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Original article

Variation of functional traits in trees from a biogeographically complex Mexican cloud forest

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ARTICLE INFO

Article history:

Received 28 September 2007

Accepted 24 April 2008

Published online 9 June 2008

Keywords:

Cross-species correlations

Mexico

Phylogenetic independent contrasts

Specific leaf area

Seed mass

Tree height

Wood density

ABSTRACT

Several studies have proposed a group of morpho-functional traits as determinants of the ecological strategy of species. Among these, four morpho-functional traits are considered to be relevant in determining a plant's ecological strategy: specific leaf area (SLA), height at maturity (Hmax), wood density (WD), and seed mass (SM). We examined the variation of these traits and attempted to identify functional groups among 33 tree species with different biogeographical affinities from a montane cloud forest. Covariation among the four traits was examined using Principal Component Analysis (PCA) and species clustering. Bivariate trait relationships were evaluated through two methods: cross-species correlations, and evolutionary divergence correlations using phylogenetically independent contrasts (PICs). Correlations between attributes were overall weak, the most obvious ones being between Hmax and SM, and between Hmax and WD; this latter trait pair was also correlated in PICs. In both analyses SLA was unrelated to all other traits. In the PCA ordination the first two axes explained 66.9% of the between-species variation. Despite a largely continuous between-species variation, species clustering allowed differentiation of two main groups. Observed trait correlations were consistent with those reported for other floras, with the important exception of the independent behaviour of SLA. This study indicates a variety of comparable successful life history strategies among the studied species. The effect of phylogeny in trait covariation was unimportant, in fact, a mixture of clades was represented in several groups among the species they contained, suggesting among-lineage convergence.

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doi:10.1016/j.actao.2008.04.006

1. Introduction

The quantitative study of plant traits has revealed the existence of an extremely large across-species variation, some of which seems to reflect the occurrence of trade-offs in plant life histories (Wright et al., 2004); therefore plant traits provide a useful base for the classification of plants in functional groups (Díaz and Cabido, 1997). Functional groups have been defined as sets of species sharing biological traits and playing similar roles in ecosystem processes (Gitay and Noble, 1997; Lavorel et al., 1998). The benefits of classifying plants in functional groups have been recognized by many authors (Lavorel et al., 1997; Díaz et al., 1999); for example, such groups may be viewed as plant life strategies, inasmuch as they represent different ways in which plants secure carbon profit during vegetative growth, and acquire, use, and conserve resources (Westoby et al., 2002). A fruitful approach in developing functional classifications of plants is represented by ecological strategies schemes, which consists in grouping species in categories, according to a varying number of ecological traits (Raunkiaer, 1934; Drury and Nisbet, 1973; Grime, 1977; Noble and Slatyer, 1980).

Several studies have proposed a group of morpho-functional traits that have proven to be appropriate, independent predictors of a species ecological behaviour (Westoby, 1998; Westoby et al., 2002; Wright et al., 2006b). Among these, four have received much attention because of their ease of measurement and interpretation: (a) specific leaf area (SLA); (b) maximum height (Hmax); (c) wood density (WD); and (d) seed mass (SM). SLA is an important determinant of growth rate because the larger SLA, the larger the area for capturing light per unit of previously captured mass (Lambers and Poorter, 1992).

There is empirical evidence that SLA is weakly related with plant height and seed size, and that it often shows no relationship with WD and leaf size across many species and community types (Díaz et al., 2004; Wright et al., 2006b). However, site-specific studies based on controlled protocols and on an ample knowledge of the system's ecology have succeeded in finding relationships of SLA with other traits, e.g. with WD and leaf size (Wright et al., 2006b). These contrasting results imply a lack of a strong basis to support the existence of significant correlations between SLA and other traits. In turn, Hmax is linked to strategies that ensure carbon gain through light interception, e.g. slow growth in low light levels vs. fast growth in gap conditions (a trade-off between height gain and shade tolerance) (Falster and Westoby, 2005b). Apparently due to mechanical reasons, Hmax is tightly associated to WD (Lawton, 1984; Muller-Landau, 2004; King et al., 2005); a higher WD provides more resistance against xylem cavitation (Cavender-Bares and Holbrook, 2001; Maherali et al., 2004) and pathogens (Coley, 1988). WD is positively correlated with tree height along successional gradients, with the opposite being true along light-availability gradients (Falster and Westoby, 2005a), and in general, negatively correlated with leaf size across different vegetation types (Cavender-Bares et al., 2004; Wright et al., 2006a). Also, a trend has been reported for bigger plants to bear bigger seeds (Moles et al., 2004).

Finally, SM is a regenerative trait playing a central role for reproduction and the seedling establishment phase because it

determines the amount of resources available for seedlings' early growth (Paz and Martínez-Ramos, 2003; Moles and Westoby, 2004b; Paz et al., 2005). SM has been shown to be positively correlated with dispersal mode, leaf size, seedling functional type and plant height (Leishman et al., 1995; Kitajima, 1996; Falster and Westoby, 2005b).

The occurrence of multiple trade-offs involving these attributes allows visualization of a gradient of ecological strategies, ranging from fast-growing, short-lived pioneer species on one extreme, to slow-growing, long-lived, late successional species, associated with increased shade tolerance, on the other (Muller-Landau, 2004). According to existing theory and available empirical information, often contradictory as shown above, it is difficult to propose specific hypotheses establishing a definite directionality for the relationships between the four attributes. However, based on the results of the majority of studies analysing between-trait correlations, it is reasonable to state that most small-seeded trees are fast growing species, while the opposite will be true for large seeded trees. Because growth rate of a tree is usually positively associated to a larger light interception area per leaf and negatively to WD, we predict here that species with small seeds should tend to have high SLA, relatively low WD and a wide variation in total height, whereas species bearing large seeds should tend to have medium to high WD, low SLA, and a large Hmax.

It has been demonstrated that patterns of species distribution and functional covariation in an ecological community can reflect both species' inherited traits from a common ancestor (phylogenetic effect) and adaptive convergences among distantly related species (Webb et al., 2002; Ackerly, 2003; Chazdon et al., 2003). The evolutionary comparative methods that incorporate a phylogenetic approach have proven useful in solving questions about ecological significance of functional variation among plant species (Ackerly, 1999). For example, the question whether the trend toward a shorter leaf life-span and a high SLA in more recent cloud forest taxa reflects ecological variation, or if it is rather related with the phylogenetic relationships among species (Williams-Linera, 2000). In general, more related taxa tend to be more similar, which implies a lower level of evolutionary divergence between related taxa (Ackerly, 2000).

An underlying assumption of the general relationships discussed above is that they derive from the evolution of many species in common communities, and that strategies have emerged through the appearance of different trade-offs (Westoby et al., 2002; Wright et al., 2006a). However, the possibility of generalizing trait correlations may be limited; for example, the significant correlation between SLA and WD observed in tropical rain forests may not be valid for other forest types (Wright et al., 2006b). This uncertainty is particularly relevant for cloud forests (CF) of the mountains of southern/central Mexico, which is a highly complex community from a biogeographical point of view, as it is composed of a mixture of both tropical and temperate Laurasian elements, together with tropical and temperate taxa of Gondwanic origin (Wendt, 1998). In addition to this particular concoction, these are not post-glacial communities, since they have existed since at least 20 Ma ago (Miranda and Sharp, 1950; Axelrod, 1975; Rzedowski, 1991), so that the appearance of

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