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INSIGHTS

Deciduousness Influences the Understory Community in a Semideciduous Tropical Forest

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ABSTRACT

We investigated how deciduousness of overstory tree species influences the community structure and species composition in the understory. The results suggest that deciduous overstory trees have positive effects on light-demanding species, and that the processes underlying such effects may involve reduced competition for light or facilitation through increased water availability.

Abstract in Portuguese is available in the online version of this article.

Key words: Brazil; competition; ecological filter; ecological group; facilitation; light; plant-plant interaction; tropical forest.

Ecosystem engineering by organisms has been recognized as a key driver of environmental heterogeneity (Pickett *et al.* 2000, Jones *et al.* 2010). Plants are among the most important ecological engineers, since they can create, maintain, or modify habitats, thus influencing the physical environment and local biota (Jones *et al.* 1997). Trees, for instance, can play a fundamental role in the heterogeneity of many ecosystems, as they alter numerous environmental characteristics beneath their canopies. These include light regimes (Lee 1989, Mejía-Domínguez *et al.* 2011), soil properties (Garbin *et al.* 2006), litter depth (Mejía-Domínguez *et al.* 2011), and availability of water and nutrients (Jones *et al.* 1997). Variations in morphological (Niinemets 2010), architectural (Chazdon & Fetcher 1984, Wang & Augspurger 2006) and phenological traits (Tomita & Seiwa 2004, Ishii & Asano 2010) of canopy trees may regulate the intensity and the way they influence the microhabitat of the understory.

Light is one of the main factors determining the survival, establishment, and growth of plants (Dupuy & Chazdon 2006, Augspurger 2008). Several authors have shown that low light intensity may have negative effects on different ontogenetic plant stages (Clark & Clark 1992, Tomita & Seiwa 2004, Dupuy & Chazdon 2006). Subtle changes in understory light, such as the infiltration of sunflecks through the canopy, may positively influence the survival and recruitment of young plants (Montgomery & Chazdon 2002). Studies in temperate deciduous forests have found that the deciduousness of canopy trees has an important function for the supply of light to seedlings and saplings in the understory (Miyazawa & Kikuzawa 2005, Augspurger 2008). Since leaf fall has a potential to increase the quantity of light reaching the shaded environment of the understory (Lee 1989), the deciduousness of overstory trees may facilitate the regeneration of plants that have higher light requirements and are shade-intolerant (Taylor *et al.* 2004).

The consequences of the microenvironmental modifications promoted by plants on the community structure are extensively documented for harsh environments such as deserts, prairies, and dunes (see reviews in Callaway 1995, 2007). The dynamics of these ecosystems are usually driven by facilitative mechanisms, by which a nurse plant allows the establishment of another plant, mainly through the amelioration of stressful abiotic conditions, such as high light intensity, drought, strong winds, etc. (Callaway 2007). However, in tropical and subtropical ecosystems, the interactions of tree species and their effects on community assembly are still poorly known (Villela & Proctor 2002, Peters *et al.* 2004, Dias *et al.* 2005, Wang & Augspurger 2006, Mejía-Domínguez *et al.* 2011).

We conducted this study to investigate the influence of deciduous overstory trees on the understory community structure and species richness in a seasonal semideciduous tropical forest (Veloso *et al.* 1991, or tropical wet forest *sensu* Holdridge 1967). The study site was located at the Caetetus Ecological Station, in the westcentral region of São Paulo state, Brazil (22°41′ S; 49°10′ W), which comprises *ca* 2200 ha of preserved vegetation. The mean annual temperature is 21.4°C; the mean maximum temperature is 30.6°C, occurring in February, and the mean minimum temperature is 9°C, occurring in July. The annual rainfall at the site is ~1300 mm and the dry season (precipitation <100 mm, *sensu* Walsh 1996) occurs between April and September, when 20–50 percent of individuals lose their leaves (Veloso *et al.* 1991).

The field survey was carried out in a 10.24-ha permanent plot, in which all trees and treelets with diameter at breast height (dbh) ≥ 4.8 cm were tagged and identified. All overstory trees with a dbh ≥ 4.8 cm were censused, except palms, broken, or bent trees, trees with canopies covered by lianas, and trees inside or at the edge of gaps. Pioneer species were also excluded from

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the sampling of the overstory, since their life cycle is short (Swaine & Whitmore 1988) and their effects on both young and adult understory trees would most likely be of little significance. Underneath each overstory tree, we recorded all trees and treelets with dbh ≥ 4.8 cm, which included understory and midstory individuals (hereafter referred to as 'understory' individuals). We classified the overstory trees as either deciduous or evergreen (Morellato 1991, Morellato & Leitão-Filho 1992). We also classified the understory species according to their light requirements, as either light-demanding or shade-tolerant based on work done by Gandolfi (1991, 2000), Souza and Válio (2001), and more than two decades of expert knowledge from researchers at the study site (G. Franco and G. Durigan, pers. comm.). To calculate the crown area of the overstory trees (Mueller-Dombois & Ellenberg 1974), so as to estimate the density of understory individuals, we took two perpendicular measurements of the crown, the first one corresponding to its greatest length.

Each overstory tree was considered as a sample unit. The total density of understory individuals, and the proportion of species and individuals of the light-demanding group were compared between the deciduous and evergreen trees using a *t*-test, since the variances were homogeneous. We transformed the proportions using a slight modification of the Freeman and Tukey formulae, since it provides better results than the common arcsine square root transformation (Zar 1999). To compare the total species richness in the understory between deciduous and evergreen overstory trees, we constructed rarefaction curves (Magurran 2004) with 1000 iterations, using the EcoSim 7.0 software (Gotelli & Entsminger 2001).

We recorded 67 deciduous and 47 evergreen trees in the overstory (dbh range: ~19–117 cm), comprising a total of 22 species of which 16 were deciduous and six were evergreen. Underneath the deciduous overstory trees, we found 506 individuals and 59 species (35 light-demanding, 19 shade-tolerant and five unclassified). Under evergreen trees, we recorded 436 individuals and 57 species (31 light-demanding, 22 shade-tolerant and four unclassified).

The total density of understory individuals did not differ between deciduous and evergreen overstory trees (mean ± standard error = 0.16 ± 0.01 individuals/m^2 under deciduous trees and 0.17 ± 0.02 individuals/m^2 under evergreen trees; $t = -0.3446$; df = 83; $P = 0.7313$). However, the proportion of light-demanding understory trees was higher underneath the deciduous trees than under the evergreen trees ($t = 3.3195$; df = 112; $P < 0.001$; Fig. 1A). The total species richness in the understory did not differ between deciduous and evergreen trees (Fig. 2), but the proportion of light-demanding species was higher underneath the deciduous overstory trees ($t = 3.0314$; df = 112; $P = 0.002$; Fig. 1B).

Our results showed that deciduousness of overstory trees does not affect the overall density and species richness of the plant community beneath their canopies, but instead seems to act on individual understory species depending on their light requirements. The higher proportion of light-demanding species and light-demanding individuals underneath the deciduous

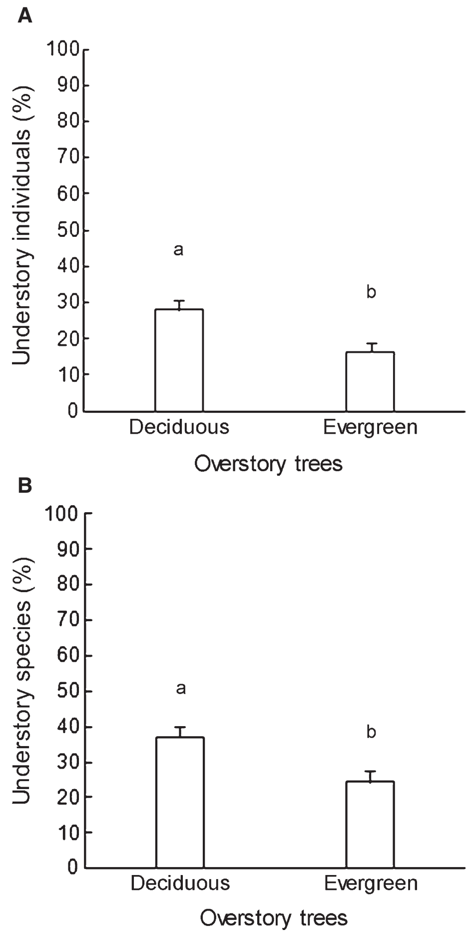

FIGURE 1. Proportion of light-demanding individuals (A) and light-demanding species (B) recorded under deciduous and evergreen overstory trees in a semideciduous tropical forest (mean ± standard error). Different letters indicate significant differences between deciduous and evergreen overstory trees ($P < 0.05$, *t*-test).

overstory trees suggests that deciduousness favors this group of plants, and that the consequences of the interactions occurring between overstory and understory individuals in the initial life phases (*e.g.*, seedling phase) persist until the later stages of development.

The positive effect of deciduous trees on light-demanding plants is most likely related to alterations in the light regimes in the understory, which is caused by the canopy openness formed by the leaf fall during the dry season. Studies conducted in deciduous forests have shown that the quantity and quality of light reaching the understory are affected by the level of canopy cover and are highly influenced by seasonal phenological events, such as leaf fall and sprouting of the overstory species (Lee 1989, Tomita & Seiwa 2004, Lopez *et al.* 2008). Most of the light that reaches the forest floor comes from the short-duration sunflecks that pass through the overstory canopies (Chazdon & Fetcher 1984, Way & Pearcy 2012). These small increases in light are of great importance to the carbon balance of the seedlings (Chazdon

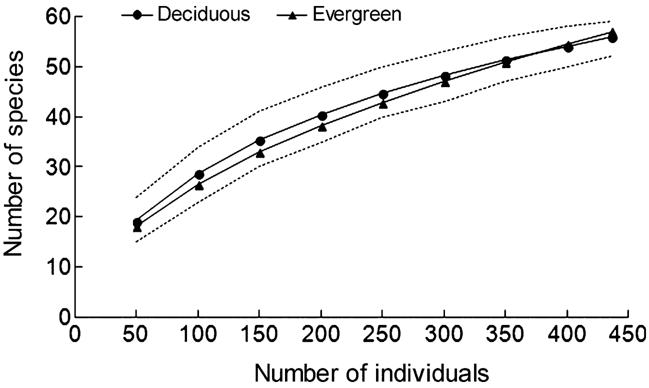

FIGURE 2. Rarefaction curves for the understory plant community underneath deciduous (understory plants sampled = 506) and evergreen overstory trees (understory plants sampled = 436). The solid lines show the mean species richness below deciduous and evergreen trees; the dotted line shows the 95 percent confidence interval for the understory community underneath deciduous trees rarefied down to 436.

& Fetcher 1984, Way & Pearcy 2012) and, as a consequence, play an important role in the survival and growth of the plants in the forest (Augspurger 2008). When the leaf fall of deciduous species occurs, the levels of photosynthetic photon flux density (PPFD) in the understory can potentially increase by a magnitude of seven compared to when the trees have leaves (Lee 1989). Therefore, light-demanding species probably experience much less competition for light under deciduous overstory trees than under evergreen trees.

Although deciduousness seems to favor light-demanding species by the augmentation of radiation, it may also negatively affect shade-tolerant plants. High levels of radiation can cause photoinhibition, impairing the efficiency of photosynthesis (Way & Pearcy 2012). In addition, shade-tolerant species tend to allocate energy to defenses against herbivory and to the storage of resources, which can limit their growth even when resources are abundant (Wright *et al.* 2003). Since light-demanding species grow faster than shade-tolerants (Swaine & Whitmore 1988), light demanders most likely have a competitive advantage over shade-tolerants beneath deciduous trees, where light is more abundant. Therefore, the higher proportion of light-demanding individuals under deciduous trees may be a consequence of an improved performance or lower mortality of these species in this environment than in the densely shaded habitat beneath evergreen trees.

Most of the deciduous trees lose their leaves during the dry season, which could potentially reduce the benefits that understory species experience under their leafless canopies. However, the water consumption and transpiration of a leafless tree are lower than that of an evergreen tree, and at the same time, the absence of canopy reduces water interception, thus promoting a higher input of water into the soil. In addition, leaf fall increases litter accumulation and helps maintain soil humidity (Facelli & Pickett 1991). Furthermore, the water content of the subsuperficial horizons of the soil at the study site during the dry season is still within the range of that which is considered available to plants (M. Cooper, unpubl. data).

Our results indicate that deciduous overstory trees have positive effects on light-demanding tree species in the understory and that the processes underlying these effects may be reduced competition for light, facilitation through increased water availability, or both. Therefore, we believe that deciduousness plays an important but underappreciated role in the dynamics of semideciduous forests, and that the relationship between deciduous trees and the different groups of plants that establish beneath their canopies should not be overlooked.

These findings raise a number of questions that should be investigated in more detail, such as the magnitude of the changes in abiotic factors (*e.g.*, water, light, litter depth) underneath the different canopy types and the responses of the understory plants to such alterations. In these studies, it is important to take into account not only the functional groups but also the identity of each species, since the response of a species to varying conditions may depend on the combination of its traits (Eviner 2004). Additional investigations should also consider the different ontogenetic stages, as shifts in the direction of interactions (positive or negative) are known to occur during the plant-life cycle (Soliveres *et al.* 2010, le Roux *et al.* 2013). A more profound knowledge of plant-plant interactions is essential to better understand how these interactions affect the abundance and distribution patterns of plant populations, and also to predict community dynamics in species-rich tropical ecosystems.

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