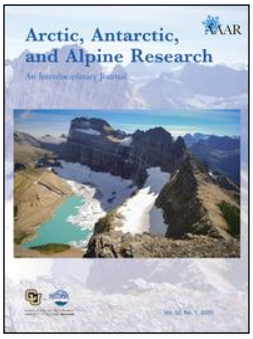

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Alpine plant community diversity in species–area relations at fine scale

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ABSTRACT

Observations of diversity in alpine vegetation appear to be scale dependent. The relations of plant species richness with surface processes and geomorphology have been studied, but patterns of beta diversity are less known. In Glacier National Park, Montana, diversity has been examined within 1 m^2 plots and for 16 m^2 plots across two ranges, with within-plot and across-range explanatory factors, respectively. The slopes of species–area equations for nested 4, 8, 12, and 16 m^2 plots were used as an indicator of beta diversity in Glacier National Park, where smaller and larger scales have been examined. The slopes were negatively related to a field assessment of surface stability and positively to the presence of talus—two sides of the same coin. A positive relationship with bedrock outcrops may be due to a misrepresentation of area for plants. The relationship of species–area slopes to plot-level gamma diversity was negative, weak, and marginally significant, and this variable did not enter the general linear model (GLM). Beyond simple differences in diversity with differences in environment, examination of beta diversity at a scale between that of earlier studies revealed surface processes and geomorphology as drivers that were also at a scale between those previously reported.

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Alpine; beta diversity; Glacier National Park; spatial scale; species–area

Introduction

Alpine plant communities are floristically diverse at multiple scales. In alpine plant communities, more functional types can be found in the same area given steep environmental gradients and high environmental heterogeneity, and alpine plants are small and thus more individuals and more species can fit per unit area (Körner 2003). These factors are scale dependent. Therefore, alpine plant community composition and diversity vary across and within regions and mountain ranges, and how the diversity of this habitat varies with spatial scale could inform fundamental theory in biogeography. In addition, understanding the underlying determinants of the diversity of alpine vegetation will help anticipate the effects of climate change (Amagai, Kudo, and Sato 2018; Malanson et al. 2019). Although increases in diversity in Europe have been reported (e.g., Pauli et al. 2012), species are mostly shifting their distributions upward, with an acceleration of such range shifts (e.g., Steinbauer et al. 2018). Thus, local diversity may be reduced by climate warming in the future (e.g., Dirnbock, Dullinger, and Grabherr 2003; Klanderud and Totland 2005; Engler et al. 2011). In the United States, Diaz and Eischeid (2007) reported that the alpine type of climate probably will not exist in the American West in the near future. This change would endanger many species, although not necessarily eliminate all areas of alpine vegetation. A complicating factor is the multiscale heterogeneity caused by geomorphology (e.g., Johnson and Billings 1962; Malanson, Bengtson, and Fagre 2012; le Roux, Virtanen, and Luoto 2013; le Roux and Luoto 2014). We aim to fill a gap in the scales at which plant species diversity has been analyzed in the alpine vegetation of the Rocky Mountains, United States.

McGill (2010) argued that a greater understanding of scale dependence was needed to explain biogeographic patterns. For species diversity, scale is foundational. In emphasizing the species–area relationship as perhaps the strongest biogeographic principle, Rosenzweig (1995) focused on change over space, the slope of the species–area equation. Chase et al. (2018) recently developed Rosenzweig's argument that more useful

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information could be derived from the species–area equation per se than from analysis of alpha diversity alone. The slope of the species–area equation captures the beta diversity of the observed scale. Other measures of beta diversity are common, however, and may also be informative (Tuomisto 2010).

Studies in alpine diversity can be difficult to generalize because of the differences in their geographic and historical settings and resulting flora. Carlson et al. (2013) noted the scale dependence of the determinants of alpine plant distributions, and Meier and Hofer (2016) reported effects of plot size on observations of alpine diversity. Bhatta, Grytnes, and Vetaas (2018) reported that the effects of regional gamma diversity did not differ with the scale of nested quadrats on an elevation gradient in the Himalaya. A number of studies point to topographically determined environmental heterogeneity as an important factor at multiple scales. At about 1 m scale, microtopography affects temperature (Scherrer and Körner 2011) and soil water (Litaor, Williams, and Seastedt 2008) and can indicate disturbance (Bruun et al. 2006). At this scale, species interactions and species characteristics, such as spread by cloning, will be important (Choler, Michalet, and Callaway 2001). At 10 to 100 m scale, factors such as roughness and slope aspect, angle, and shape (and their effect on snow and soil moisture) play a role (Randin et al. 2009; Malanson, Bengtson, and Fagre 2012; Jiménez-Alfaro et al. 2014; Takahashi and Murayama 2014; Opedal, Armbruster, and Graae 2015; Wu et al. 2018). Across mountain ranges, variation in alpha and beta diversity again reflects general topography (Wehn, Lundemo, and Holten 2014) but in relation to broader factors such as synoptic climatology (Winkler et al. 2016). At yet larger scales, patterns of climate and evolutionary biogeography are probable factors but are not yet well described (Anthelme et al. 2014; Malanson, Cheney, and Kinney 2015).

We focused on a local area for which we have a broader context. Rose and Malanson (2012) examined species richness within 1 m^2 plots in Glacier National Park (GNP), Montana. They found that microtopographic heterogeneity constrained rather than supported species richness. For the richness sampled in 16 m^2 plots across GNP, Malanson, Fagre, and Zimmerman (2018) reported that low diversity occurred only where precipitation was highest. However, those results were set within the context of similar size plots across the Rocky Mountains, and at that scale temperature was the determining factor. Here, we examined diversity at a scale between those two scales—that is, within the 16 m^2 plots—by focusing on species–area equations. Our aim was to uncover the environmental factors affecting diversity at this in-between scale. We can interpret not only the specific results of an improved quantification but also how factors differ from other scales in the same vegetation.

Additional context for GNP indicates that this location has the environmental variability that could produce a wide range of species–area slopes. The plots in GNP were also part of a larger study that included similar plots in the Beartooth Range, Wyoming, the Indian Peaks Area, Colorado, and Taos, New Mexico (Malanson et al. 2017). Comparisons of the four regions are reported in Appendix A. The species–area slopes for GNP were higher than those for the other three locations (but not significantly from the Beartooth). The continuous environmental measures differed in some respects, but GNP was never the most extreme. GNP did tend to be more variable, however, with the highest coefficient of variation for soil depth and for the standard deviation of soil depth. In addition, the stratified sample design for the four regions was based on preliminary analyses in GNP, where the number of species in ninety-six plots exceeded the number reported by Damm (2001) for a thorough coverage of the alpine with 525 releves. The total regional diversity was also relatively high, possibly because of its biogeographic position, with species from both the southern cordillera and the arctic floras (Harris 2002; Lesica and McCune 2004). Thus, GNP provided the best data to examine the question of beta diversity at the in-between scale.

Methods

We reexamined the data used by Malanson, Fagre, and Zimmerman (2018): species identified in ninety-six 16 m^2 quadrats distributed across the Lewis and Livingston Ranges in GNP. The original 16 m^2 plots were recorded in four 2 × 2 m subplots. We used the species–area procedure in PC-ORD ver. 6 to compute the average number of species per single subplot, every pair of subplots, and every triplet of subplots; the total number per plot provided a fourth point. This approach constitutes an average nesting rather than a true one. We calculated the species–area equation for these four points with the usual log–log transformation from $S = cA^z$ to $\log S = \log c + z \log A$ (where S is species richness, A is area, and c and z are parameters). We used the slopes of these equations, z, as our initial dependent variable. Slope indicates the rate of increase in diversity among the four subplots and is an indicator of beta diversity at this scale. For comparison, we also calculated the simplest original indicator of beta diversity (Whittaker 1960), the total species per plot, or plot gamma diversity, divided by the average of the four subplots.

Following Damm (2001), for each plot Malanson, Fagre, and Zimmerman (2018) recorded the elevation, slope angle, and slope aspect, and they measured an indicator of soil depth at the center and four corners of the plot and calculated its mean and standard deviation. For indicators of surface condition and microtopography they recorded the following characteristics or conditions for each quadrat:

- Slope relief: smooth, rolling, outcrop, convex, concave, irregular, terrace, other
- Microclimate/exposure: cold air drainage, upslope warm air, wind blasted, snow catchment
- Position: upper, middle, low or foot of a slope
- Topography: ridge, saddle, valley bottom, slope, summit, other
- Soil surface: stable–well vegetated, stable–poorly vegetated, unstable
- Special features: talus, scree, wet meadow, swale, seep, avalanche, open water.

They used these binary observations in categorical principal components analysis to produce two vectors for each of the six categories and an additional two for all combined; here, we used the binary variables directly after removing those for which fewer than five plots were recorded. For soil surface we collapse the categories into stable or unstable; our assessment was based on walking on the surface, not a visual estimate.

We first computed correlations among the two indicators of beta diversity, species–area slope and Whittaker's beta; the intercept of the species–area equations; and the total species richness of the 16 m^2 plots (plot gamma diversity). For the species–area slope, in Minitab ver. 19 we derived a general linear model (GLM) using a stepwise procedure with the categorical variables as factors and the continuous variables as covariates. We used GLM because of the mix of continuous and categorical variables. The stepwise procedure enters and removes variables at each step depending on p value, which we set at .05 to enter and .10 to remove. For the significant variables in the GLM, we used commonality analysis (Ray-Mukherjee et al. 2014) to partition the variance. Although it did not appear as a predictor in the model, we also examined the relationship between slope and plot gamma diversity.

Results

The descriptive statistics for the variables and correlations among species–area slope, Whittaker's beta, plot gamma and alpha diversities, and the slope intercepts are shown in Appendix B. Because of a high correlation between the slopes and Whittaker's beta, the intercept and alpha and gamma, and alpha and gamma we thereafter analyzed only species–area slope and gamma diversity. The species–area slopes ranged from 0.057 to 0.604, and their R^2 ranged from 0.923 to 0.999.

The GLM and commonality analysis revealed that the independent variables explained only a modest proportion of the variance in beta diversity at this scale as represented by species–area slope (Tables 1 and 2). The surface stability indicator alone accounted for <15 percent of the variance in species area slope; talus added <10 percent and bedrock outcrops 3.25 percent. Shared effects of talus and outcrops with stability were <3 percent each, and their combination was <0.0, as was the interaction of all three variables (commonality analysis reveals negative contributions to explained variance). Species–area slope was negatively related to surface stability and the presence of talus, whereas it was positively related to the presence of outcrops. Although it was not significant in the GLM, when species–area slopes were regressed on plot gamma diversity (16 m^2), the weak negative relationship was signficant (R^2 = 0.047; p = .035; Figure 1).

Discussion

The species–area slopes are useful metrics of diversity at a small scale. Although much of the information is in the species richness of the plots, these slopes capture the internal heterogeneity of the plots and represent their beta diversity. The slopes are related to factors other than plot gamma diversity per se. The analysis of

Table 1. GLM results for the dependent species–area slope with the independent site variables. The contribution is the percentage that each source in the analysis of variance table contributes to the total sequential sums of squares.

	Contribution (%)	p
Stability	14.60	.000
Talus	9.37	.001
Outcrops	3.26	.045
Total R^2	27.22	

Table 2. Commonality analysis, which partitions the R^2 in simple and multiple regressions, for the three independent variables that were significant in the GLM.

	Variance partitioned (%)
Stability	11.94
Talus	9.37
Outcrops	3.25
Stability + Talus	2.72
Stability + Outcrops	2.01
Talus + Outcrops	−0.58
All three	−2.07

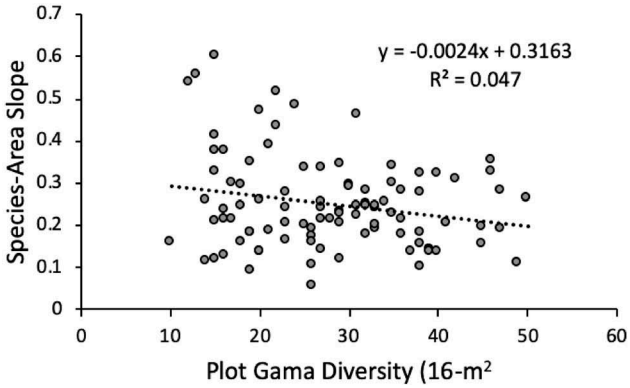

Figure 1. The species–area slope regressed on the plot gamma diversity; the relationship is significant at $p < .05$.

the other variables may help separate beta diversity from gamma diversity (cf. Tuomisto 2010; Ulrich et al. 2017). This analysis should perhaps complement those of Chase et al. (2018).

The site-specific conditions that affected the species heterogeneity of plots were related to geomorphic heterogeneity at this scale. Of the potential explanatory factors, aspects of slope stability had larger effects. Surface stability, from an indicator based on field assessment, led to lower beta diversity. A moving surface creates diffferences in the subplots that account for this heterogeneity. Beta diversity is also higher with more talus, another indicator of slope instability. The influence of outcrops is an aspect of topography that differs from others. In subplots with an outcrop, the area for plants is actually less, and the steeper species–area slopes may misrepresent the relationship. A subquadrat with an outcrop has less inhabitable area (we did not include lichen in this study), and the area used as a basis for the analysis might not be meaningful.

Bhatta, Grytnes, and Vetaas (2018) reported a gradient in diversity with elevation, but they were looking at patterns for broad gamma diversity among scales instead of environmental effects within a scale. Here, elevation had a small indirect effect on diversity. At the highest elevations, fewer species coexist in any case because of the more extreme conditions of exposure, more likely dry sites, and less soil. Though these factors did not individually affect diversity across their ranges, their combination at the highest elevations is a possible explanation; elevation can also represent spatiotemporal disequilibria (e.g., Roland and Schmidt 2015).

Rose and Malanson (2012) analyzed diversity in 1 m^2 plots distributed across GNP, and Malanson, Fagre, and Zimmerman (2018) used 16 m^2 plots similarly but not identically distributed. Here, we examined diversity in four 4 m^2 plots comprising those 16 m^2 plots. Analysis of the smaller plots revealed that diversity was lower where microtopographic variability was greatest, possibly because it increased the nonvegetated surface area. Analysis of the larger plots found that diversity was related to a precipitation gradient across GNP. This precipitation gradient is, however, also related to topography but at the scale of the major ranges that make up GNP: The climate of the northwestern portion of GNP is more directly affected by the Pacific Ocean, with a more maritime climate. The east side of GNP is in a rainshadow and is dominated by a more continental climate. Thus, topography at the scale of the mountain range may be a factor that differentiates diversity across GNP. The slope of the species–area equations based on the 4 m^2 subplots within the 16 m^2 plots reveals an intermediate scale of geomorphic patterns that control diversity. Where nonvegetated surface area reduced diversity in the 1 m^2 plots, the presence of outcrops increased beta diversity within the 16 m^2 plots, and it was further affected by mesoscale topography and slope instability.

That beta diversity varies with the environment is trivial, but identifying the specifics of scale dependence is a challenge (Carlson et al. 2013; Suding et al. 2016; Malanson, Fagre, and Zimmerman 2018). The factors that matter to ecological patterns must be those that affect processes at the individual plant level, but studies in alpine vegetation display scale dependence because of the multiple scales at which processes vary and interact. Spatial heterogeneity in environments creates complex intersections of these factors. These will include broad environmental patterns, such as continental gradients in precipitation (Malanson, Cheney, and Kinney 2015), but it is likely that the factors that matter, other than general temperature or precipitation, will be those that are scaled to modify those two drivers or their effects on individual plants (Carlson et al. 2013). Geomorphic and topographic features are likely to matter at this scale (e.g., Bruun et al. 2006; Litaor, Williams, and Seastedt 2008; Scherrer and Körner 2011; Malanson, Bengtson, and Fagre 2012; Rose and Malanson 2012; le Roux, Virtanen, and Luoto 2013; Jiménez-Alfaro et al. 2014; Takahashi and Murayama 2014; Wehn, Lundemo, and Holten 2014; Winkler et al. 2016; Wu et al. 2018).

In this study, processes and patterns at a scale within slopes affected the within-plot heterogeneity, a scale-specific measure of beta diversity. Surface processes that led to nonvegetated area, notably talus, complemented the presence of bedrock outcrops.

Together they produced low alpha diversity in some subquadrats, which in turn resulted in steeper species–area slopes. Although its importance was documented by Johnson and Billings (1962), further study of the relations of surficial geomorphic processes and the diversity and structure of alpine vegetation is needed (cf. le Roux and Luoto 2014). These patterns can change with climate because freeze–thaw proceses are important drivers (Benedict 1970), and how they create the heterogeneity on which alpine diversity depends should be better understood.

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