

Can functional traits explain species habitat specialization? The case of a Central Amazon forest

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Introduction

The high diversity of trees found in tropical forests is significantly driven by habitat specialization¹, yet the mechanisms that restrict species to particular habitats are still uncertain. These mechanisms can play important roles in diversification², biodiversity maintenance³, and predicting climate change ramifications⁴. For example, habitat specialization across small-scale topo-edaphic gradients is likely to be especially important for the fate of tree species in the Amazon basin, where there is little large-scale topographic variation to provide future climatic refugia^{5,6}.

In Amazon, topography determines soil physicochemical properties and creates spatial heterogeneity in soil fertility⁷. Central Amazon, a hyper-diverse region⁸, is composed of clayey plateaus intercut by sandy valleys⁹. These are very infertile soils, with very low phosphorus concentrations⁷, the most limiting soil nutrient for plants in the region and a major driver of forest composition¹⁰, biomass^{9,11} and dynamics¹² and tree species distribution¹³. Additionally, clayey soils contain relatively high levels of aluminium and iron, which can be toxic for plants⁷ and soil microbes⁷ and make phosphorus less available for plants⁷, respectively. Sandy soils, on the other hand, may constitute a less stable substrate for large trees and consequently increase tree mortality rates⁷. Interestingly, though, some species seem to successfully establish in both sandy valleys and clayey plateaus⁷.

Plants in infertile soils cannot cope with leaf tissue loss¹⁴ caused by herbivores or falling debris and should, therefore, adopt conservative strategies like reduced nutritional quality (low leaf P concentration, LPC) or increased protection (high leaf toughness, LT)¹⁵. Conversely, plants in P-rich soils should have acquisitive strategies in order to compete with fast-growing neighbours¹⁴. Therefore, they should have lower leaf production costs (low LT) and leaves with higher photosynthetic capacity (high LPC)¹⁵ (Table 1, Figure 1). Generalist species, in turn, should either have higher intraspecific variation in these traits (ITV)¹⁶ than specialists or somehow escape the growth-defense trade-off (high LPC, high LT)¹⁷ in order to occur at both habitats. Other explanations would be that generalist species are actually a mid-gradient (slope) specialist, and therefore occurs in low abundance in both habitats¹⁷, or even gap specialists, in which case they should be distributed in relatively small clumps in both habitats¹⁸. Finally, there is the possibility that generalists are simply better dispersers and can exploit ecological opportunities (win by default due to dispersal failure of specialist species) in both habitats¹⁹.

Table 1: Table 1. Predictions for the main hypotheses that explain how generalist species (G) manage to establish both in sandy valleys (V) and in clayey plateaus (P) and compete with local specialists (S). Predictions are made in terms of the values of the functional traits leaf phosphorus content (LPC) and leaf toughness (LT), performance (local abundance), and spatial distribution (clumpiness) within each habitat. * Abundance of a gap specialist depends on how dynamic the forest in each habitat is. ** Abundance of an opportunistic species depends on how much each forest is limited by dispersal.

Hypothesis	LPC	LT	Abundance	Clumpiness
Trait plasticity	$G \sim S$	$G \sim S$	$G \sim S$	$G \sim S$
Hutchinsonian demon	$G > S$	$G > S$	$G > S$	$G \sim S$
Mid-gradient specialist	$G < Sv; G > Sp$	$G > Sv; G < Sp$	$G < S$	$G \sim S$
Gap specialist	$G > S$	$G < S$	$G < S^*$	$G > S$
Opportunistic	$G ? S$	$G ? S$	$G < S^{**}$	$G < S$

Methods

I will sample 60 abundant species (20 valley specialists, 20 plateau specialists, and 20 generalists) in a 25-ha permanent plot near Manaus, Brazil (Figure 2A). In order to plan the sampling, I divided the plot into three types of habitats: valley (elevation ≤ 15 m), slope ($15 < \text{elevation} < 35$ m), and plateau (elevation ≥ 35 m; Figure 2B). This cut was made in a such a way that it maximized differences in soil texture between the valley and the plateau (Figure 3A). I will sample ten saplings from specialist species in their respective habitats, and 20 saplings from generalist species, ten in each habitat. To determine LPC, I will bulk samples from different individuals sampled in each of the habitats (1-5 leaves per plant, depending on leaf size). Following standardized protocols¹⁵, I will measure LT using a penetrometer (three punches in two leaves from each sampled plant) and also leaf size, leaf specific area, leaf dry matter content, and stem specific density, for those saplings that have branches.

Because the valleys have more fertile (Figure 3B) and less toxic soils (Figure 3C) than the plateau (although the sandy valley soils have lower field capacity; Figure 3D), valley-specialists should have higher LPC but lower LT, while plateau-specialists should have lower LPC but higher LT (Figure 1). Generalists may have trait values that are higher, lower or similar to those of specialists, depending on the mechanism that makes them generalists (Table 1; Figure 1).

Preliminary results

Spatial point-pattern analysis showed that there are in the plot 108 plateau-specialist species, 67 valley-specialists, and 124 generalists (Figure 4A). Abundance ranks shift between specialists, while generalists tend to have a constant, intermediary abundance (Figure 4B,C), but when all generalist species are considered together, they are the most abundant ones across the gradient (Figure 4D).

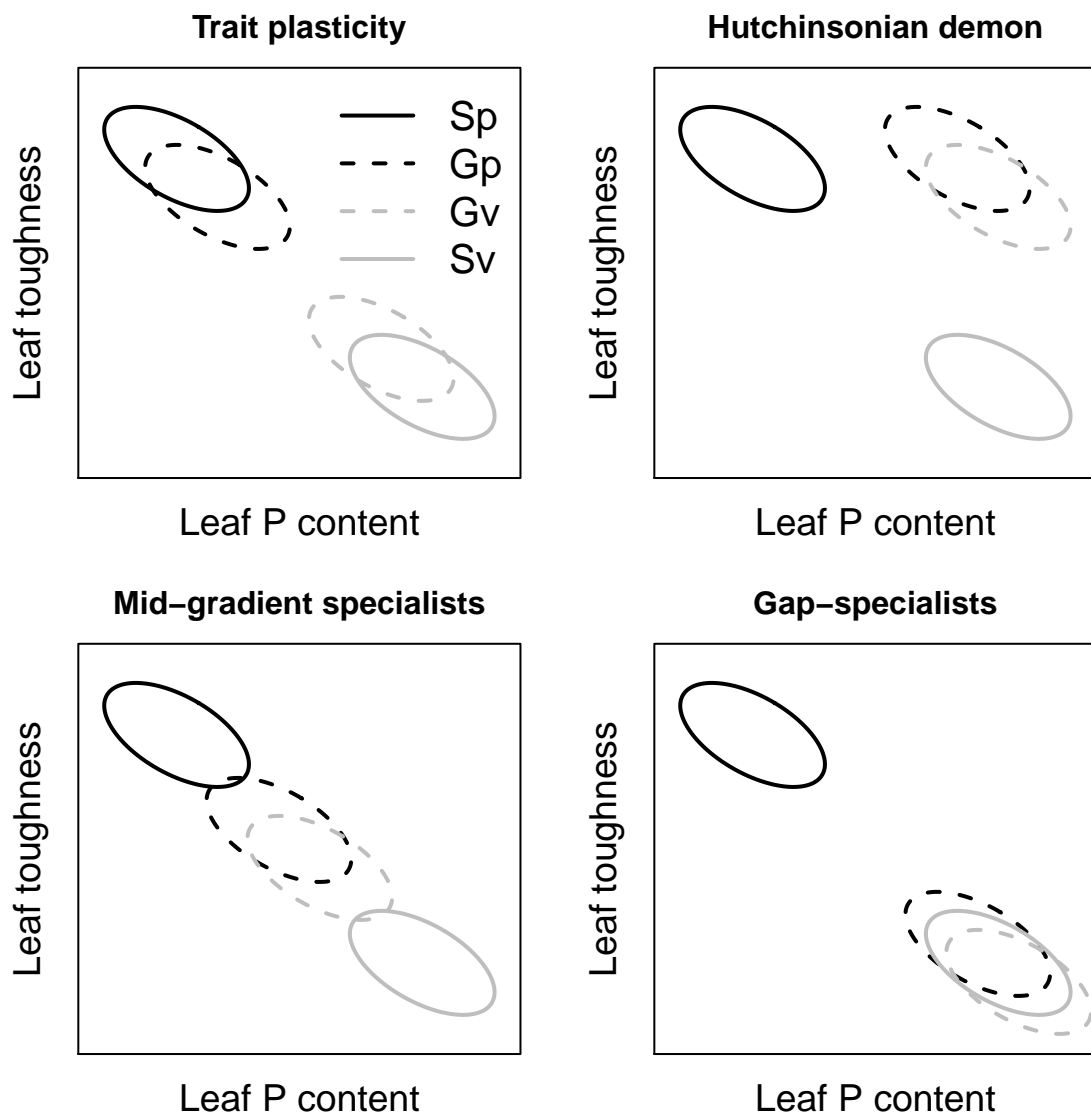


Figure 1: Predictions for generalism hypotheses in a trait space formed by leaf toughness and leaf phosphorus content for species that are plateau-specialists (Sp), valley-specialists (Sv), and generalists sampled in each of these habitats (Gp and Gv).

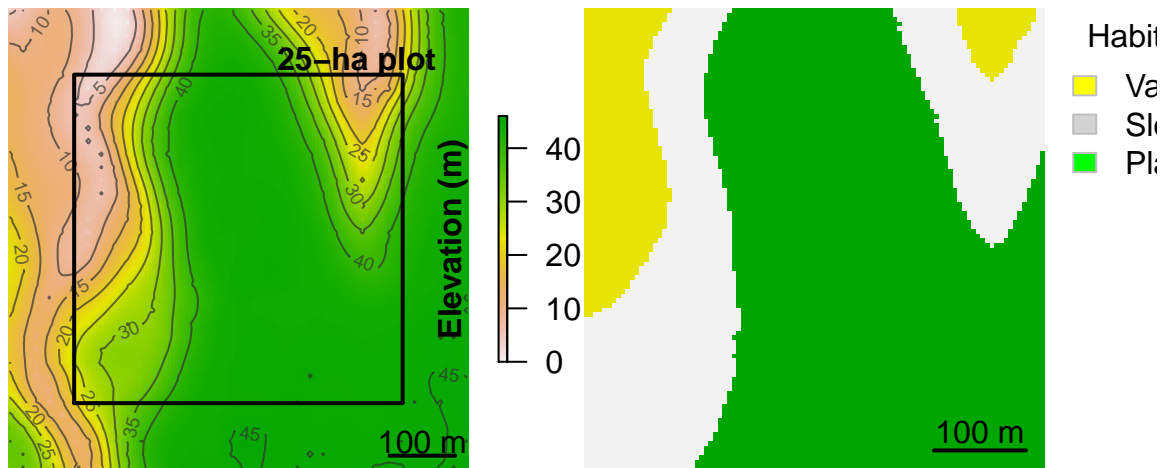


Figure 2: Topographic map of the 49-ha plot where the central 25-ha one is located (A), and the classification of the central plot into three contrasting habitats according to soil texture and topography: valley, slope, and plateau (B).

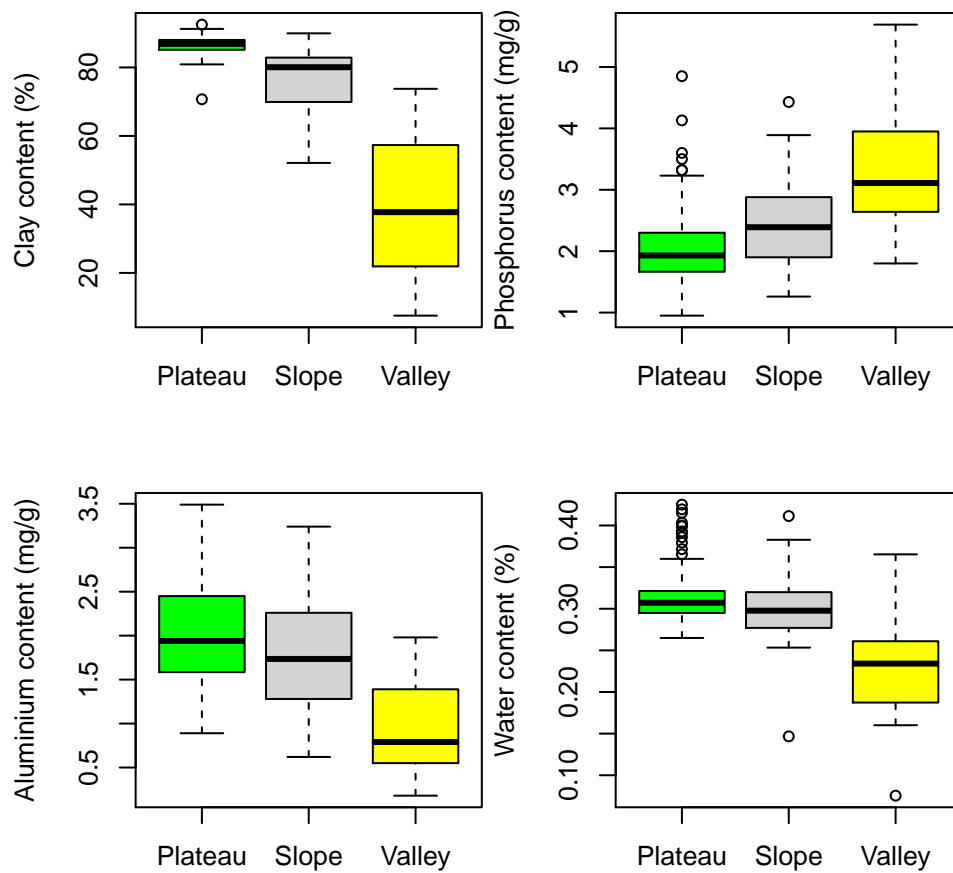


Figure 3: Soil differences between plateau and valley. Slopes show as a transition between these two habitats.

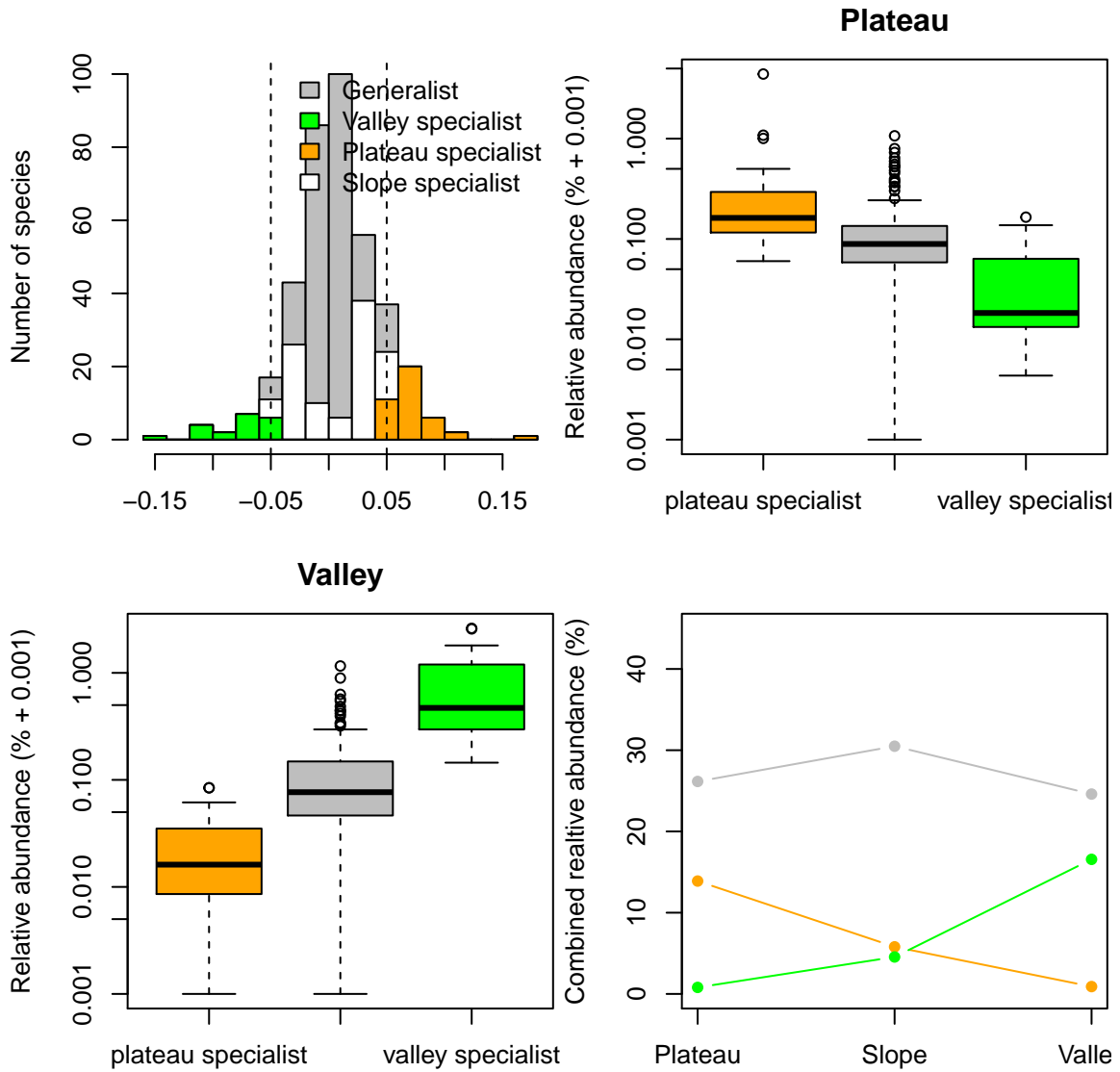


Figure 4: Species classification into habitat specialists (plateau, slope, and valley) and generalists (A) and their relative abundances in the plateau (B) and in the valley (C). Combined abundance of these species are also shown (D)

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