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TECHNICAL COMMENT

Tree diversity in relation to maximum tree height: evidence for the harshness hypothesis of species diversity gradients

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Abstract

Marks *et al*. (Ecology Letters, 19, 2016, 743) showed tree species richness correlates with maximum tree height, and interpret this as evidence that the environmental stressors that limit tree height also act as ecological filters on species richness. Here, we strengthen these arguments by further addressing the roles of environmental covariates and beta diversity.

Keywords

Canopy height, environmental filters, favourability hypothesis, moisture gradient, shade tolerance.

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Our previous work showed that maximum tree height is a strong predictor of tree species richness and may be a useful proxy for richness in the absence of diversity data (Marks *et al*. 2016). We further suggested that maximum tree height is a convenient biological indicator of environmental harshness for the tree life form that integrates the effects of multiple stress factors sufficiently accurately to be useful in appropriate contexts (i.e. within a region and in contexts that exclude stands of immature trees). We thus concluded that the close relationship between maximum height and tree species richness supports the *harshness hypothesis* that environmental stresses act as filters on the traits and thus also the species that are viable on a site, and thereby reduce richness.

When Givnish (2017) suggests that analyses of the effects of tree height on tree diversity should control for environmental covariates of both, he appears to have misunderstood our approach. We did not argue that tree height has a direct effect on tree diversity, but rather that environmental harshness limits both tree diversity and maximum tree height in parallel ways, thus making tree height a good proxy for environmental harshness. To support this idea, we showed how species richness and maximum height respond in qualitatively similar ways to the various stress gradients (Marks *et al*. 2016). Maximum tree height is not exclusively a function of productivity as Givnish suggests; it is also affected by seasonality for example (Larjavaara 2014; Klein *et al*. 2015).

Givnish (2017) agrees that greater maximum height is associated with an increase in the available trait space, but disagrees that this will necessarily result in more species coexisting, as a few dominant species may exclude others. Givnish (2017) further argues that classic research by Whittaker (1956, 1960) is inconsistent with the harshness hypothesis because it shows a rise and then a decline in tree species richness with moisture. We argue that the harshness hypothesis predicts a decline in richness on the most hydric sites with soil hypoxia, as well as on late-successional mesic sites in which the dense overstory has resulted in deep understory shade, an endogenously created environmental stress that can prevent seedling recruitment of some species (Marks *et al*. 2016). That is, we agree that the most competitive species could eventually exclude others in mesic sites, but they will do so by exacerbating an environmental stress such as shade (i.e. lowest R*, Tilman 1988), which makes the lowered diversity consistent with the harshness hypothesis. To avoid the confounding effects of shade in late-successional plots when testing the harshness hypothesis on moisture gradients, one could consider the total number of species supported by a site type over the course of succession, which the harshness hypothesis predicts to be greater in more productive environments (e.g. Coomes *et al*. 2009).

Though declines in tree richness in late succession on the most productive sites can in this way be interpreted as consistent with the harshness hypothesis, patterns in tree height at these sites may in some cases be contrary to our secondary hypothesis that maximum tree height is a general indicator of environmental stresses for trees. Givnish is correct that maximum tree height does not necessarily decline as species are competitively excluded, because the most competitive species could be the tallest. In eastern North America, the tallest tree species are mostly deciduous angiosperms that are intolerant of shade, implying a decline in maximum height with succession, but in western North America, the tallest species are usually evergreen conifers that can be shade tolerant (Table S1). This difference may be a function of the degree to which the tallest tree species achieve their exceptional stature due to rapid growth vs. great longevity and associated trade-offs in traits (Wright *et al*. 2010; Marks & Canham 2015). Therefore, height by a certain age may be a more accurate measure of environmental harshness for trees than maximum height (see 'site index' in Marks *et al*. 2016), although maximum height is more practical to apply.

Givnish proposes that the closer relationship between maximum height and diversity at the regional rather than local

Table 1 Pearson correlation coefficients of 100 × 100 km^2 grid cell data from Marks *et al.* (2016) for eastern and western North America

	height.range	height.max	Alpha	Beta	Gamma
Eastern					
height.range	1.000	0.990	0.624	0.450	0.774
height.max	0.990	1.000	0.632	0.437	0.771
Alpha	0.624	0.632	1.000	−0.014	0.687
Beta	0.450	0.437	−0.014	1.000	0.707
Gamma	0.774	0.771	0.687	0.707	1.000
Western					
height.range	1.000	0.999	0.721	0.598	0.809
height.max	0.999	1.000	0.724	0.581	0.800
Alpha	0.721	0.724	1.000	0.311	0.780
Beta	0.598	0.581	0.311	1.000	0.828
Gamma	0.809	0.800	0.780	0.828	1.000

Height.max and height.range are the maximum and range of maximum plot tree heights respectively. Alpha is the mean plot species richness for the grid cell, gamma is the species richness for the entire grid cell, and beta species richness is computed by dividing gamma by alpha.

scale reflects the influence of beta diversity. He suggests that higher regional values of maximum tree height reflect higher variance in environmental conditions, which is associated with elevated regional diversity because different species dominate under different conditions. Here, we explicitly test this idea by quantifying correlations of the range and maximum of tree height with alpha, beta and gamma diversity (Table 1). These analyses show that height range and beta diversity are correlated as expected based on the regional variance hypothesis, but not as strongly as are maximum height and alpha diversity, the signature of the harshness hypothesis (Table 1). This implies that the effect of regional maximum height on beta diversity may be of secondary importance to increasing gamma diversity, consistent with our original interpretation.

DATA ACCESSIBILITY

All supporting data are available from the USDA Forest Service's FIA website.

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