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Tropical cyclones disrupt the relationship between tree height and species diversity: Comment

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In a recent report on the patterns of tree species richness in eastern and western North America, Marks et al. (2016) claimed to have identified an operational indicator of environmental harshness (maximum tree height) and concluded that environmental stressors that limit tree height also act as ecological filters on species richness. Marks et al. (2017) attributed the positive association between species richness and maximum tree height to both the direct effects of environmental harshness on species richness and the indirect effects of environmental harshness on species richness as mediated by maximum tree height.

This finding overlooked the fact that many environmental stressors such as cyclonic disturbance affect tree height and tree species diversity in different directions. In a study of elevational patterns in Taiwan, Chi et al. (2015) reported sharply contrasting relationships between tree species diversity and canopy tree height in sites that were subject to tropical cyclone disturbance vs. those that were not. In the mountains of southeastern China beyond the reach of tropical cyclones, both tree species richness and canopy tree height decreased with increasing elevation (Zheng et al. 2004, Chi et al. 2015), supporting the harshness hypothesis (Marks et al. 2016, 2017). In contrast, in Taiwan, where tropical cyclones occur annually, tree species richness decreased but maximum tree height increased with increasing elevation, the opposite of the predictions of the harshness hypothesis (Fig. 1). We attributed the contrasting elevational patterns and associations between tree diversity and canopy tree height in Taiwan to topographic mediation of tropical cyclone disturbance. The shorter tree stature in lower elevations was attributed to more severe tropical cyclone damage (Chi et al. 2015). Although tropical cyclones limit tree height, tree mortality is very low, possibly a result of both evolutional and ecological responses of these forest ecosystems through the long-term interaction between cyclones and the forest ecosystems (Lin et al. 2011). As an example, multiple category three tropical cyclones on

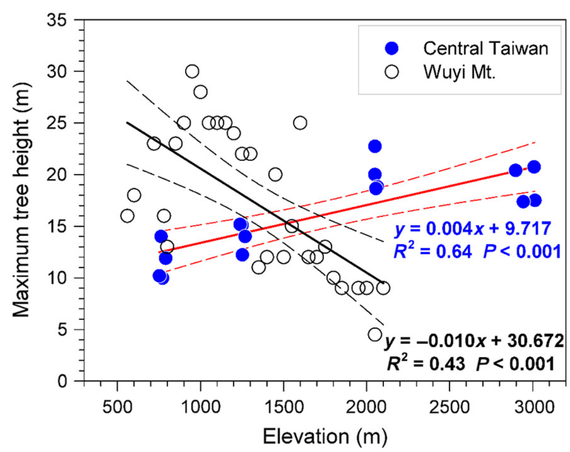

Fig. 1. Elevation and maximum tree height in central Taiwan and Wuyi Mt. of southeastern China. Note the increases of maximum tree height at Wuyi Mt. at elevations <1000 m may reflect decreases in human disturbance. Data of Wuyi from Zheng et al. (2004).

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the Saffir-Simpson scale (Simpson and Riehl 1981) caused <2% tree mortality in low-elevation evergreen broadleaf forest in northeastern Taiwan in 1994, a record year of tropical cyclone frequency and intensity (Lin et al. 2011). However, taller trees were selectively killed and defoliation was severe, both of which contributed to the low stature of the forest even though the mean annual temperature (18°C) and precipitation (3800) mm are high (Lin et al. 2011). Cyclone disturbance limits vertical development of trees but does not lead to their elimination. Thus, more tropical cyclone disturbance at lower elevations overrides climatic controls on elevational patterns of tree height but does not change the elevational pattern of tree species richness. We suggest that there is an important difference between actual maximum tree height and potential maximum tree height in the presence of disturbance (e.g., tropical cyclone).

Across an elevational gradient (700–3000 m) in Taiwan, we found that maximum tree height was not a good predictor of tree species alpha richness (i.e., richness of each plot; Fig. 2a), whereas components of environmental harshness, moisture index (Fig. 2b), and warmth index were (Fig. 2c). Moreover, the relationship between maximum tree height and either of the two components of environmental harshness was not significant (Fig. 2d, e). Such results challenge the fundamental assumption (i.e., factors that limit tree height also limit species richness and the effects are in the same direction) underlying the use of maximum tree height as a predictor of tree species richness in disturbance-prone regions. As such, our results of increasing canopy tree height and decreasing species diversity of trees along the 2300-m elevational gradient in central Taiwan (Chi et al. 2015) demonstrate that tree height is not a universal indicator of environmental harshness. The cumulative consequences of the components of environmental harshness may be different for richness and maximum tree height, especially in disturbance-mediated systems.

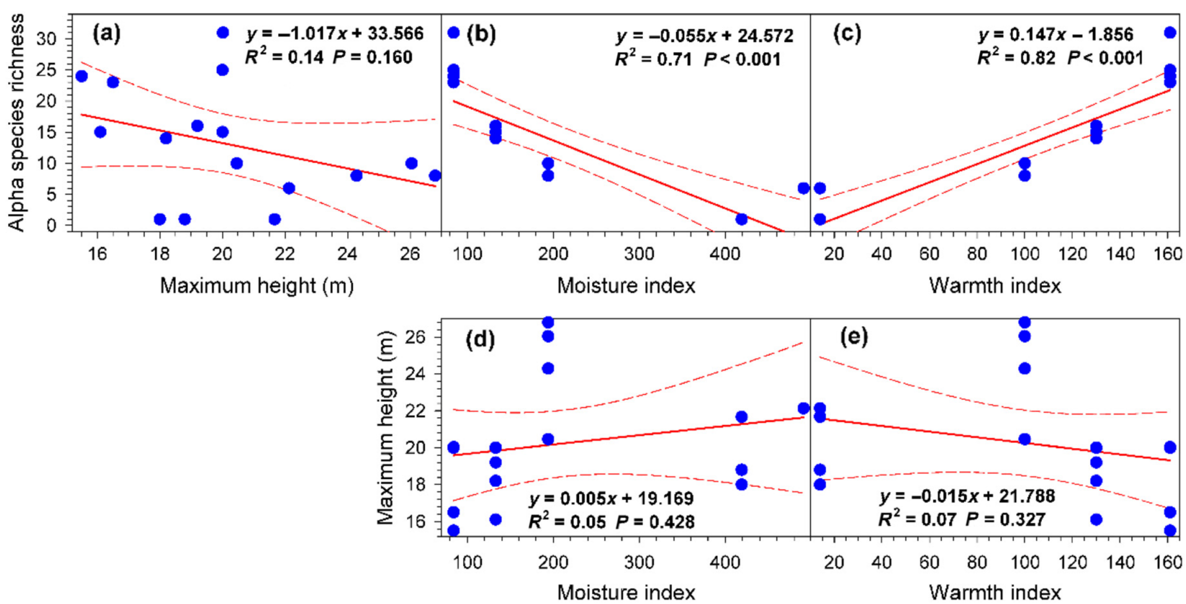

Fig. 2. Relationship between alpha tree species richness and maximum tree height (a), moisture index (b), and warmth index (c) as well as between maximum tree height and moisture index (d) and warmth index (e) along a 2300-m (700–3000 m) elevational gradient in central Taiwan. The moisture index was calculated following Thornthwaite (1948) (moisture index = 100 × [(P/PET) − 1], where P is annual precipitation and PET is annual potential evapotranspiration). The warmth index is a temperature-based index and is the summation of monthly mean temperature minuses five for temperatures that are >5°C (Kira 1991). Tree height and species were surveyed in four 10 × 15 m plots at each of four elevation categories. For details about plot selection and tree survey, please see Chi et al. (2015). Dashed lines delineate 95% confidence intervals.

In summary, we argue that tropical cyclones and maybe other types of disturbance (e.g., outbreak of insects that damage apical buds) could have different impacts on species richness and maximum tree height. Consequently, caution should be exercised when using maximum tree height as a useful surrogate of environmental harshness to predict large-scale patterns of tree species richness within ecoregions. We suggest that application of the surrogate be constrained to regions without frequent disturbances that affect tree height and tree species richness in different directions.

Acknowledgments

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