

REPORT

## Size-dependent species richness: trends within plant communities and across latitude

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### Abstract

We examine how species richness and species-specific plant density (number of species and number of individuals per species, respectively) vary within community size frequency distributions and across latitude. Communities from Asia, Africa, Europe, and North, Central and South America were studied (60°4'N–41°4'S latitude) using the Gentry data base. Log–log linear stem size (diameter) frequency distributions were constructed for each community and the species richness and species-specific plant density within each size class were determined for each frequency distribution. Species richness in the smallest stem size class correlated with the *Y*-intercepts ( $\beta$ -values) of the regression curves describing each log–log linear size distributions. Two extreme community types were identified (designated as type A and type B). Type A communities had steep size distributions (i.e. large  $\beta$ -values), log–log linear species-richness size distributions, low species-specific plant density distributions, and a small size class (2–4 cm) containing the majority of all species but rarely conspecifics of the dominant tree species. Type B communities had shallow size distributions (i.e. small  $\beta$ -values), more or less uniform (and low) size class species- richness and species-specific density distributions and size-dominant species resident in the smallest size class. Type A communities were absent in the higher latitudes but increased in number towards the equator, i.e. in the smallest size class, species richness increased (and species-specific density decreased) towards the tropics. Based on our survey of type A and type B communities (and their intermediates), species richness evinces size-dependent and latitudinal trends, i.e. species richness increased with decreasing body size and most species increasingly reside in the smallest plant size class towards the tropics. Across all latitudes, a trade-off exists between the number of species and the number of individuals per species residing in the smaller size classes.

### Keywords

Community ecology, plant size, species packing, species richness.

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### INTRODUCTION

Understanding how species coexist and occupy space is a fundamental issue in ecology. A wide range of hypotheses for species packaging and coexistence have been advanced (see Palmer 1994; Sollins 1998; Wright 1999, 2002). However, testing these alternative hypotheses has proven difficult and it is uncertain whether any one taken in isolation provides a sufficient explanation for observed patterns of species coexistence and packaging (Palmer 1994; Sollins 1998; Wright 1999,2002; Kelly *et al.* 2001; Sheil & Burslem 2003).

One important piece of information relevant to understanding these phenomena is how species richness and species-specific plant density (number of conspecifics per sampled area) vary as a function of body size and latitude. Arguably, species richness might be expected to increase with increasing total plant density merely as a result of sampling effects (McGeoch & Gaston 2002). Likewise, for even-aged populations, plant density is expected to decrease with increasing body size as a consequence of how individuals compete for limited space and resources (White & Harper 1970). However, the relationships among all three

of these parameters are far more complex for communities of mixed species because the numbers of species and conspecifics can vary as a function of body size and many plant species occupy a range of body sizes owing to indeterminate growth (Kohyama 1993; Niklas 1994; Roberts & Gilliam 1995; Kelly *et al.* 2001).

Here, we explore the relationships among species richness, body size and plant density empirically by tabulating and comparing the number of species and the number of individuals per species residing in the different stem size (diameter) classes of 226 plant communities using the world-wide Gentry data base (see Phillips & Miller in press). The objective of this study was to determine if species richness is correlated with body size and to see if it varies as a function of latitude (here used as a crude surrogate measure of environmental diversity). The size frequency distributions of the Gentry communities have been shown to be statistically well described by log–log linear regression formulas with numerically well-defined (and correlated)  $Y$ -intercepts and slopes ( $\beta$ - and  $\alpha$ -values, respectively; see Enquist & Niklas 2001; Niklas *et al.* 2003). These statistical features permit the ‘shape’ of each community size distribution to be defined by the numerical value of  $\beta$ . In turn, the extent to which  $\beta$ -values correlate with species richness and species-specific plant density in different community size classes can be evaluated.

Our analyses indicate that there is continuous variation in the pattern of species richness and species-specific plant density across all 226 forested plant communities. However, this variation has two extremes differing in a variety of ecologically important ways (designated here as type A and type B communities). Specifically, type A communities are characterized by steep size distributions (i.e. large  $\beta$ -values), log–log linear species-richness size distributions, low species-specific plant density distributions for the majority of size classes and have a small stem size class (2 cm < stem diameter  $\leq$  4 cm) containing the majority of species but rarely those of the size-dominant tree species. In contrast, type B communities have shallow size distributions (i.e. small  $\beta$ -values), more or less uniform (and low) size class species richness and species-specific density distributions, and size-dominant species residing in the smallest size classes. Importantly, type A and B communities manifest a latitudinal trend. Type A communities become progressively more rare towards the higher latitudes.

These findings indicate that species richness is a size-dependent phenomenon, that the majority of species increasingly resides in the smallest size class towards the tropics and that the species in progressively smaller size classes become more numerically rare such that a trade-off exists between species richness and individuals per species.

Our results also indicate that the dominant tree species are unlikely understory constituents towards the tropics. In practical terms, plant biodiversity can be increasingly underestimated towards the equator unless sampling protocols include the evaluation of very small and potentially overlooked stem size classes. In terms of competing hypotheses for species coexistence and packaging, the trade-off between species richness and species-specific plant density suggests that ‘coexistence’ may come at some cost in terms of population size.

## MATERIALS AND METHODS

To examine how species are distributed within different community size classes, we explored the world-wide Gentry data base (see Enquist & Niklas 2001; Niklas *et al.* 2003), which is available online (at <http://www.mobot.org/MO-BOT/research/gentry/welcome.shtml>) and in published form (Phillips & Miller in press). For each of 226 communities, this data base provides the species identification, number and diameter for all (liana and self-supporting monocot and dicot) stems measuring  $\geq 2.54$  cm in diameter (at breast height dbh, but not necessarily above buttress height) within 10 closely spaced transects each measuring 2  $\times$  50 m in area (total sampled area per site = 0.1 ha).

Stem size (diameter) distributions were constructed for each community sample (based on histograms with a 2 cm bin size). The number of all individuals  $N_i$  in each stem size class  $D_i$  were tabulated,  $\log_{10}$ -transformed and regressed as  $\log N_i$  vs.  $\log D_i$  to determine the best-fit regression curve for each community (see Enquist & Niklas 2001). Comparisons between log–log linear and nonlinear regression models indicated that the general regression curve:

$$\log N_i = \log \beta - \alpha \log D_i, \quad (1)$$

provided the best fit for each community (see Enquist & Niklas 2001; Niklas *et al.* 2003). Noting that  $\alpha$ - and  $\beta$ -values are autocorrelated mathematically (Niklas *et al.* 2003), the ‘shapes’ of distributions were specified by the numerical values of  $\beta$ .

The different size classes for each community were then examined to determine the number of species in each size class (size class species richness), the stem size range occupied by each species (species size range), and the number of individuals per species in each size class (size class species-specific plant density). Species size-ranges were determined by plotting the occurrence of each species across the different stem size classes; gaps in the size distribution of each species (unoccupied size bins) were noted but not counted as contributing to either size class species richness or species-specific plant density.

## RESULTS

Our analyses indicate that  $Y$ -intercepts ( $\beta$ -values) of log–log linear size frequency distribution regression curves are good indicators of the species richness and species-specific plant density in the smallest size class of community size distributions, that species diversity in the smallest stem size class increases towards the equator, species-specific plant density evinces the reverse trend with latitude and that high density and species-rich (typically tropical) communities appear to be unfavourable to the survival of the size-dominant tree juveniles.

Species richness correlated positively with the ‘shape’ of each size frequency distribution as gauged by  $\beta$ -values (Fig. 1a). Ordinary least squares regression indicated  $\beta$  scales as the 0.867 power of the number of species in the smallest size class ( $r^2 = 0.315$ ,  $F = 102.0$ ,  $P < 0.0001$ ). As expected, the  $\beta$ -values of size frequency distributions also correlated with the total number of individuals in the smallest size class (Fig. 1b), i.e.  $\beta$  scaled as the 1.92 power of this parameter ( $r^2 = 0.760$ ,  $F = 707.4$ ,  $P < 0.0001$ ). This correlation is an emergent property of the structure of log–log linear size frequency distributions, because the  $Y$ -intercept of the regression curve approximating such a distribution is a crude gauge of the total number of individuals in the smallest size class (see Niklas *et al.* 2003).

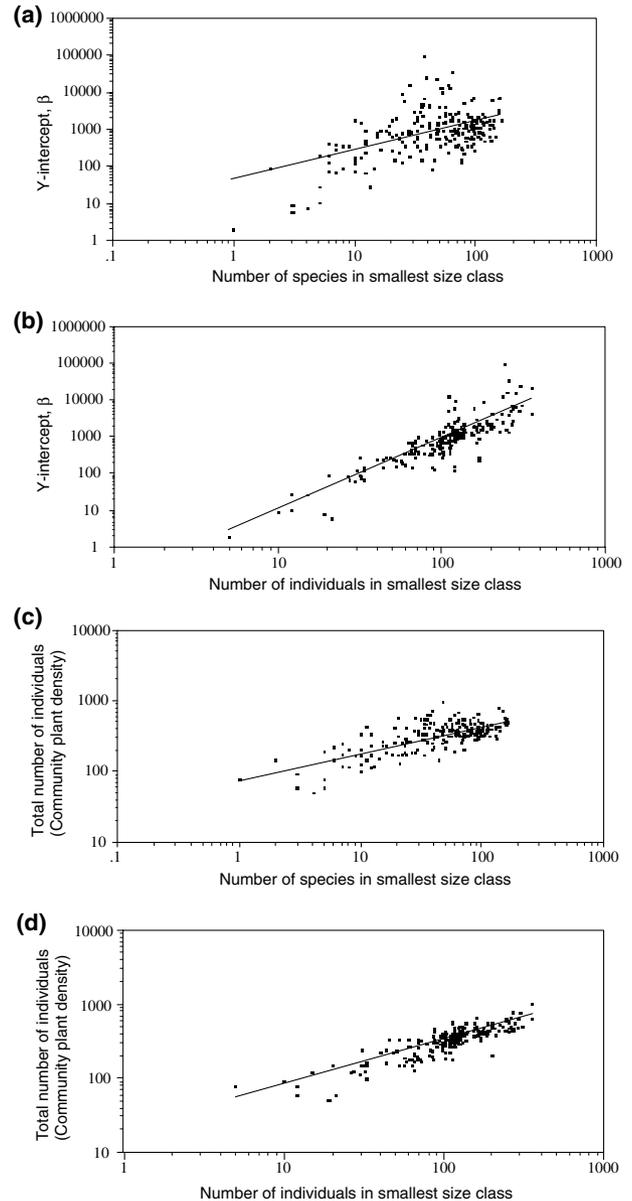
Regression analyses showed the total community plant density scales as the 0.372 power of the number of species in the smallest size class ( $r^2 = 0.529$ ,  $F = 248.9$ ,  $P < 0.0001$ ) and as the 0.640 power of the total number of individuals in this size class ( $r^2 = 0.761$ ,  $F = 708.5$ ,  $P < 0.0001$ ) (Fig. 1c,d). Although the first of these two relationships is strictly empirical, the relationship between total community density and plant density of the smallest size class is once again mathematically predictable. Specifically, we have shown that total community plant density  $N_T$  is approximated well by the formula:

$$N_T = \frac{\beta}{\Delta x(1 - \alpha)} (D_{\max}^{1-\alpha} - D_{\min}^{1-\alpha}), \quad (2)$$

where  $\Delta x$  is the size frequency bin size,  $\alpha$  is the slope of log  $N_i$  vs. log  $D_i$  (see eqn 1), and  $D_{\max}$  and  $D_{\min}$  are, respectively, the maximum and minimum stem diameters in a distribution (Niklas *et al.* 2003). Noting from eqn 1 that the number of individuals in the smallest size class  $n_{it}$  equals  $\beta D_{\min}^{-\alpha}$ , it follows from eqn 2 that:

$$n_{it} = N_T \frac{\Delta x(1 - \alpha)}{D_{\min}^{\alpha} D_{\max}^{1-\alpha} - D_{\min}^{1-\alpha}}. \quad (3)$$

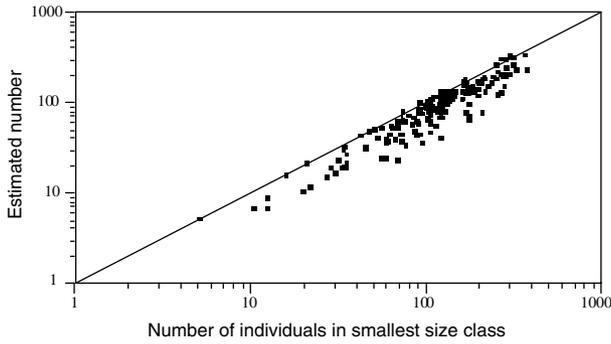
This formula obviates the autocorrelation between  $N_T$  and  $\beta$  (see Niklas *et al.* 2003) and predicts observed values of  $n_{it}$  reasonably well (Fig. 2). Across the numerical ranges of  $\alpha$ ,  $D_{\min}$  and  $D_{\max}$  observed for the Gentry data base,  $n_{it}$  scaled



**Figure 1** Bivariate plots showing the relationships between the  $Y$ -intercepts ( $\beta$ -values) of log–log normal size frequency distributions and the number of species (species richness) and number of individuals in the smallest size classes of 226 community size frequency distributions (a, b) and the relationships between total number of individuals (community plant density) and the number of species and individuals in the smallest size classes (c, d). Solid lines are log–log linear ordinary least squares regression curves.

as the 1.62 power of  $N_T$  (95% CI = 1.55 and 1.71;  $r^2 = 0.886$ ,  $F = 1701$ ,  $P < 0.0001$ ) such that, on average,

$$n_{it} \propto N_T^{5/3}. \quad (4)$$



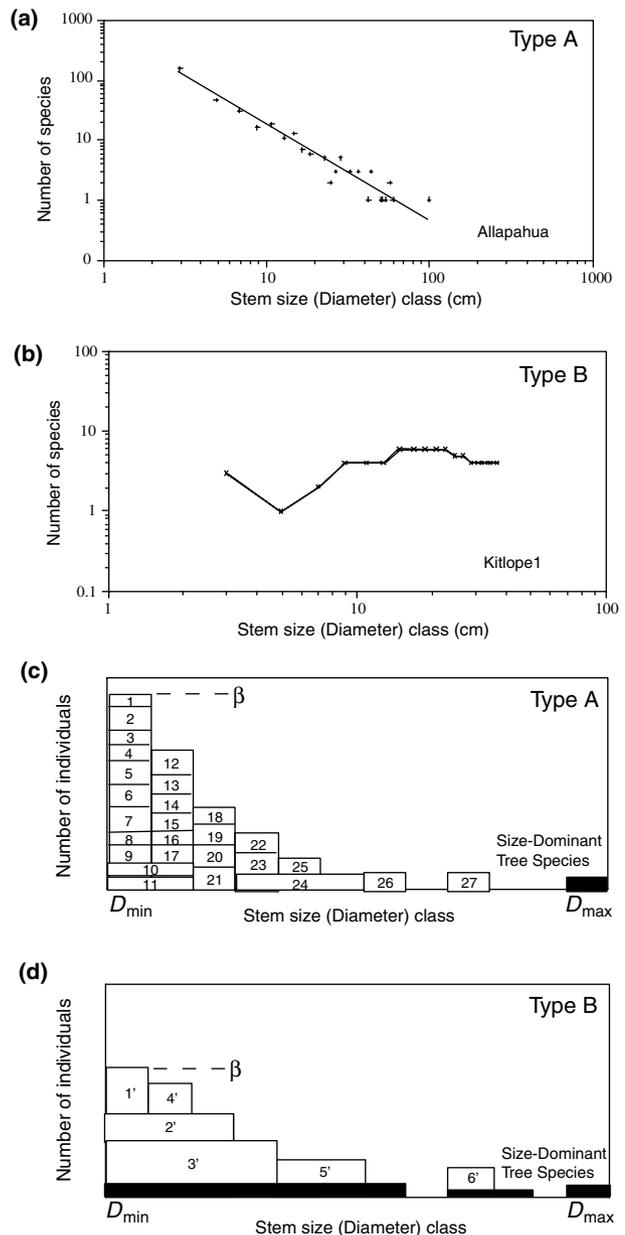
**Figure 2** Bivariate plot of estimated vs. observed number of individuals in the smallest size class of 226 community size frequency distributions. Estimated numbers are predicted from eqn 3 (see text). Solid line has a slope of one (the isometric condition). Data points falling below the line reflect under-estimated numbers.

This scaling relationship indicated that the plant density of the smallest size class increases disproportionately as the total community plant density increases across the 226 Gentry community samples.

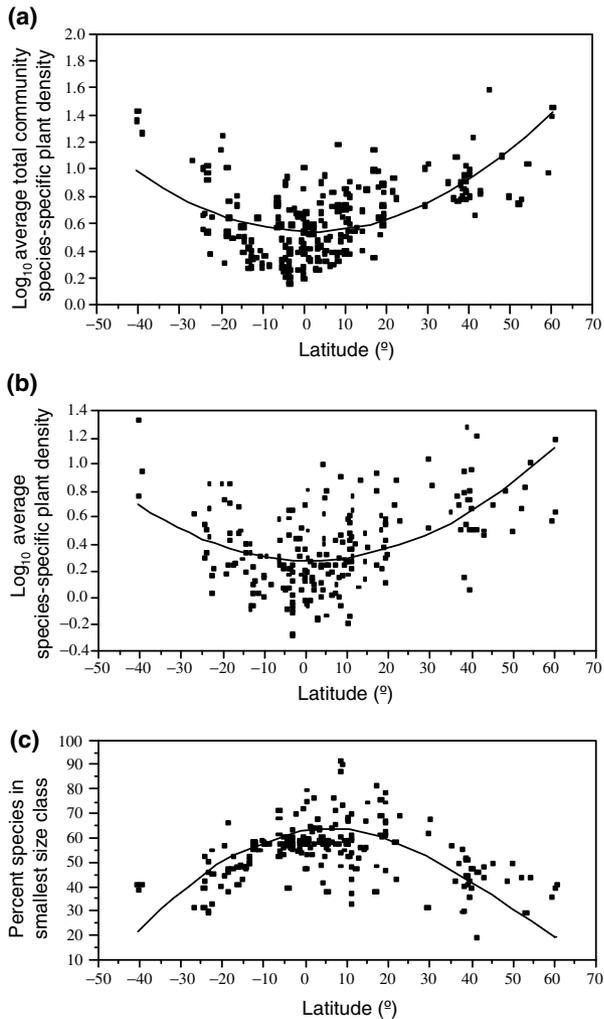
The size frequency distribution of species richness was complex but varied predictably across the 226 communities which were sorted into two extreme categories. Specifically, communities with high  $\beta$ -values characterizing steep size frequency distributions had log-log linear size class species richness distributions (type A communities), whereas those with shallow size class distributions had log-log convex or a more or less ‘flat-line’ size class species richness distributions (type B communities) (Fig. 3). Across all type A communities, species richness scaled, on average, as the 1.52 power of  $D_i$ , i.e. roughly as the  $-3/2$  power of stem size class. A consistent feature of type A communities was the general absence of dominant tree conspecifics in the smallest and intermediate size classes (e.g.  $4 \text{ cm} < D_i <$

10 cm). In contrast, type B communities with log-log convex or flat-line species richness distributions had conspecifics of the larger species residing in the smaller size classes, suggesting that the progeny of dominant tree species have lower probabilities of survival towards lower latitudes.

A latitudinal pattern was also observed across type A and B communities in terms of species-specific plant density and species richness. The average species-specific plant density across each community (and within the smallest size class) decreased towards the equator (Fig. 4a,b). Likewise, the percentage of total community species diversity increased in the smallest size class towards the equator (Fig. 4c). Thus, an



**Figure 3** Species-richness size frequency distributions typical of type A and B communities. (a) log-log linear species-richness distribution characteristic of a community with a steep size frequency distribution (Allapahua community from Mesoamerica) (example of type A community). (b) log-log ‘flat-line’ species-richness distribution characteristic of a community with shallow size frequency distributions (Kitlope 1 community from N. America) (example of type B community). Community designations those of Gentry. (c, d) Hypothetical species-richness distributions for stereotypical type A and B (high and low  $\beta$ -values, respectively) communities showing species-specific size range distributions and plant densities of species (denoted by different numbers and heights of cells, respectively). Size-dominant species indicated by black cells. Note that species 10, 11, and 24 extend into two or more size classes (see c) and that species 2’, 3’, and 5’ extend into two or more size classes, whereas size-dominant species extend into the majority of size classes (see d).



**Figure 4** Latitudinal trends in average species-specific plant density and average species richness. (a) Total community average species-specific plant density vs. latitude. (b) Average species-specific plant density for the smallest size class in each community vs. latitude. (c) Per cent of total species in the smallest community size class. Curves are best-fit ordinary least squares (second order polynomial) curves.

inverse latitudinal relationship was observed between species richness and species-specific plant density.

## DISCUSSION

Our analyses do not address why species richness increases towards the tropics or why the reverse trend is observed for average species-specific plant density (see Fig. 4). Indeed, a variety of hypotheses have been advanced to explain species coexistence and packaging, e.g. phenotypic discontinuities (MacArthur & Levins 1967; Grubb 1977; Denslow 1987; Chesson 2000) and environmental stochasticity or hetero-

geneity (Connell 1978; Huston 1994; Hubbell 1979; see also Loehle 2000). Our objective here was to explore empirically how species richness and species-specific plant density vary as a function of body size within individual communities and across communities differing in latitude.

Nevertheless, our findings are relevant to hypotheses concerning species coexistence and packaging because these parameters evidence size-dependent and latitudinal variation. Although there is a considerable range to average species richness and species-specific plant density within the tropics (see Fig. 4), perhaps as a result of abiotic factors (e.g. elevation, temperature, rain fall and soil conditions), a clear inverse relationship exists between the latitudinal trends observed for these two ecologically important parameters. Indeed, within the context of limiting resources and available space, an *a priori* trade-off logically exists between the number of species with comparatively small adult body sizes and the numbers of coexisting conspecifics per unit area. In this sense, 'coexistence' appears to come at some cost in terms of the size of individual species populations.

Unfortunately, the Gentry data base provides neither information about the spatial distribution of plants or species nor fluctuations in the recruitment of individuals into adult size classes, both of which are important parameters to understanding species rarity and productivity (see Kelly *et al.* 2001; Cook *et al.* 2002; Mouquet *et al.* 2002). Therefore, we cannot determine to what extent conspecifics are 'clustered' or scattered spatially. Such information would allow us to comment on the extent to which individual species coexist in the sense of sharing similar or dissimilar sites. However, our data indicate that individuals, regardless of species, are increasingly more densely packed towards the tropics and that the number of conspecifics decreases in a nearly proportional way. Taken at face value, these two opposing trends indicate that, although species richness may be fostered in the tropics, the size of species populations decreases in comparison with those in higher latitudes.

In regard to the packaging of individual plants across different stem size classes, we wish to draw attention to the relationship between the slopes of size frequency distributions ( $\alpha$ -values) and the manner in which total basal stem area ( $TBA_i$ ) varies as a function of stem size class regardless of species composition. Referring to the untransformed form of eqn 1, we see that  $N_i = \beta D_i^{-\alpha}$ . As stem cross sectional area equals  $D_i^2$  it follows that  $TBA_i = \beta D_i^{2-\alpha}$ . Thus, when  $\alpha = 2$ , total basal stem area is invariant across all stem size classes in a community, i.e.  $TBA_i = \beta D_i^0$ . Prior work indicates that, on average,  $\alpha = 2$  across the Gentry community samples such that  $TBA_i$  is constant (see Enquist & Niklas 2001). However, across the Gentry community samples, the numerical value of  $\alpha$  varies significantly and predictably, i.e.  $\alpha$  increases towards the higher latitudes and decreases towards the equator (see Niklas *et al.* 2003). This

latitudinal trend indicates that, on average,  $TBA_i$  decreases with increasing stem size class in higher latitude communities, whereas the reverse holds for progressively more tropical communities, i.e. the smallest size class in tropical communities, on average, has a larger total basal stem area than progressively larger size classes, whereas the largest size class in higher latitude communities has a larger total basal stem area than progressively smaller size classes. Thus, the biodiversity residing in the smallest stem size class is more densely packaged in the tropics than in higher latitudes.

Our findings raise an obvious concern with regard to the estimates of biodiversity. The Gentry data base typically does not provide measurements for stem diameters < 2.5 cm. Yet, even with this stem size truncation, our data indicate that the bulk of species diversity resides in the smallest size class of tropical communities and that these species are numerically rare (regardless of their clustered or scattered distribution). Therefore, estimates of tropical plant biodiversity can be seriously jeopardized whenever surveys neglect very small individuals, which are typically ignored in surveys of forested communities.

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