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Availability and species diversity of forest products in a Neotropical rainforest landscape

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ABSTRACT

Tropical rainforests harbor a high diversity of tree species, offering a potentially rich array of timber (TFP) and non-timber (NTFP) forest products. The supply of such products has been commonly evaluated at the local (plot) scale; however, little is known about how their availability and diversity change at the landscape scale, particularly in heterogeneous environments. This information is critical in designing landscape forest management programs. Here, we assess the extent to which the frequency, abundance, diversity, composition and productivity (aboveground biomass) of tree assemblages with potential forest products (PFPs) change across three landscape units (LUs) that differ in soil and topographic conditions. The study was carried out in a well-conserved old-growth tropical rainforest in southeastern Mexico. Three plots (0.5 ha each) were established per LU, in which all trees ≥ 10 cm were inventoried, taxonomically identified and assigned to eight forest product categories. General linear models, multiple regression and ordination analysis (CCA) were used to assess structural and compositional changes in the tree assemblages supplying different PFPs among LUs and along soil physicochemical gradients. More than half (94 species, 57%) of the total number of identified species (165) had one or more PFPs, mostly related to timber products. Ordination analysis showed that the abundance of species with different PFPs has a heterogeneous distribution among LUs, mostly related to changes in soil nitrogen, pH and aluminum saturation. Variation among LUs in terms of tree biomass was strongly driven by soil available phosphorus and soil physiological depth. Each LU had a different potential to provide forest products, producing a diverse mosaic of PFPs within the landscape. Decisions concerning sustainable forest management should consider such variability in the availability and diversity of forest products across landscapes, as well as the environmental factors that govern this spatial variation.

1. Introduction

Tropical rain forests (TRF) are mega-diverse ecosystems that supply a wide array of goods and benefits for human well-being (de Groot et al., 2012). Among such goods are the timber (TFP) and non-timber (NTFP) forest products. The latter includes any biotic resource that does not imply the logging of trees, such as edible fruits, fuelwood, materials for construction (e.g. roofing leaves), as well as ornamental and medicinal plants (Belcher, 2003; de Groot et al., 2010). Considering the classification of ecosystem services established by MEA (2005), forest products are an important provision ecosystem service that adds to the other support, regulation and cultural services supplied by TRF (Daily, 1997).

In the Anthropocene, global demand for food and expansion of agriculture has driven severe deforestation in tropical regions (Gibbs et al., 2010). Deforestation has produced a critical reduction of global biodiversity and the loss of ecosystem services of local, regional and global importance (Foley et al., 2011). Satisfying the present and future demand for food, without compromising the biodiversity and ecosystem services of TRF, is therefore vital for the sustainable management of

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these forest ecosystems (Harvey et al., 2008). Sound management of forest products requires an assessment of their availability and diversity, as has been conducted in some tropical forests (e.g. Dattagupta et al., 2014; Ibarra-Manríquez et al., 1997; Peters et al., 1989). Some studies have shown a positive relationship between plant species diversity and the number of potential forest products at plot level (e.g. Quijas et al., 2010). There are studies that address the landscape-scale variation of tropical forest products and their relevance to forest management (e.g. Newton et al., 2012; Salo and Toivonen, 2009; ter Steege et al., 2002). However, most studies focused separately on timber or non-timber products. Therefore, there is a need of studies assessing changes in the availability, diversity and composition of forest products at landscape scales considering both forest product types. This approach is important for designing management strategies of forest products in an integral way, especially in areas with high environmental heterogeneity.

The extraordinary tree species diversity in TRF is a result of the fact that most species have low population densities, which in turn causes a low availability of species-specific forest products. Since the population density and spatial distribution of species supplying forest products can affect harvesting quotas at the local and landscape scales, documenting these demographic attributes should help with the design of appropriate sustainable management programs for TRF products (Fortini et al., 2006; Newton et al., 2012; Ribeiro et al., 2014; Ticktin, 2004). Sustainable TRF management also addresses the biological and environmental complexity of these forest ecosystems (Ros-Tonen, 2000). For example, most TRF tree species require specific resources (e.g. quantity and quality of light, availability of soil nutrients and water), conditions (temperature, humidity) and biotic interactions (mutualistic associations with animals, bacteria and fungi) in order to germinate, establish, grow and reproduce (Gravel et al., 2011; Wright, 2002). Sustainable forest management therefore not only requires basic information about the availability and diversity of forest products but also about the ecological factors that determine the spatial variation of these attributes (Guariguata et al., 2010).

Several studies have documented important levels of tree species turnover associated with environmental heterogeneity in TRF landscapes (e.g. Baldeck et al., 2013; Condit et al., 2013; John et al., 2007; Phillips et al., 2003; Toledo et al., 2012). Soil nutrient content (Baldeck et al., 2013; John et al., 2007; Phillips et al., 2003; Swaine, 1996) and soil water retention capacity (Sollins, 1998) have been identified as important variables affecting tree species distribution and species turnover. Soil variables could therefore also play an important role in determining spatial variation in the availability and diversity of potential forest products (PFPs). It is possible to map spatial changes in soil nutrient content and water availability using topographic variation, since topography affects soil water availability and the biogeochemical processes that influence soil nutrient availability (Baldeck et al., 2013; Brown et al., 2013). Topographic and soil variables can be integrated within discrete, relatively homogenous, LUs, through a process of geopedological delimitation (Zinck et al., 2016). When LUs are recognized, it is possible to evaluate the effect of soil variables on the spatial distribution and population density of plant species (Phillips et al., 2003). This, in turn, helps to identify soil and topographic factors that influence the potential spatial availability of forest products. This potential availability can be assessed through the abundance (trees per unit area), frequency of occurrence, and aboveground biomass (AGB, hereafter referred to as "biomass") of the tree species that provide the PFPs. Abundance and frequency give an idea of the spatial attainability of the forest products while biomass reflects the potential productivity of tree species (Clark et al., 2001).

The Lacandon forest in southeast Mexico is one of the largest tropical rainforests of Mesoamerica; it is broadly representative of the TRF of southern Mexico and Central America (de Jong et al., 2000; Meli and Carabias, 2015). It has a high species diversity [120 plant species in 0.1 ha (Dirzo et al., 2009) and more than 200 tree species with stems ≥10 cm DBH in 7 ha (Martínez-Ramos, 2006)], which is related to its edaphic and topographic heterogeneity (Siebe et al., 1995). The historical cover of the Lacandon forest has decreased by 66% over the last four decades as a result of conversion of the land to agriculture (Meli and Carabias, 2015; Zermeño-Hernández et al., 2015) and the Mexican government has decreed part of the forest (331,200 ha) as the UNESCO Montes Azules Biosphere Reserve (MABR) in 1978. This reserve aims to preserve the biodiversity and ecosystem functions and services of old growth forest ecosystems, limiting any extractivism or other human activity. In the area surrounding the MABR, where same forest topographic and soil formations exist (Martínez-Ramos, 2006; Navarrete-Segueda et al., 2015) (Appendix A, supplementary material), governmental programs involving ecotourism and payment for environmental services have been conceived as part of the sustainable management of human modified landscapes (HMLs). However, accelerated demographic growth and human activities cause intense pressure, on remaining forest fragments surrounding MABR landscapes (Carabias et al., 2015). An ecological analysis of the availability and distribution of forest products that considers environmental heterogeneity is urgently required in such HMLs.

In this paper, we assess changes in the abundance, frequency, biomass, diversity and composition of tree assemblages that supply PFPs across LUs that contrast in terms of soil and topographic characteristics, in the Lacandon tropical rainforest. We use areas of the MABR as a study system in an attempt to provide an ecological basis for the extractivism potential and management of forest products in HMLs. The objectives of the study were to: i) evaluate the potential availability (abundance, frequency and biomass) and diversity of forest products supplied by tree assemblages present in an environmentally heterogeneous landscape, ii) document the variation in such potential within and among types of LU, and iii) assess the extent to which such changes are associated with variation in the soil (water and nutrient availability) and topographic attributes of the landscape.

2. Methods

2.1. Study site

This study was conducted in the Montes Azules Biosphere Reserve (16°04′N and 90°45′W), located in the region of the Lacandon tropical rainforest, in Southeastern Mexico. Total annual precipitation in this area is *ca.* 3000 mm and mean annual temperature is 22 °C; there is a short dry season from February to April, with less than 60 mm of precipitation per month (Martínez-Ramos et al., 2009). The composition, structure and diversity of the forest are influenced by variation in the geology, soils and topography (Ibarra-Manríquez and Martínez-Ramos, 2002; Siebe et al., 1995).

The geology of the region comprises sedimentary rocks affected by folding and fracturing, such that outcrops of limestone, claystone and sandstone, as well as conglomerates, are structured in systematic patterns. Limestone outcrops occur on mountain ranges covering an altitudinal gradient of 150–700 m, affected by a karstification process. Low-hill areas occupy the depressions between karst-ranges in which claystone, sandstone and conglomerate outcrops alternate (García-Gil and Lugo-Hupb, 1992). Landscape units can be identified within this complex geological system, based on lithology, topography and soil properties (Siebe et al., 1995). The density and distribution of plant species respond to these contrasting landscape attributes (Ibarra-Manríquez and Martínez-Ramos, 2002; Martínez-Ramos, 2006).

2.2. Landscape units

Landscape units (LUs) were characterized based on the hierarchical geopedological classification system proposed by Zinck et al. (2016). These units were delimited by visual interpretation of the external characteristics of landforms in aerial photographs at scale 1:20,000 and