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Neotropical White-sand Forests: Origins, Ecology and Conservation of a Unique Rain Forest Environment

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Neotropical white-sand forests are unusual environments found throughout tropical South America that often occur as habitat islands surrounded by more familiar rain forests growing on clayey soils. Their namesake sandy soils can greatly reduce nutrient and water availability, leading to stunted forests with unique physiognomies and endemic species assemblages. Although white-sand forests have fascinated biologists since the 19th century (Spruce 1908, Janzen 1974), it was not until the 1980s that efforts to describe their unique nutrient cycling, forest structure, plant adaptations, and biological diversity began in earnest (*e.g.*, Anderson 1981, Medina & Cuevas 1989, Duivenvoorden & Lips 1995, Coomes & Grubb 1996, ter Steege *et al.* 2000, Álvarez Alonso & Whitney 2003). In this Special Section, we present original research, reviews and synthesis to detail the current state of knowledge of Neotropical white-sand forests, as well as identify research and conservation priorities for the future.

The eleven articles in this Special Section are a multinational effort with lead authors from Brazil, Peru, Ecuador, France, and the United States. The taxonomic and geographic focus of these articles is impressive, with articles on terrestrial plants, epiphytes, insects, birds, and fungi based on fieldwork conducted in the Amazon Basin, the Guianas, and Brazil's Atlantic Forests. Beyond the individual advances these articles put forth, considering them as a whole also reveals three persistent themes. The first is the realization that while some of the white-sand soils are ancient—over 100 million years in some areas of tropical South America—the recent history of the habitat islands we see today is quite dynamic. Their current biota is shaped in part by the expansion and contraction of white-sand areas, the large-scale movement of sediments by rivers, and geologic subsidence during the Pleistocene (Adeney *et al.* 2016). This combination of ancient origin with recent dynamism has had important consequences for the biota of white-sand habitats. On the one hand, many plant lineages have had long associations with white-sand forests, and have evolved traits that preclude them from expanding their distributions into other forest types (Vicentini 2016). As detailed by Fine and Baraloto (2016), these traits are likely related to adaptations to low nutrient availability, drought, and defense against natural enemies. The discontinuous nature of white-sand habitats across the landscape, which could also have been promoted by Pleistocene changes, may have also resulted in allopatric isolation and subsequent speciation in many of these plant lineages (Guevara *et al.* 2016); a similar signal of recent divergence may also be seen in the phylogeographic structure of white-sand bird species (Matos *et al.* 2016). However, other plant and animal lineages appear to exhibit much less niche conservatism, with clades of white-sand forest specialists that are closely related to specialists from other habitat types (Fine & Baraloto 2016, Lamarre *et al.* 2016).

A second, related theme is that many species associated with white-sand forests also occur in other forest types—especially forests with similar structure or resource limitations. Thus, many organisms that are abundant in white-sand forests may not be entirely restricted to these habitats, including species of trees (Garcia-Villacorta *et al.* 2016), epiphytes (Marí *et al.* 2016), birds (Borges *et al.* 2016), and ectomycorrhyzal fungi (Roy *et al.* 2016). These other marginal habitats, including seasonally flooded black-water forests (*igapó*) and disturbed open habitats (*caatinga*), may serve as corridors between isolated white-sand forest islands, resulting in greater gene flow and metacommunity dynamics that buffer against local extinction.

Finally, white-sand forests are unique and fragile habitats that are especially vulnerable to anthropogenic change. Many of the contributions highlight specific regions of white-sand forest that should be priorities for conservation initiatives (*e.g.*, Daly *et al.* 2016); particularly notable among these is Adeney *et al.* (2016), which also includes the first comprehensive map of Amazonian white-sand ecosystems. We hope the articles in this Special Section make a compelling case for why tropical biologists should continue to study and strive to conserve the fascinating biota of Neotropical white-sand forests.

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