



## Original article

## Commonness of Amazonian palm (Arecaceae) species: Cross-scale links and potential determinants

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## ABSTRACT

The mechanisms that cause variation in commonness (abundances and range sizes) of species remain debated in ecology, and a repeatedly observed pattern is the positive relation between local abundances and larger scale range sizes. We used the Amazonian palm species (Arecaceae) to investigate the dependence between and potential determinants of commonness across three (local, landscape, continental) spatial scales. Commonness at the smaller scales (local abundance, landscape frequency) was estimated using data from 57 transects (5 × 500 m) in primary, non-inundated (*terra firme*) rainforest in a western Amazonian landscape, while commonness at the largest scale (continental range size) was estimated from digitized distribution maps. Landscape frequency was positively related to both local abundance and continental range size, which, however, were not related to each other. Landscape frequency was positively related to topographic niche breadth. Stem height correlated with continental range size and was the only species life-history trait related to any commonness measure. Distance from the study area to a species' range centre did not influence any of the commonness measures. The factors determining commonness in the Amazonian palm flora appear to be scale-dependent, with the unrelated local scale abundance and continental range size probably being controlled by different driving factors. Interestingly, commonness at the intermediate, landscape scale seems linked to both the smaller and the larger scale. Our results point towards topographic niche breadth at the smaller scales and stem height, possibly reflecting species' dispersal potential, at the continental scale as important determinants of commonness.

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## 1. Introduction

It is a near universal feature of biological communities that species differ substantially in their abundances and distributional ranges: a few species are common and many are rare (Gaston, 2003). In tropical rainforests, known for housing large proportions of the World's species and for having high richness of species at all scales from local to continental, a large proportion of the species are rare and narrowly distributed and far fewer species are common and widely distributed. The pattern is well documented, but the mechanisms that underlie this pattern remain poorly understood, although some progress has been made (Hubbell et al., 1999; Pitman et al., 2001; Tuomisto et al., 2003; Svenning et al., 2004; Condit et al., 2005). Understanding the mechanisms governing commonness and rarity is a fundamental challenge for conservation

biology (Gaston, 2003), e.g., for predicting extinction risk from continued deforestation (Hubbell et al., 2008).

Commonness and rarity can be defined in terms of number of individuals, ultimately the product of a species' local abundance and its overall range size (Gaston, 1994), i.e., its commonness across multiple scales. In many different taxa and over various ecological settings abundance is positively related to range size, i.e., locally abundant species tend to be widespread at larger scales, whereas species with narrow distributions tend to have low local abundances (Gaston, 2003). Given their generality, one should search for general ecological determinants of these cross-scale commonness links (Kolb et al., 2006).

Several hypotheses have been proposed to explain species differences in abundance and range size as well as the cross-scale links between these commonness measures. The niche breadth hypothesis (Brown, 1984) suggests that species that are able to utilize a broader variety of resources will achieve higher local densities, and be able to spread across larger areas. The related niche availability hypothesis posits that abundance and distribution of the

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resources used, rather than the range of resources, determine species' abundances and distributions. Hence, the species that utilize the most available resources will be the most abundant and the most widely distributed (Hanski et al., 1993; Gaston et al., 1997). Life-history traits may also underlie differences in abundance and range size between common and rare species (Kunin and Gaston, 1997; Murray et al., 2002). For example, fecundity and propagule dispersal may strongly affect both abundance and distribution (Murray et al., 2002). According to the 'abundant-centre' rule both abundance and occupancy decline towards a species' range edge (Brown, 1984); and thus species' commonness can be influenced by the distance to their range centres and a positive abundance-range size relationship among species could be observed when a spatially limited study area comprises varying parts of species' ranges (Bock and Ricklefs, 1983; Bock, 1984). However, the generality of the 'abundant-centre' rule has been challenged (Sagarin and Gaines, 2002; Murphy et al., 2006). When investigating commonness patterns, cross-scale links, and the mechanisms underlying them, interpretations should be carried out with explicit reference to spatial scale, as the mechanisms involved are likely to be scale-dependent (Willis and Whittaker, 2002).

In the present study we investigate the consistency of commonness for western Amazonian palm species across three spatial scales (local, landscape, continental), and we assess potential underlying ecological determinants of commonness. The palm family (Arecaceae) is an important component of American tropical rainforests and is particularly dominant in the western Amazon basin (Henderson, 1995; Ter Steege et al., 2000). Palm species richness strongly peaks in this region (Bjorholm et al., 2005), just as woody plants do in general (Gentry, 1988). Palms vary greatly in abundance and distribution, they have developed a number of different life forms (Henderson, 1995), and have a well resolved phylogeny (Asmussen et al., 2006), which make them a suitable model group for studying the determinants of commonness and the variation in commonness across scales (Vormisto et al., 2004a; Macía and Svenning, 2005).

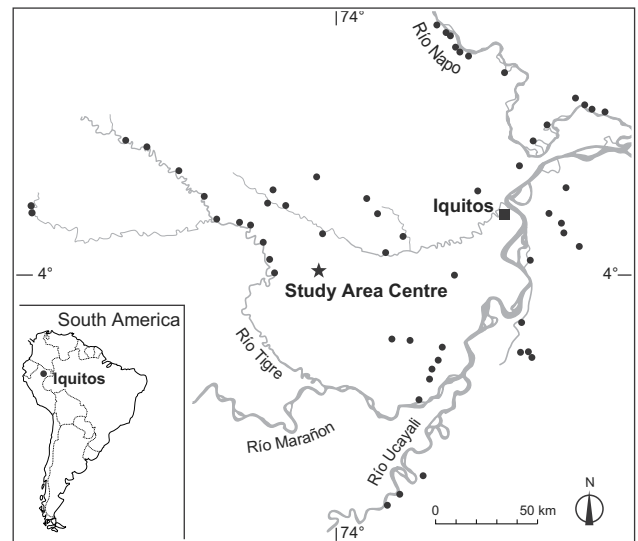
More specifically, we address the following questions: 1) Are commonness measures on different spatial scales (local abundance, landscape frequency, continental range size) positively related to each other? 2) Are commonness measures related to species' niche characteristics (i.e., habitat preference, niche breadth, and niche position), to species' life-history traits, or (only local abundance and landscape frequency) to the relative distance from the study area to the species' range centres?

## 2. Materials and Methods

### 2.1. Study area and sampling design

Fieldwork was carried out in a 290 × 240 km region around Iquitos, Peru (Fig. 1). The area has a wet, tropical climate with 2900 mm mean annual precipitation and 26 °C mean annual temperature (<http://www.worldclimate.com>). The elevation is 100–200 m above sea level and the terrain is generally flat, although rather steep hills sometimes occur.

We placed 57 transects of 5 × 500 m, subdivided into 100 subunits of 5 × 5 m, in non-inundated (*terra firme*), tall, primary rainforest, avoiding major vegetation disturbance and white-sand soils. All individuals of the palm family (Arecaceae) were recorded in each subunit and assigned to one of three developmental stage classes: seedling, juvenile or adult. Seedlings were individuals with leaves still undivided (or very small individuals in species with entire leaves), juveniles were individuals large enough to have divided leaves, but too small to reproduce (according to H. Balslev's many years of field experience with western Amazonian palms), and adults were individuals large enough to at least potentially reproduce (see Appendix A for nomenclature). *Socratea exorrhiza* and



**Fig. 1.** Map of the study area. Dots indicate the location of 57 transects placed on *terra firme* around Iquitos, Peru. Square indicates the location of Iquitos. Star indicates the centre of the study area (see Methods).

*Socratea salazarii* could not be distinguished as seedlings and juveniles and were lumped as *S. exorrhiza/salazarii*. Among adult *Socratea* 41% were *S. salazarii*. We encountered 62 species and identified 69,799 individuals. An additional 326 individuals, that we could not identify, were excluded from the analysis. Five species occurred only in a single transect, and one species, *Bactris concinna*, which was abundant in adjacent floodplains, was present with only one individual in our *terra firme* transects. On average, within the first 250 m we had encountered more than 87% of the total number of species found per transect, suggesting that the chosen transect length of 500 m provides a fair estimate of the local *terra firme* species pool.

### 2.2. Commonness measures

Commonness was measured at three distinct scales: (i) At the local scale, commonness was measured by local abundance, the mean number of individuals of all stages per hectare, including only those transects where a species was found. (ii) At the landscape scale, commonness was measured by landscape frequency, defined as the number of transects in which a species was found. Again all stages were considered. (iii) At the continental scale, commonness was measured by continental range size, defined as the number of occupied 1 × 1° grid cells across the Americas based on distribution maps from Henderson et al. (1995) and digitized in Bjorholm et al. (2005). As these are outline maps, continental range size represents extent of occurrence, not area of occupancy (Gaston, 2003). In order to assess the robustness of the relationships between commonness measures, we alternatively quantified abundance and landscape frequency with only juveniles and adults included and with only adults included.

### 2.3. Niche characteristics

Topography and the associated hydrology have been shown to control species distributions and community structure in palm communities at local scales in the Amazon basin (Kahn and de Granville, 1992; Svenning, 1999, 2001; Vormisto et al., 2004b; Normand et al., 2006) as well as in numerous plant communities elsewhere (e.g., Silvertown et al., 1999). We therefore chose topographic position and hydrology as a key niche axis for the Amazonian palm species. We defined three niche measures in relation to this niche

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