich than the ridge tree community. The upper slope species-individual curve leveled off at a slightly lower number of species than the cumulative number of cove tree species. A comparison of the lower slope and cove species-individual curves is impossible since neither curve leveled off due to the low tree density at those terrain types. However, overall, the same trends seem to be evident in tree species-individual curves as in the herb species-area curves.

Discussion:

The 900 feet maximum change in elevation between coves and ridges in the study area was not enough to cause extensive specialization of herbs to the cove or ridge habitat. Furthermore, species richness per plot was greatest in coves rather than on slopes, suggesting that slopes were not an ecotone between two distinct habitats for herbaceous species. However, some species were absent from ridges which were well represented in other terrain types, suggesting that the herbaceous community in coves contains more well-represented specialists than does the herbaceous community on ridges.

Species richness per plot (Figure 1) and cumulative species richness over all plots (Figure 2) decreased along the topographical gradients from coves to ridges. Since the number of recent treefall gaps showed a similar trend, treefall gaps could have caused the greater species richness in coves in either of two ways. Treefall gaps are most likely to increase the cumulative herbaceous species richness by allowing the presence of early successional species which are unable to become established under a closed canopy. In this study, only two potential gap specialists were found and species-area curves which excluded plots containing recent treefall gaps (Figure 3) showed the same trend as did curves which included all plots, so gap specialists were not the cause of the trend of species richness along the topographical gradients. Treefall gaps could also increase species richness per plot if the greater availability of light increased the number of individuals found in the plot and thus increased the species richness. However, species richness was approximately the same in gap and non-gap plots of the same terrain type (Figure 4). Therefore, gaps were not the cause of the greater species richness observed in coves in this study.

Recruitment limitation may be very high in the study area, which would explain the lack of early successional species in plots with recent treefall gaps. Studies have shown that recruitment limitation for trees in the southern Appalachians is quite high (Clark et al., 1998; although Clebsch and Busing (1989) concluded that recruitment limitation was low for trees in secondary forests adjacent to old growth stands). Recruitment limitation for herbs in the area has not been studied, but since herbs use many of the same (wind, mammal, bird) or slower (ant, vegetative) dispersal methods as do trees (Bierzychudek, 1982), recruitment limitation is likely to be even greater for herbs.

Although recent treefall gaps did not explain the differential herbaceous species richness along the topographical gradients, soil heterogeneity resulting from past treefalls may have had an effect. Beatty (1984) showed that understory plant species segregate spatially with species specializing in pits or mounds from fallen trees. Since the pits and mounds resulting from treefalls may remain on the forest floor for centuries, a greater incidence of treefalls in coves than on ridges could result in a more heterogenous forest floor with more opportunities for spatial segregation of herbs leading to a greater species richness. Coves also often contain creeks which would allow more spatial segregation along the moisture gradient. Although no quadrats in this study were within creeks, segregation along the moisture gradient could have increased the herbaceous species diversity in coves. Therefore, although recent treefall gaps did not seem to be the cause of the greater species richness in coves, we cannot reject the hypothesis that greater heterogeneity in the coves is the cause of the trend of species richness.

Productivity, measured as the herbaceous percent cover per plot, was the best predictor of herbaceous species richness (Figure 6). The trend of decreasing cover along the topographical gradients from coves to ridges (Figure 5) is likely to be due to either soil moisture or soil nutrients. Coves are assumed to be more moist than ridges, but no analysis of soil moisture content was performed, so we cannot determine whether amount of water was the cause of the trend in productivity.

Depth of the A soil horizon was used as a rough indicator of the soil nutrient concentrations. The A horizon was deepest in coves and shallowest on ridges (Figure 8), suggesting that the depth of the soil may be the cause of the trends in productivity. Deeper A horizons in coves are likely to develop due to faster decomposition of leaves from cove hardwood trees than from the oaks and hickories found on ridges. This hypothesis is supported by the negative correlation between the depth of the A and O horizons (Figure 9) which suggests that a similar amount of organic matter is deposited in coves and on ridges, but that the leaves in coves decay more rapidly, resulting in a deeper A horizon and less leaf litter (O horizon) while the ridges have slower decomposition with more nutrients bound up in the leaf litter. However, the depth of the A horizon was not a good predictor of the herbaceous percent cover or species richness. A more precise measure of the actual concentrations of different nutrients in the soil of coves and ridges would be necessary to determine whether soil nutrients are the cause of greater productivity in coves.

Although herbaceous percent cover is a very good predictor of herbaceous species richness, the correlation between the two factors is more complicated. Productivity could influence species richness by changing the number of individuals found in each quadrat. Condit *et al.* (1996) showed that species richness is better predicted by the number of individuals surveyed than by the area surveyed. Therefore, the greater richness in coves could simply be due to the greater percent cover sampled in coves. This hypothesis assumes that cover is merely a measure of the number of individuals inhabiting the area, but cover is also a measure of size of individual plants. Figure 7 showed that 1% cover in a ridge quadrat contained more species than 1% cover in a cove quadrat. Therefore, if we assume that species richness is proportional to number of individuals surveyed, 1% cover in a ridge quadrat contains more, smaller individuals than 1% cover in a cove quadrat. This extrapolation suggests that productivity is greater in coves and that, even though a smaller total amount of cover was surveyed on ridges due to the sparse growth there, the discrepancy in number of individuals surveyed between coves and ridges was not as large as it may have appeared.

The lack of a statistically significant relationship between cover and richness in most terrain types on the scale of the quadrat lends further credence to the idea that productivity is not affecting richness merely by increasing the number of individuals sampled in more productive areas. Instead, productivity is likely to be increasing species richness by increasing heterogeneity. Tilman *et al.* (1996) have suggested that a more productive environment with greater concentrations of nutrients increases the heterogeneity of the concentrations of soil nutrients and thus creates more niches and a greater species richness. This hypothesis suggests that the absence of a trend between cover and richness at the quadrat level is due to resource heterogeneity at a larger scale than 1 m^2.

Species-individual curves (Figure 11) for trees showed a similar trend as species-area curves for herbs. However, the tree communities showed more specialization to the cove and ridge habitats than did herbaceous species. The specialization of trees is not unexpected since Braun (1950) noted the specialization of trees along topographical gradients when she distinguished between the oak-hickory community of ridges and dry slopes and the cove hardwood community of coves.

The greater tree species richness in coves could directly influence the herbaceous species richness through microsite soil chemistry effects under individual trees, creating a more heterogenous environment which could be used by more herbaceous species. However, the total number of trees found in this study in coves and on ridges differed by only two species; the trend of more tree species in coves was extrapolated from the species-individual curves in which the cove curve was almost linear and the ridge curve had levelled off. Since the total number of trees found in coves and ridges in the study was very similar, the trend in tree species richness is unlikely to be a direct cause of the trend in herbaceous species richness and is instead likely to be a result of the same cause.

The differences between the tree species-area (Figure 10) and species-individual (Figure 11) curves raises an important procedural point. The increased number of data points in a species-individual curve provides a finer resolution, resulting in curves with 95% confidence intervals which are less likely to overlap when small areas but large numbers of individuals are sampled from populations with different total numbers of species. However, the different trends along the topographical gradients which are seen in tree species-area and species-individual curves raises the possibility that the herbaceous species might show different trends if species-individual curves were plotted. The cause of the changing trends for tree curves was the much greater tree density on ridges which allowed the ridge species-individual curve to level off within 8 plots and the upper slope curve to level off in 7 plots while the cove curve did not level off. The opposite trend is evident among herbaceous individuals with the greatest herbaceous percent cover in coves. Since the ridge herbaceous species-area curve had the lowest slope, suggesting that it was beginning to level off despite the lower amount of cover surveyed, the trends evident in the herbaceous species-area curves are unlikely to change. Furthermore, the species richness/percent cover ratio discussed previously suggests that the ridge curve does not contain as many fewer individuals than the cove curve as might be expected due to the great difference in percent cover between the two areas. Therefore, the trend of greater herbaceous species richness in coves is likely to be maintained when a larger area is surveyed.

The hypothesis which best explained the evident trends of species richness along the topographical gradients was that greater heterogeneity in soil resources as a result of greater productivity allowed the coexistence of more herbaceous species. Although this study only explored differences in herbaceous species richness along a topographical gradients in the ridge and valley province of the southern Appalachians, the tremendous species richness of the entire province may be due to productivity as well. Although specialization along the topographical gradients was not strongly evident among herbs in this study, such specialization may be a cause of the southern Appalachians' diversity on a larger scale.

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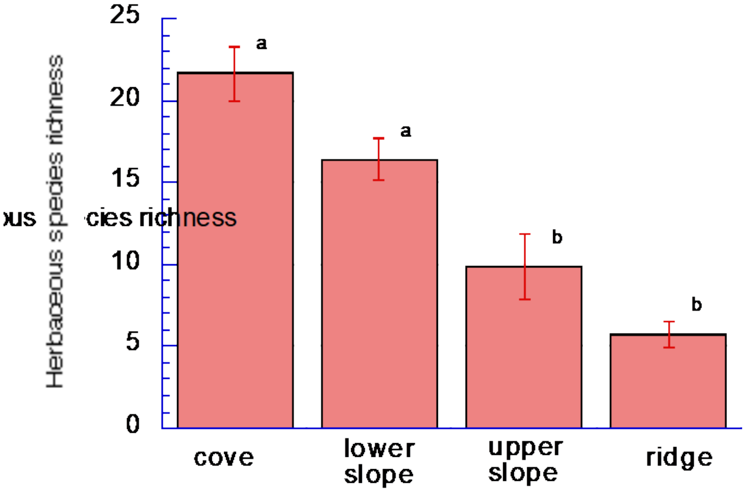

Figure 1: Herbaceous species richness versus terrain type. ANOVA showed a statistically significant difference in the herbaceous species richness per plot at different terrain types ($p<0.0001$). Letters refer to statistically significantly different means (using Tukey/Kramer post hoc, $p<0.05$). Error bars indicate standard error.

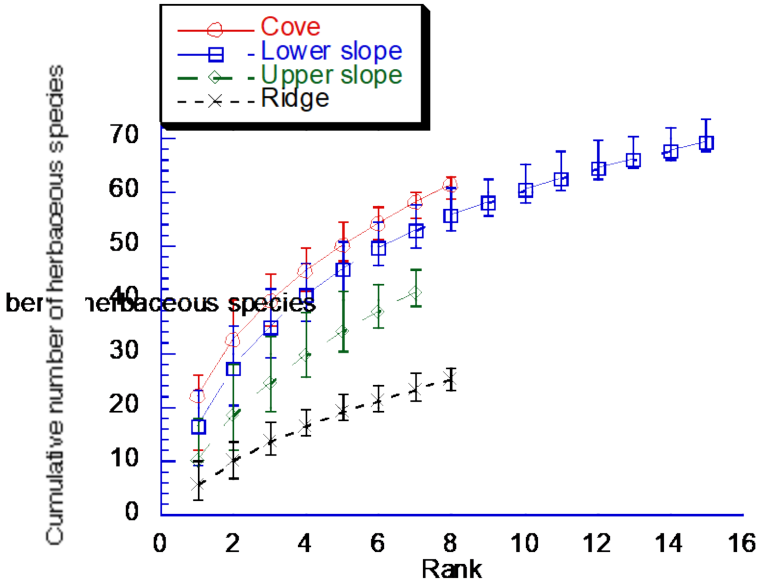

Figure 2: Each curve represents 1000 random rearrangements of the order of the plots. The mean and 95% confidence intervals are plotted.

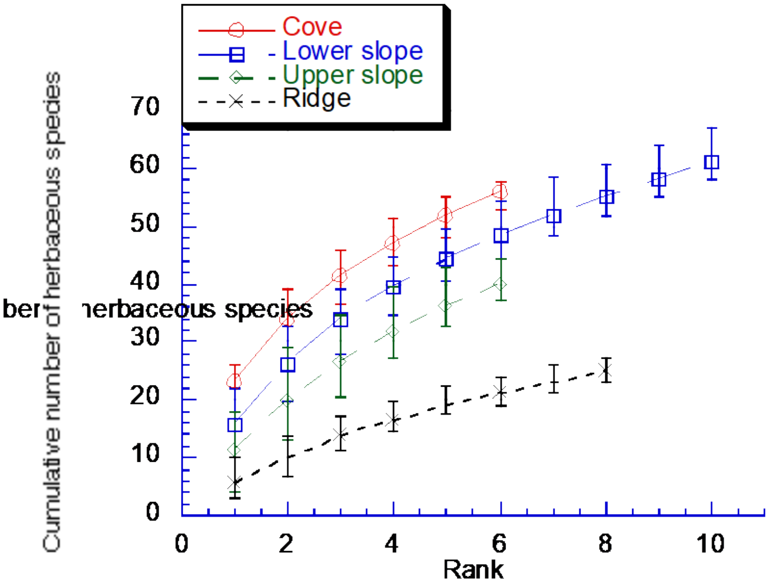

Figure 3: Species-area curves excluding plots which contained recent treefall gaps. Each curve either represents all of the possible arrangements of the order of the plots or 1000 random rearrangements. The mean and 95% confidence intervals are plotted.

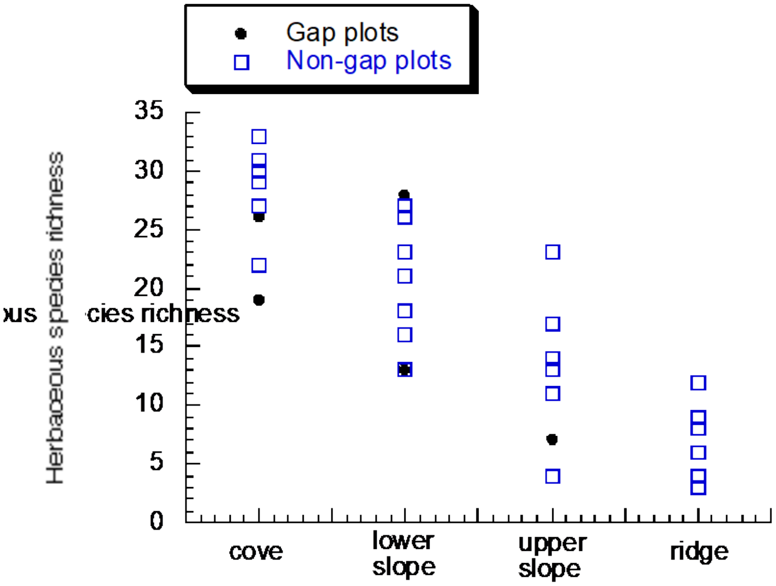

Figure 4: Herbaceous species richness for sites with and without recent treefall gaps. Within each terrain type, gap sites seem to have randomly distributed species richness.

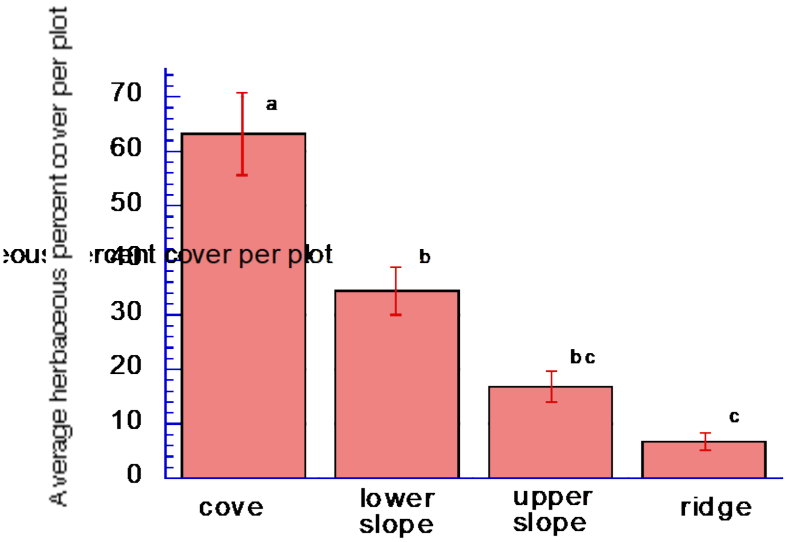

Figure 5: Herbaceous percent cover versus terrain type. ANOVA showed a statistically significant difference in the herbaceous percent cover per plot at different terrain types ($p<0.0001$). Letters refer to statistically significantly different means (using Tukey/Kramer post hoc, $p<0.05$). Error bars indicate standard error.

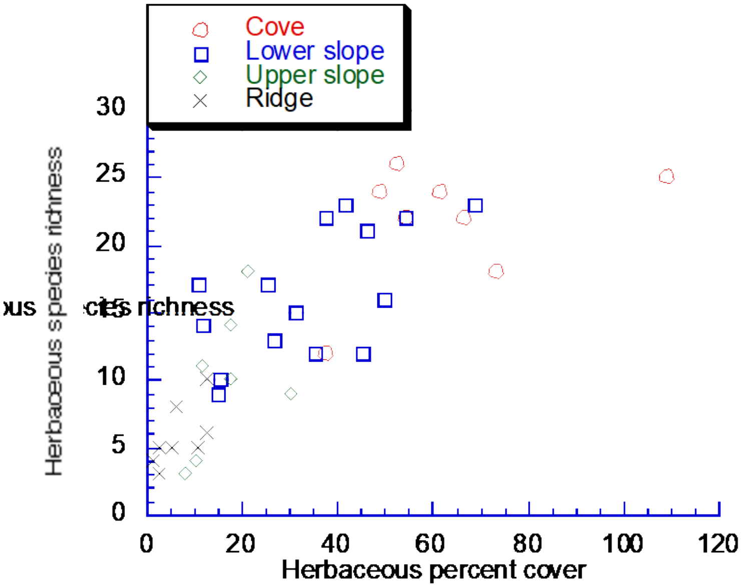

Figure 6: Herbaceous species richness versus herbaceous percent cover. Cover has a statistically significant effect on richness (ANCOVA; $p=0.0272$). ANCOVA showed no statistically significant interaction ($p=0.529$) between cover and terrain, so cover has the same effect on species richness at all terrain types.

Table 1: ANCOVA on the effect of plot and herbaceous percent cover on the herbaceous species richness per quadrat.

Terrain	plot * cover interaction	plot	cover
Cove	p=0.4331	p=0.8067	p=0.2339
Lower Slope	p=0.1762	p=0.0701	p=0.0006
Upper Slope	p=0.3378	p=0.0091	p=0.1737
Ridge	p=0.0087	---	---

Figure 7: The ratio of herbaceous species richness to herbaceous percent cover versus terrain type. ANOVA showed a statistically significant difference in the ratio per plot at different terrain types (p=0.0027). Letters refer to statistically significantly different means (using Tukey/Kramer post hoc, p<0.05). Error bars indicate standard error.

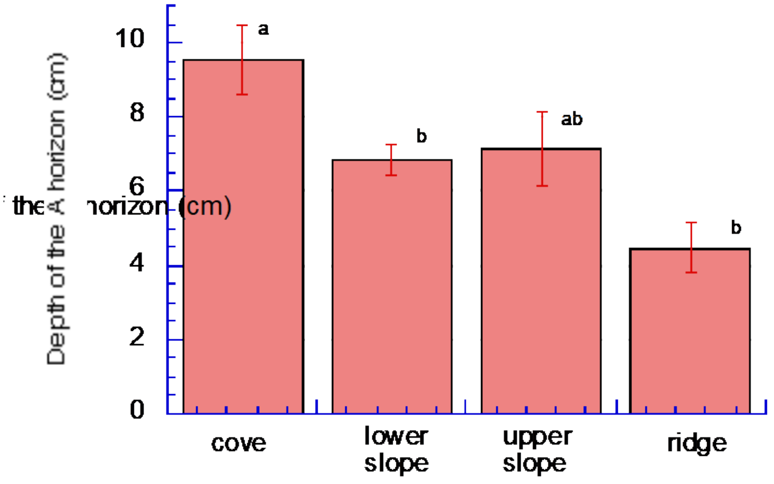

Figure 8: The depth of the A horizon versus terrain type. ANOVA showed a statistically significant difference in the depth of the A horizon at different terrain types ($p=0.0005$). Letters refer to statistically significantly different means (using Tukey/Kramer post hoc, $p<0.05$). Error bars indicate standard error.

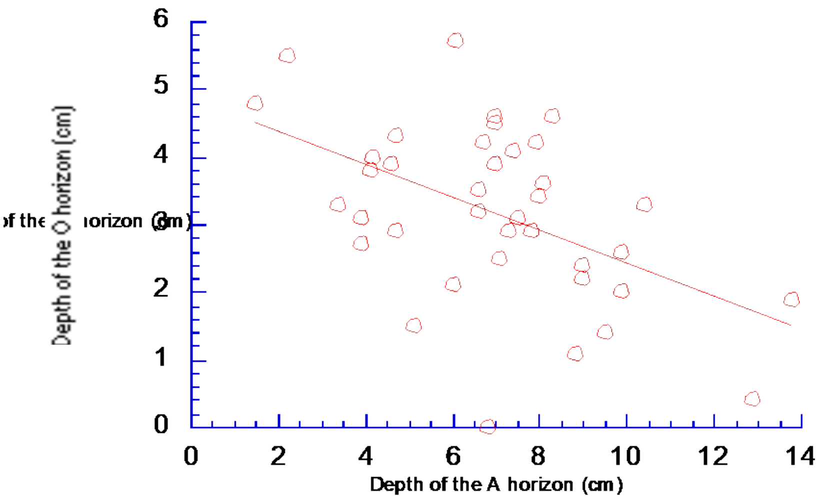

Figure 9: There is a statistically significant negative correlation between the depth of the A and O horizons ($p=0.0013$; Correlation=-0.495).

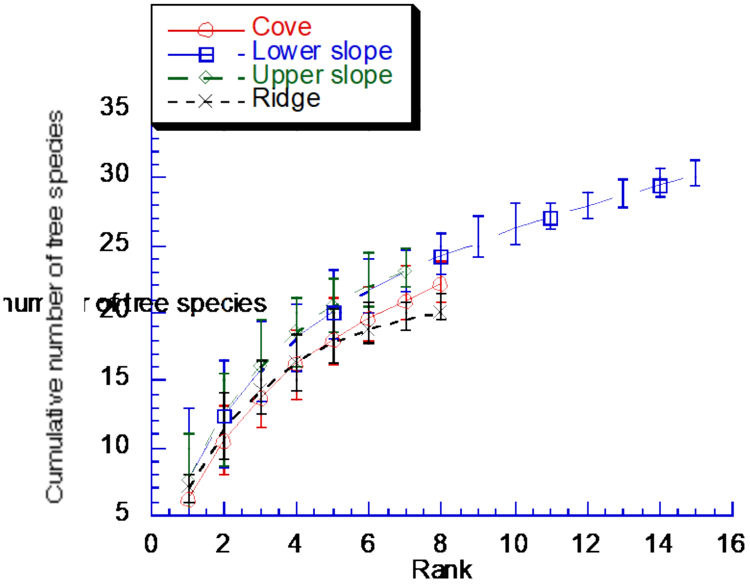

Figure 10: Species-area curves for trees with dbh ≥ 6 cm. Each curve represents 1000 random rearrangements of the order of the plots. The mean and 95% confidence intervals are plotted.

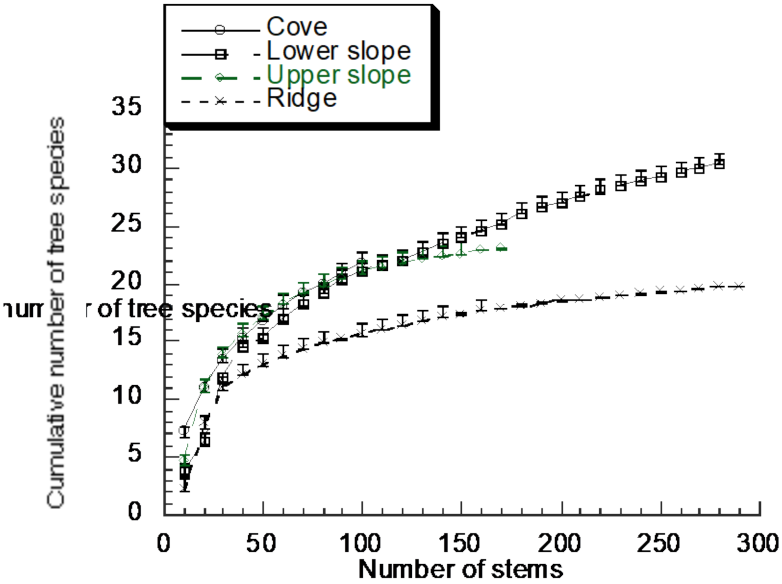

Figure 11: Species-individual curves for trees with dbh ≥ 6 cm. Each curve represents 1000 random rearrangements of the order of the trees. The mean and 95% confidence intervals are plotted.