Habitat Endemism in White-sand Forests: Insights into the Mechanisms of Lineage Diversification and Community Assembly of the Neotropical Flora

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ABSTRACT

White-sand forests represent natural laboratories of evolution over their long history throughout Amazonia and the Guiana Shield and pose significant physiological challenges to the plants and animals they host. The study of diversification in plant lineages comprising species endemic to white-sand forest can therefore give insights into processes of evolution and community assembly in tropical forests. In this article, we synthesize recent studies of white-sand forests to integrate patterns of plant species distribution with processes of lineage diversification and community assembly in the white-sand flora. We contrast lineages that have radiated uniquely in these habitats (*e.g.*, *Pagamea*, Rubiaceae), with cosmopolitan lineages comprising specialists to white-sand forests and other habitats that may have arisen via ecological speciation across habitat gradients (*e.g.*, *Protium*, Burseraceae). In both cases, similar suites of functional traits have evolved, including investment in dense, long-lived tissues that are well-defended structurally and chemically. White-sand endemics, therefore, play an important role in biodiversity conservation because they represent unique combinations of functional and phylogenetic diversity. Furthermore, white-sand endemics may respond differently than other tropical forest plant species to contemporary global changes because they comprise resilient functional types that may better withstand increased drought, temperature, and invasions of exotic pests in these regions.

Abstract in Spanish is available with online material.

Key words: Amazon; endemic; functional traits; habitat specialization; niche conservatism; speciation.

WHITE-SAND FORESTS GAINED PROMINENCE IN THE 1970S AND 1980S DUE TO A SERIES OF CLASSIC PAPERS describing their unusual structure, function, and species compositions (Janzen 1974, Anderson 1981, Medina & Cuevas 1989). These discrete, island-like formations of the most nutrient-poor soils known, surrounded by rainforests growing on more typical soils, captured the attention of biologists who hypothesized that they represented laboratories of evolution producing a unique white-sand flora and fauna. The initial wave of studies mainly focused on describing forest physiognomy and nutrient cycling but also included many hypotheses about the abiotic and biotic factors that may be driving the evolution of these unusual floras (Janzen 1974, Gentry 1986). However, although some of the most unusual and dominant species were described, there were no published accounts about how many endemic white-sand specialist plant species exist in the Amazon basin and how strictly these species were associated with white-sand habitats.

In the past 20 yr, several floristic studies from many different white-sand forests found in Peru, Colombia, Brazil, Guyana, Suriname, and French Guiana have been published, offering new insight into patterns of diversity and dominance across the continent. In addition, the advent of molecular phylogenetics has given us a wealth of new knowledge on the timing and patterns of relatedness of Amazonian plant lineages, including many white-sand specialists. Finally, advances in functional trait research have allowed us to match environmental data with plant traits at a variety of different scales to examine how white-sand plants differ functionally from those found in other forests. Here, we review and synthesize recent studies concerning white-sand floristics, species-level phylogenies, and functional traits to gain a broader understanding of (1) white-sand endemism; (2) white-sand forest historical biogeography and the evolution of specialization; and (3) the abiotic and biotic factors underlying the unique functional composition of white-sand plants.

EVALUATING ENDEMISM IN THE WHITE-SAND FLORA

Throughout this article, we refer to 'endemism' in the sense of a species being restricted to white-sand forests and not to any particular geographic locality (*i.e.*, 'geographic endemism'). It is common to find tourist recruits in adjacent habitats, so we consider an endemic as a taxon with significant habitat association with

some proportion of observations (*e.g.*, 90%) restricted to that habitat. To evaluate habitat endemism, it is, therefore, necessary to know not only which species of plants are found in white-sand forests but also whether these species are also found in other forest types in the same geographic region. In general, these types of studies are rare. Instead, most investigators have compiled lists of plants found in the white-sand forests of their study area (Anderson 1981, Duivenvoorden & Lips 1995, Coomes & Grubb 1996, García Villacorta *et al.* 2003, Kelloff & Funk 2004, Guevara *et al.* 2016). While these lists contribute greatly to our knowledge of which species and genera are dominant across South American white-sand forests, they do not allow us to strictly evaluate endemism.

Another limitation is that most comparisons of white-sand forests with other forests have compared turnover at the community level, rather than testing each species for its degree of habitat specialization. These community comparisons have been done in two different, but related ways. First, investigators have placed transects across environmental gradients and correlated species composition with environmental variables (Damasco *et al.* 2013) or visualized dissimilarity clusters of species composition against axes of environmental variables (Tuomisto *et al.* 1995, 2003, Ruokolainen *et al.* 1997, Vormisto *et al.* 2000). Alternatively, some studies have compared species compositions of geographically separated plots of different soil types (ter Steege *et al.* 1993, Banki 2010, Fine *et al.* 2010, Stropp *et al.* 2011, Peñuela-Mora 2014). For example, Fine *et al.* (2010) reported significant differences between white-sand forest plots and terra firme plots in northeastern Peru. However, endemism per se, in other words which particular species were actually endemics to white-sand forests, was evaluated on a more ad-hoc basis, by comparing the number of plots in which a plant species was found in white-sand forests to the number of plots in non-white-sand forests or by confirming whether or not the plant was included in a recently published Catalogue of Ecuador which at the time was not known to harbor white-sand forests (Jørgensen & Léon-Yánez 1999). Similarly, Stropp *et al.* (2011) reported strong differences between white-sand and non-white-sand (terra firme) forests of the Rio Negro, Brazil, at the community level. Indicator species analysis, which is a statistical procedure that finds non-random association with a habitat or a geographic area (Dufrene & Legendre 1997, De Caceres *et al.* 2010), was used to delimit species, genera, and families that had greater than expected numbers of individuals in white-sand forests (Stropp *et al.* 2011). Ter Steege *et al.* (2013) provided a similar analysis at the scale of the entire Amazon region. Although this approach is useful to depict habitat associations, it must be interpreted in light of the sampling design and lack of taxonomic standardization used to generate the data. Generally, few white-sand forests have been sampled in these studies, and often white-sand forests are sampled without paired forest sites in adjacent non-white-sand areas. Therefore, some true endemics have probably been missed for a lack of adequate sample size, and some geographically restricted species have probably been mistakenly labeled as white-sand endemics. Moreover, many white-sand taxa may represent cryptic species

(Fine *et al.* 2013a) or when morphologically distinct have been labeled as 'morphospecies' that have generally been excluded from these larger meta-analyses (ter Steege *et al.* 2013), and thus remain undescribed as endemics.

Although we lack a comprehensive picture of the white-sand endemic flora across the Amazon, there are several consistent patterns. First, white-sand forests generally are significantly more species-poor than non-white-sand forests. On average, 1-ha tree plots contain fewer than 61 species (Guevara *et al.* 2016), whereas Amazonian terra firme forests generally contain at least twice and up to five times as many species (ter Steege *et al.* 2013). Second, white-sand forests are dominated by a subset of tree species that achieve extremely high relative abundances. For example, in Peru, 62.4 percent of the individuals across 16 plots in seven geographically separated white-sand forests were made up of only 17 species (Fine *et al.* 2010). In the upper Rio Negro, the most abundant eight species (led by two species of *Eperua* and *Aldina heterophylla*) accounted for more than 51 percent of the trees sampled in four white-sand plots (Stropp *et al.* 2011). This pattern has been reported again and again from all sides of the Amazon basin (ter Steege *et al.* 2013). At the same time, there are reports of many non-endemic species occurring in white-sand forests at low abundances. For example, about half of the 221 species registered in the Peru study were also found in neighboring terra firme plots or included in the Catalogue of Ecuador (Fine *et al.* 2010). We interpret this pattern to indicate that many species can survive in white-sand forests, but to achieve dominant species status, they need to have a suite of traits that confer success in these unique and challenging environments. Interestingly, the dominant species in Peru are rarely (if ever) reported in non-white-sand forests, pointing toward a link between dominance in white-sand forests and endemism. If there are evolutionary trade-offs that confer advantages in white-sand forests, the same traits that lead to dominance may be strongly disadvantageous in other soil types, leading to the exclusion of these species by either physiological intolerance or competition with other plants (Fine *et al.* 2006). This pattern of white-sand dominants not occurring in non-white-sand forests is not as clear in the Upper Rio Negro or in the Guianas where the contrast between white-sand forests and other forest soil types is not as marked. For example, the two species of *Eperua* and *Aldina heterophylla* that so thoroughly dominate some white-sand forests of that region were also found in lateritic forests (Boubli 2002, Stropp *et al.* 2011). Nevertheless, these (non-white-sand) terra firme forests of the Guiana Shield are less starkly contrasting in soil texture and nutrient limitation with regional white-sand forests than their terra firme counterparts in the western Amazon that have much higher clay content and nutrient availabilities (Baraloto *et al.* 2011).

We can extend our thinking of endemism (or habitat association) by using herbarium records and floras to ask whether these taxa have close relatives that occur in other habitats or alternatively, whether taxa generally belong to clades that are associated with white-sand or similar forest types. This broader definition of endemism may allow us to increase our understanding of the factors that are most likely driving the evolution of diversity and

dominance in white-sand forests (Guevara et al. 2016). By including phylogenetic information in community comparisons, we can compare white-sand and non-white-sand forests at deeper phylogenetic depths. For example, Fine and Kembel (2011) compared phylogenetic community structure and phylobetadiversity of the Peruvian white-sand and terra firme plots mentioned above. They found a list of nodes that were significantly overrepresented in the phylogenetic assemblage that occurs in white-sand forests, corresponding to the dominant species, genera, and families reported in Fine et al. (2010). Stropp et al. (2011) conducted a similar analysis using indicator species analysis at the genus and family level. These types of analyses would be promising to extend to all white-sand plots across the Amazon (e.g., ter Steege et al. 2013), but will require improved standardization of vouchers across plot networks and phylogeographic studies to resolve species complexes.

CONTRASTING PROCESSES OF DIVERSIFICATION GENERATING THE ENDEMIC WHITE-SAND FLORA

Although they cover a relatively small area representing 3 percent or less of the total forest cover, white-sand forests occur throughout the Amazon basin, Guiana Shield, and the Atlantic Forests of Brazil (ter Steege et al. 2000, de Oliveira et al. 2014, Adeney et al. 2016). In the lowland Amazon basin, white-sand forests cover the largest and most contiguous area in the Rio Negro basin, in Brazil, Colombia, and Venezuela (Medina & Cuevas 1989, Adeney et al. 2016). In the Western Amazon in Acre (Brazil), Peru, Ecuador, and in western Colombia, white-sand forests are often island-like patches of just a few hectares surrounded by other terra firme forest types of much more fertile soils (Duivenvoorden & Lips 1995, Fine et al. 2010, Neill & Asanza 2012, Peñuela-Mora 2014). Adeney et al. (2016) include a map of lowland white-sand areas of the Amazon Basin. In the Guiana Shield of Venezuela, Guyana, Suriname, and French Guiana, white-sand forests are distributed both toward the coast and on and adjacent to the quartzite rocks that make up the Shield itself (Hammond 2005). Coastal white-sand forests are common in the Guianas as well as in Brazil, where they are called restingas (de Oliveira et al. 2014). These forests grow on top of ancient sand dunes and beaches that were formed by the higher sea levels in the Pleistocene.

Several recent publications have reviewed the geology of Amazonian sediments, and the events of the Miocene remain the subject of much debate (cf. Hoorn et al. 2010, Latrubesse et al. 2010). Nevertheless, some general patterns that are relevant to the evolution of white-sand endemic flora can be summarized. Some white-sand soils likely have formed in-situ, within the past million years via podsolization or subsidence (Rossetti et al. 2012). Other white-sand soils derive from ancient, Pre-Cambrian sediments that make up the Guiana and Brazilian Shields that have been exposed to rainfall and eroded for many tens of millions of years (Hoorn 1993). These quartz sediments have been carried from the Shields by rivers, and some were deposited as

far west as the Peruvian Amazon when major northern South American rivers flowed across the continent in the westerly direction (Hoorn 1993, Hoorn et al. 2010). Due to the extremely dynamic nature of Amazonian floodplains, however, these sand deposits have likely been moved many times since their first deposition, meaning that although the sand itself and the presence of white-sand forest habitat in South America may be extremely ancient and continuously present since its origin, the precise location of any particular present-day white-sand forest (outside of the core areas on or near the Shields) may not be older than a few million years or in some cases, much younger. This combination of the extreme antiquity of white-sand soils along with highly dynamic histories of geologic strata of the Amazon means that plants endemic to white-sand forests may include lineages with very different evolutionary trajectories.

Indeed, in the white-sand flora, we see dominant taxa belonging to two categories (Table 1), exemplified by *Pagamea* (Rubiaceae) on the one hand, a genus almost entirely restricted to white-sand forests, and by *Protium* (Burseraceae) on the other, which is a clade that contains habitat-specialist species in a multitude of habitat types. These two different patterns suggest entirely different processes underlying species diversification of the groups. Clades like *Pagamea* have extremely large geographic distributions, yet only occur in poor-soil habitats, suggesting that there is some intrinsic constraint on the entire lineage that prevents the plants from thriving in more fertile substrates. Addi-

TABLE 1. *The 13 most dominant white-sand specialist species from the 91 ATDN white-sand plots (Guevara* et al. *2016) and whether these species belong to clades restricted to white-sand forests or whether they have close relatives specialized to other habitat types.*

Species dominant in WS plot network (number of individuals registered)	Contain congener in other forest types?
Eperua falcata (Fabaceae) (3343)	Yes, but only in poor-soil areas (Guiana shield)
Catostemma fragrans (Malvaceae) (1665)	Yes, but only in poor-soil areas (Guiana shield)
Eperua leucantha (Fabaceae) (1260)	Yes, but only in poor-soil areas (Guiana shield
Eperua grandiflora (Fabaceae) (1074)	Yes, but only in poor-soil areas (Guiana shield)
Pachira brevipes (Malvaceae) (1065)	Yes
Micrandra sprucei (Euphorbiaceae) (839)	No
Licania buxifolia (Chrysobalanaceae) (743)	Yes
Haploclathra cordata (Calophyllaceae) (543)	No
Swartzia bannia (Fabaceae) (536)	Yes
Aspidosperma excelsum (Apocynaceae) (509)	Yes
Dicymbe uaiparaense (Fabaceae) (491)	Yes, but only in poor-soil areas (Guiana shield)
Matyayba opaca (Sapindaceae) (441)	Yes
Pradosia schomburgkiana (Sapotaceae) (440)	Yes
Lecythis corrugata (Lecythidaceae) (432)	Yes

TABLE 2. *Hypothesized relationship between niche conservatism and intrinsic factors influencing speciation in the clade-level patterns of habitat endemism of white-sand specialists.*

Amount of clade-level trait conservatism associated with white sand	Intrinsic clade-level factors promoting diversification	Predicted pattern	Example clade
High	Present	Species-rich clades composed of many WS specialists, with different species in different regions	*Pagamea* (Rubiaceae)
High	Absent	Species-poor clades composed of a few WS specialists, with large geographic distributions	*Haploclathra* (Calophyllaceae)
Low	Present	Species-rich clades composed of WS specialists but also many specialists to other soil types	*Protium* (Burseraceae)
Low	Absent	Species-poor clades composed of a few species of WS specialist(s) closely related to specialists of other soil types	*Mauritia* (Arecaceae)

tionally, there is a strong geographic component to *Pagamea*'s species distribution, indicating allopatric speciation among the different South American regions that contain white-sand soils likely driving diversification (Vicentini 2016). Thus, we suggest that the combination of trait conservatism that leads to white-sand specialization together with the isolated nature of white-sand patches within and among regions in South America leads to patterns found in clades like *Pagamea*. (Table 2). There are other clades that dominate white-sand forests of the Upper Rio Negro and Guiana Shield that have a more restricted geographic distribution, like *Eperua* and *Aldina* (Stropp *et al*. 2011, Guevara *et al*. 2016). In these examples, it is difficult to know whether these lineages are actually constrained from inhabiting more fertile soils because the entire region is composed of low-nutrient soils (Hammond 2005).

The opposite pattern of habitat specialization within clades is much more common, that of white-sand specialists being closely related to other congeners that occur in a wide variety of habitats (Table 1). Examples of this pattern were first noted by Gentry (1981) who described four closely related edaphic specialists of *Passiflora*, one occurring in white-sand, one in seasonally flooded forest, one in non-inundated alluvial soils, and one in terra firme lateritic soils. Gentry (1986) was convinced that such rampant edaphic specialization represented an important mechanism for diversification in many different tropical clades. Subsequent works in *Protium* (Fine *et al*. 2005, 2014), *Adelobotrys* (Schulman 2003), and *Potalia* (Frasier *et al*. 2008) have described clades with white-sand specialists closely related to edaphic specialists to other soil types. For some of these clades, white-sand specialists appear to be ancient (Frasier *et al*. 2008); for others, the white-sand specialists likely have evolved much more recently, from non-white-sand specialist ancestors (Fine *et al*. 2005).

For clades such as these that include many different habitat specialists, there appears to be little niche conservatism with respect to soil type. Indeed, specialization to a variety of different habitats including clay, terra firme soils, or flooded forests in addition to white-sand forests is common, with different congeneric species occurring parapatrically. It is important to note that for lineages like *Protium*, *Pachira*, *Micropholis*, and many others,

while there appears to be little edaphic niche conservatism at the clade level, individual species themselves are generally strict edaphic specialists, not habitat generalists. Such habitat specialization could evolve by at least two different mechanisms. First, habitat-generalist populations could be isolated by some barrier (a mountain, a river, or a grassland, etc.), and one of these allopatrically separated populations could undergo selection to specialize onto white-sand soils while the other would not. This would be equivalent to the vanishing refuge model (Vanzolini & Williams 1981) or ecogeographic speciation (Glennon *et al*. 2012). Subsequent dispersal (or disappearance of the former barrier) would lead to current parapatric distributions. Moreover, any tradeoff in growth or survival on different substrates would lead to selection for reinforcement if gene flow between soil types is still possible (Kay *et al*. 2011).

A second possibility is that white-sand specialist species are produced by ecological speciation (parapatric speciation with gene flow) across a habitat gradient. Here, specialization to white-sand habitats would involve an evolutionary tradeoff such that success in white-sand forests comes at a cost to being successful in non-white-sand forests. Fine *et al*. (2006) hypothesized that there was a tradeoff to investment in growth and defense that limited habitat generalization in white-sand and terra firme forests. White-sand specialists were found to have significantly greater investment in physical and chemical defenses and slower growth rates than their congeners from clay, terra firme habitats (Fine *et al*. 2006). If selection were strong enough, habitat-mediated speciation could ensue even in the face of some gene flow, through strong selection against intermediate phenotypes (Endler 1982). Alternatively, if intrinsic isolating mechanisms evolve rapidly, habitat-mediated differentiation and speciation could occur even when selection against intermediate phenotypes was not so strong (Misiewicz 2014).

Protium subserratum Engl. has been the subject of several in-depth studies because this taxon is a complex of different lineages that include ecotypes that are morphologically (Daly & Fine 2011, Fine *et al*. 2013a, Misiewicz & Fine 2014) and chemically distinct (Lokvam & Fine 2012, Fine *et al*. 2013b, Lokvam *et al*. 2015) with these differences corresponding to white-sand or terra

firme soils. Misiewicz and Fine (2014) used nuclear microsatellite markers to show that populations of ecotypes found in adjacent and divergent soil types (<3 km apart) exhibited extremely low levels of gene flow compared to populations of ecotypes that were from the same soil type 100 km distant, even though all populations overlapped considerably in their flowering times and pollinators (Misiewicz 2014, Misiewicz et al. 2014). Hand pollination studies revealed that some mechanism of intrinsic genetic incompatibility between white-sand and terra firme ecotypes was occurring to prevent hybrid formation, either directly before or directly after fertilization (Misiewicz 2014).

Could there be a link between the rapid evolution of reproductive isolating mechanisms (or other intrinsic clade-level traits that promote speciation) and the formation of habitat-specialist lineages from more habitat-generalist progenitors? Besides some direct pleiotropic link between genes that confer reproductive incompatibility and other genes that are related to edaphic specialization (which is indeed possible, Kay et al. 2011), one could imagine that any factor that promoted reproductive isolation of spatially discontinuous populations within a large, edaphically heterogeneous area like the Amazon would increase the chances of habitat specialization to evolve given the mosaic-like arrangement of soil types. Even small selective differences due to different biotic enemies or nutrient availabilities of the soils could cause local adaptation and thus morphological and chemical divergence of the different ecotypes.

For example, in Protium subserratum, Fine et al. (2013b) found that white-sand ecotypes (1) grew significantly slower than clay-soil ecotypes, (2) had leaves containing more secondary metabolites (phenolics, flavones, quinnic acid derivatives, and oxidized terpenes), and (3) harbored completely different assemblages of insect herbivores. White-sand ecotype leaves also had different relative abundances of shared chemicals (Fine et al. 2013b, Lokvam et al. 2015), suggesting that selection by natural enemies may be a very important factor driving habitat specialization. Because these ecotypes have similar flowering times and share many insect pollinators (Misiewicz 2014, Misiewicz et al. 2014), we suggest that without fast-evolving incompatibility mechanisms, gene flow across habitat boundaries should maintain habitat-generalist phenotypes; or alternatively, intermediate phenotypes must be a large selective disadvantage in both habitat types, driving the evolution of pre-zygotic isolating mechanisms.

ENVIRONMENTAL FILTERING AND THE FUNCTIONAL COMPOSITION OF WHITE-SAND FLORA

No matter the mechanism of diversification, species that successfully establish in white-sand forests are subject to several strong abiotic and biotic environmental filters (Adeney et al. 2016). As a result, white-sand floras comprise a unique functional composition (Fortunel et al. 2014a), suggesting important differences in important ecosystem processes related to carbon and nutrient cycles. For example, Chave et al. (2010) found more than 40 percent less litterfall in white-sand forests than other old-growth

forests across South America and Panama, indicating significantly reduced net primary production and slower carbon cycling in these forests.

White-sand forests also have been shown to have very low levels of soil mineral nutrients, particularly nitrogen (Coomes & Grubb 1998, ter Steege et al. 2000, Fine et al. 2010, Baraloto et al. 2011, Brearley et al. 2011). Although white-sand soils have low total phosphorus, they often have higher levels of plant-available phosphorus than more clay-rich soils (Silver et al. 2000, Baraloto et al. 2011). White-sand soils also contain low levels of exchangeable aluminum because the reservoirs of this element are in clay particles and thus low cation exchange capacity. These soils have little potential to buffer acidity, which may limit nitrogen mineralization and inhibit recruitment of some species of seedlings (Proctor 1999). Many white-sand forests also experience drought, with studies reporting low plant extractable water during seasonal events of low precipitation (Baraloto et al. 2011, Quesada et al. 2011). Many white-sand forests have also been exposed to frequent fire in regions where fire occurs regularly (Adeney et al. 2016). Natural enemies contribute to these physiological challenges by removing or coopting plant tissues rich in nitrogen (Fine et al. 2006).

These strong filters have resulted in a strong pattern of convergence in the functional strategies of white-sand endemics, across all lineages. This pattern appears to hold not only for lineages in which white-sand specialists may have arisen via ecological speciation but also in those lineages that comprise only white-sand specialists (Table 2). Abiotic and biotic filters result in convergent functional strategies. For example, soil nutrient limitation and drought stress may favor smaller, thicker leaves to avoid higher root costs associated with replacing the high transpiration rates associated with larger, thinner leaves (Givnish 1979). Furthermore, biotic filters including high costs of tissue loss to herbivory would be predicted to promote a conservative growth strategy in white-sand endemics (Fine et al. 2006, 2013b). Indeed, white-sand plants are characterized by high tissue density in their leaves, stems, and roots (Medina & Cuevas 1989, Fortunel et al. 2012). Furthermore, white-sand specialist plants tend to have conservative nutrient use strategies, with lower mass-based tissue nutrient concentrations, and high nutrient use efficiencies, measured as biomass assimilation as a function of tissue nutrient concentration, when considering community means (with and without phylogenetic contrasts) (Coomes & Grubb 1998, Baraloto et al. 2006, Fyllas et al. 2009, Fortunel et al. 2012, 2014a).

An unsettled question concerns the extent to which white-sand plants may be more drought tolerant than plants specialized to terra firme forests (Table 3). Part of the problem is that functional ecologists have not arrived at a consensus for measuring drought tolerance in woody plants that can be readily measured across many species. Instead, we rely on proxies for the risk of cavitation, such as wood density or xylem tissue characteristics (Fortunel et al. 2014b). The few studies focusing on white-sand forest trees have found much higher wood density in white-sand taxa compared with taxa from other habitats, even when controlling for phylogeny or examining congeners differing in habitat prefer-

TABLE 3. *Summary of evidence for divergent functional strategies of the white-sand flora, at the community level, with and without phylogenetically independent contrasts (PICs), and contrasts of clades containing both white-sand specialists and specialists to other forest types (see Table 2).*

Predicted trait value of white-sand endemics	True for community means?	True for community means with PIC?	True for lineage comparisons?
Thicker leaf	Yes [3,4]	Yes [3,4]	Yes [3,4]
Sturdier leaf	Yes [3,4]	Yes [3,4]	Yes [3,4]
Lower leaf [N]	Yes [3,4,6]	Yes [3,4,6]	Yes [3,4,6]
Lower leaf [P]	Yes [3,4,6]	Yes [3,4,6]	Yes [3,4,6]
Smaller seeds	Yes [7]	Yes [7]	?
Denser wood	Yes [3,4,5,9]	Yes [3,4,5,9]	Yes [9]
Thinner xylem	No [5,9]	No [5,9]	No [9]
Lower cavitation risk	?	?	?
More resin/latex	?	?	?
More defense chemistry	?	?	Yes [2]
Unique defense chemistry	?	?	Yes [2]
Slower growth rate	Yes [1]	?	?
Thicker bark	No [8]	?	?
More ECM mutualists	Yes [10]	?	?

[1]Coomes and Grubb (1998), [2]Fine et al. (2006), [3]Fortunel et al. (2012), [4]Fortunel et al. (2014a), [5]Fortunel et al. (2014b), [6]Fyllas et al. (2009), [7]Grubb and Coomes (1997), [8]Paine et al. (2012), [9]Patiño et al. (2009), [10]Roy et al. (in press).

ences (Patiño et al. 2009, Fortunel et al. 2014b). However, total xylem area and mean vessel diameter were not significantly lower in white-sand species; instead white-sand species possessed significantly more fiber, which Fortunel et al. (2014b) proposed may represent adaptations for great biomechanical strength to withstand wind, or for higher resistance to herbivores and pathogens of wood tissue.

Biotic filters of increased herbivore or pathogen pressure may also drive white-sand specialist plants to invest in more or different chemical defenses for wood or leaf tissue. Indeed, we may expect a higher abundance of species producing resins or latexes believed to represent adaptations to natural enemies (Janzen 1974, Konno 2011), but to date no study has examined patterns of latex presence and abundance at the community or lineage level in white-sand flora. Fine et al. (2006) have shown compelling evidence for increased investment in defense chemistry of seedlings. Species from six different genera from white-sand forests were found to have higher investment in defense than their congeners occurring in terra firme clay soils along with significantly slower growth rates (Fine et al. 2006). This suggests that diversification events in these lineages have resulted from ecological speciation across habitat gradients including white-sand forests with higher pressure from natural enemies. Data for chemical defenses in leaf and wood tissue remain scarce in any tropical forest, and further work contrasting white-sand taxa with other habitats across different regions will help to complete our

understanding of the functional originality of these forests and its implications for important ecosystem processes including resilience to introduced natural enemies which may represent an important contemporary threat to natural forests (Tabarelli et al. 2012, Boyd et al. 2013).

TROPHIC INTERACTIONS

Because white-sand forests are composed of plants that produce tough, chemically defended leaves, one would predict that herbivore abundances and herbivory rates would be significantly lower in white-sand versus neighboring terra firme forests. Surprisingly, the available evidence is mixed regarding herbivory comparisons between white-sand and terra firme forests. For example, Lamarre et al. (2012) reported no significant difference in leaf production rate nor herbivory rate in community samples of 68 species from 17 different plant families in Peruvian and French Guiana white-sand forests compared to terra firme and seasonally flooded forests. On the other hand, experimental manipulation of herbivory as well as artificial defoliation in reciprocal transplant experiments in Peru has yielded significant differences in plant mortality and performance (Fine et al. 2004, 2006, Fine & Mesones 2011). Yet in Brazil, similar reciprocal transplant experiments yielded no differences in herbivory rates, although they lasted for fewer months and did not control for phylogenetic relationships of white-sand and terra firme specialists (Stropp et al. 2013). Herbivore abundance data yield results more consistent with predictions, with focused collections of insect herbivores found on Protium subserratum ecotypes growing in white-sand versus clay soils finding significantly higher numbers of insects in clay forests (Fine et al. 2013b). Lamarre et al. (in press) reported a unique arthropod community composition from Peru and French Guiana white-sand forests, with significantly lower abundances of sap-feeding and leaf-chewing insects.

Vertebrate studies have generally reported much lower species diversity and lower abundances in white-sand forests (Álvarez Alonso & Whitney 2003, Vriesendorp et al. 2006, Álvarez Alonso et al. 2013, Borges et al. 2016). This suggests that the third trophic level is less important in white-sand forests, and instead, herbivore abundances are likely controlled by low plant quality or toxicity. One interesting difference between white-sand and clay forest tree communities is that density-dependent patterns are pervasive in terra firme forests in the Neotropics, yet in white-sand forests, clumped distributions of dominant tree species are very common (Fine et al. 2010, Fine & Kembel 2011, Barbosa et al. 2013). Density dependence is thought to result from dispersal-limited host-specialist enemies causing high mortality rates under mother trees (Janzen 1970, Connell 1971). Thus, if this pattern is less pronounced in white-sand forests, it could suggest lower host-specialization and/or better dispersal ability by white-sand natural enemies (Givnish 1999). It is common to observe seedling carpets and even large numbers of saplings under parent trees in white-sand forests; thus, it is possible that the fungal pathogens or insect herbivores that cause high

levels of mortality are generally absent in white-sand forests. Regarding fungi, ectomycorrhizal mutualism is much more common in white-sand forests than terra firme forests, and it occurs across a broader range of plant taxa than previously thought (Roy *et al.* 2016). If there were some interaction by which mycorrhizae compete with or somehow counteract the effects pathogenic fungi, this would be an interesting mechanism to explain the relative paucity of pathogenic fungi in white-sand forests (*i.e.*, Liang *et al.* 2015). Yet, Peay *et al.* (2013) found evidence of putative lineages of pathogenic fungi in all habitats in a small survey of white-sand, flooded, and terra firme forests, with very low overlap in OTUs across habitats. This suggests that pathogenic fungi are present in white-sand forests, yet may be less virulent. We believe that a comparison of the mechanisms underlying density-dependence and lack thereof in Amazonian forests across white-sand and terra firme forests will be an especially productive avenue for future research.

PERSPECTIVES

We conclude that the white-sand flora represents an especially good model system to investigate plant speciation and community assembly. The replicated, island-like arrangement of white-sand forests across the Neotropics has promoted repeated instances of convergent evolution, allowing investigators to discern some important general patterns. For example, whereas niche conservatism has been trumpeted as an emerging paradigm in understanding patterns of diversification (Wiens *et al.* 2010), white-sand forests offer an intriguing counterpoint – extremely challenging physical and biotic environments, inhabited by lineages that vary wildly in their degree of niche conservatism. This gives evolutionary biologists a valuable tool to use white-sand forests as a comparative framework to study mechanisms of speciation, including the traits underlying niche conservatism and how they are linked to reproductive isolating mechanisms. Similarly, geographically separated patches of white-sand forests offer robust opportunities to test community assembly mechanisms. There is an emerging consensus that host-specialist natural enemies likely play a major role in maintaining hyperdiverse density-dependent plant communities (Givnish 1999, Comita *et al.* 2010, Mangan *et al.* 2010, Terborgh 2012). Yet, within these diverse forests exist islands of low-diversity white-sand forests with distinct plant communities and very different biotic communities. Ecologists have taken advantage of ecological gradients, such as light gaps, serpentine soils, and white-sand forests to learn many important lessons about plant adaptation to contrasting environments and the inherent tradeoffs to adaptation (Coley 1983, Fine *et al.* 2004, Kay *et al.* 2011). A similar approach, but focusing more at the community scale (Comita *et al.* 2010), is likely to give us new insights on the mechanisms by which natural enemies influence the maintenance of plant diversity. Finally, the high degree of endemism and unique functional composition of the white-sand flora merit further investigation to understand the potential floristic and ecosystem consequences of contemporary global changes. These forests are particularly vulnerable to land-use change because of encroaching settlements and accompanying risk of fire. Because white-sand soil has such low capacity to retain nutrients and water, forests that are cleared or burned regenerate extremely slowly (Álvarez Alonso *et al.* 2013). On the other hand, some authors have suggested that the stress-tolerant functional strategies of dry forest or white-sand endemics might confer resilience because they may be more tolerant of predicted increases in severe droughts (Fortunel *et al.* 2014a) or to increased movement of exotic pests to which they may have broad resistance because of high investments in defense (Fine *et al.* 2006). Further research should explore the extent to which white-sand endemics may broaden their ranges under scenarios of climate change, and the resulting consequences for trophic cascades and biogeochemical cycling given their unique functional attributes.

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