Evaluation of tree diversity and utilization: the role of acculturation.
A case study in the Bolivian Amazon

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« J'ai heurté, savez-vous, d'incroyables Florides
Mêlant aux fleurs des yeux de panthères à peaux
d'hommes ! »

À mes parents, pour m'avoir ouvert la voie des forêts tropicales.
À Charlotte, pour celle de l'Amérique du Sud...
Abstract

To date, the association between biological and cultural diversity has mostly been analyzed at regional or global scales. However, studying the link at the local scale is crucial to get a thorough understanding of the processes that determine this association. This PhD thesis aims at filling a gap between ecological and cultural studies at such a scale in the territory of a native group of the Bolivian Amazon, the Tsimane’, whose culture is relatively well documented but whose territory lacks of reliable ecological data. The four chapters of this thesis answer to the following research questions: 1) what are the differences in plant diversity in the forest surrounding indigenous villages and what are the factors determining such differences? 2) How can we relate differences in plant diversity to indigenous intracultural variation?

Fifty-five 0.1-ha plots were inventoried for trees ≥2.5 cm diameter at breast height in seven Tsimane’ villages, and soil variables were analyzed in each plot. First, I quantified oligarchic patterns across villages using diversity and composition indicators, i.e., species and family importance value index (IVI and FIVI). I found a floristic gradient with north-south orientation, likely due to biogeography and to the flooding history in the area. Second, I used Mantel analyses to quantify correlations between tree diversity, proxied by species turnover broken down into different tree categories, and edaphic and geographic factors. Tree species turnover was strongly associated with geographic distances and soil variables, mainly exchangeable cations, pH, C/N and texture; canopy trees were more strongly associated to environmental variables than understory trees, but phosphorus explained only understory tree distributions.

In six of the inventoried villages I measured individual acculturation of household heads as a proxy for intracultural variation. I used multivariate analyses to relate acculturation values to alpha diversity and forest structure in the inventoried plots. I found a significant inverse U-shaped relation between acculturation and diversity, but no significant relation with structure. I discuss how acculturation can act as a cultural disturbance through the modification of traditional ecological knowledge, having only subtle effects in old-growth forests.

Lastly, to collect data on uses of 58 tree species expert informants were interviewed in 22 villages with overlapping territory with the villages inventoried for ecological data. I used multivariate analyses to highlight association patterns between the ecological importance of the species in the inventoried plots (IVI) and their overall and categorical usefulness. There was a significant positive relation between overall usefulness and IVI, but a negative association for medicinal uses and edible species. I explain these differences by discussing the likelihood that the Tsimane’ substitute species according to their properties.

The results of this dissertation illustrate the importance of the association between intracultural variation and biological diversity in indigenous territories.
Natural factors primarily explain tree diversity and composition patterns, but indigenous traditional ecological knowledge and management also seem important determinants of these distributions. Policy implications of this study include the need to consider indigenous people as drivers of part of the biodiversity, which has to be taken into account for future territorial planning and biocultural conservation.

Key words: biocultural diversity, intracultural variation, indigenous knowledge, floristic patterns, species turnover, plant uses, Tsimane’
**Resumen**

La asociación entre las diversidades biológica y cultural se ha analizado, en la mayoría de las ocasiones, a escalas regional y global. Sin embargo, el análisis a escala local es crucial para entender los procesos que determinan dicha asociación. El principal objetivo de esta tesis doctoral es llenar parte del vacío existente en lo que se refiere a la integración entre estudios ecológicos y culturales a escala local. Con este fin he utilizado como caso de estudio un grupo indígena de la Amazonía Boliviana, los Tsimane’, cuya cultura está bien documentada pero cuyo territorio carece de datos ecológicos. Los cuatro capítulos de esta tesis contestan a las siguientes preguntas: 1) ¿Cuáles son las diferencias de diversidad vegetal en el bosque alrededor de las comunidades indígenas y cuáles son los factores que determinan dichas diferencias? y 2) ¿Cómo se pueden relacionar las diferencias en la diversidad vegetal con la variación intracultural entre los indígenas?

Para contestar a estas preguntas, cincuenta y cinco parcelas de 0,1 hectáreas fueron inventariadas en siete comunidades Tsimane’, midiendo así árboles de diámetro ≥ 2,5 cm a la altura del pecho, y recogiendo muestras de suelo para analizar diversas variables edáficas. En primer lugar cuantifiqué las tendencias de oligarquía florística entre comunidades usando indicadores de diversidad y composición (índices de valor de importancia de familias y especies o *importance value index* (IVI) para especies y familias). Encontré un gradiente florístico con orientación norte-sur, probablemente debido a la biogeografía y a la historia de inundación en la región. En segundo lugar usé un análisis de Mantel para cuantificar correlaciones entre la diversidad de árboles, estimada con el *turnover* de especies dividido entre diferentes categorías, y factores edáficos y geográficos. El *turnover* de especies estuvo estrechamente asociado con las distancias geográficas y algunas variables edáficas, principalmente cationes intercambiables, pH, C/N y textura; los árboles de dosel estuvieron más asociados con las variables ambientales que los árboles de sotobosque; sin embargo, el fósforo explicó solamente las distribuciones de árboles de sotobosque.

En seis de las comunidades inventariadas estimé la aculturación individual de los jefes de hogar para analizar la variación intracultural. Llevé a cabo análisis multivariados para relacionar los valores de aculturación con la diversidad alfa y la estructura del bosque en las parcelas. Encontré una relación significativa en forma de U invertida entre la aculturación y la diversidad, pero no con la estructura. Discuto cómo la aculturación puede actuar como una perturbación cultural a través de modificaciones del conocimiento ecológico tradicional, teniendo efectos sutiles en bosques maduros. Por último, analicé las entrevistas que fueron realizadas a informantes expertos en 22 comunidades que compartían territorio con las siete comunidades inventariadas, a fin de colectar datos de usos de 58 especies de árboles. Usé análisis multivariados para resaltar patrones de asociación entre la importancia ecológica de las especies en las parcelas (IVI) y su utilidad general y por categorías para los Tsimane’.

Encontré una relación positiva
significativa entre la utilidad general de las especies y su IVI, pero una relación negativa para los usos medicinales y las especies comestibles. Explico estas diferencias discutiendo la posibilidad de sustitución de las especies por los Tsimane’, según sus propiedades.

Los resultados de esta tesis demuestran la importancia de la asociación que puede existir entre la variación intracultural y la diversidad biológica en territorios indígenas. Los factores naturales explican ante todo los patrones de diversidad y composición florística; sin embargo, el sistema de conocimiento y manejo indígena parecen determinantes importantes de las distribuciones. Las implicaciones políticas y de gestión de este estudio incluyen la necesidad de considerar a los pueblos indígenas amazónicos como determinantes de parte de la biodiversidad, lo cual ha de ser tenido en cuenta para futuras actuaciones en materia de planificación territorial y conservación biocultural.

**Palabras claves:** diversidad biocultural, variación intracultural, conocimiento indígena, patrones florísticos, *turnover* de especies, usos de plantas, Tsimane’
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General introduction

Statement of the problem: biocultural diversity

The standard approach to conservation has often failed to efficiently protect biodiversity in developing countries, in figures such as national parks or reserves (Curran 2004, Gardner et al. 2009). Some authors have argued that one of the reasons that explain this failure is that local people, living in and around protected areas, have been primarily seen as threats to biodiversity conservation (Terborgh 2000, Porter-Bolland et al. 2011). Partially as a reaction to this approach has emerged the concept of biocultural diversity. Complex in its nature, biocultural diversity encompasses many related biological and cultural processes, but its main premise is that biological and cultural diversity are intricately linked (Baer 1989). The concept of biocultural diversity emerged out of the realization that there is a geographical overlap between biological diversity and the diversity of languages as cultural representations (Harmon 1996, Posey 1999). Based on that evidence, the biocultural diversity approach proposes the strengthening of the existing forms of community-based management as an additional strategy for biodiversity conservation that could be added to the current set of strategies excluding local people (Ortega and Kral 2007, Porter-Bolland et al. 2011). Thus, with the purpose of implementing such approaches, biocultural diversity conservation has recently become a priority for international-level conservation policies (UNESCO 2008).

Most empirical studies on biocultural diversity have studied the large-scale (i.e. continental and cross-cultural) geographical overlap of cultural and biological diversity. Such studies have mainly stressed how species richness relates to the diversity of languages (Harmon 1996, Stepp et al. 2004, Maffi 2005) under the assumption that language richness is an appropriate proxy for cultural diversity at a large scale of study. This previous research has mainly found that measures of cultural diversity show a spatial correlation with measures of biological diversity. For example, based on estimations over large geographic units, Stepp et al. (2004) approximated global plant species richness and found a co-occurrence of language and plant diversity. Loh and Harmon (2005) have calculated an index to estimate
biocultural diversity distribution worldwide, using measures on a country level based on different cultural – linguistic, ethnic and religious diversity – and biodiversity proxies – mammals, birds and plant richness, and have revealed three bioculturally rich areas: the Amazonian basin, Central Africa and Southeast Asia.

However, since both biological and cultural diversity vary across scales, the analysis of the correlation between cultural and biological diversity must be similarly undertaken at different scales (Newing 2010). Since – as some authors have argued – intracultural variation, or diversity within a given cultural group, may also be associated with differences in biological diversity (Pretty et al. 2008), integrating multiple scales, particularly small scales of analysis, in the approach of biocultural diversity is crucial to get a comprehensive understanding of overall biocultural diversity (UNESCO 2008). Despite the importance of narrowing the scale of analysis in studies of biocultural diversity, there is an evident lack of studies that search for interrelationship between cultural and biological processes at local or landscape scales.

In this dissertation, I narrow down the focus of biocultural diversity to a smaller scale. Specifically, (i) I study differences of biodiversity at the landscape scale, looking at forest tree diversity as a proxy for biodiversity in the territory of an indigenous group, and then (ii) I test the relation between biodiversity differences in this landscape and intracultural variation, proxied by acculturation. The study area was centered on an understudied part of the Bolivian Amazon, a land traditionally inhabited by the Tsimane’, a native group of hunter-gatherers and small-scale horticulturalists. Many indigenous people are still dependent on natural resources for their subsistence (Toledo 2001). Therefore, indigenous people represent an ideal case study for addressing the link between culture and biodiversity because this link is likely to be more visible than in non-indigenous societies, where management of natural resources for subsistence is less evident and often disrupted by access to market economy.

This study brings significant insights, both at theoretical and methodological levels. On a theoretical level, it contributes to the ongoing debate of which natural factors influence species distributions. In explaining plant species distributions, researchers debate on the relative role of neutral (random factors, mainly through dispersal limitation by geographical distances) versus niche factors, or
environmental determinism (Tilman 1994, Hubbell 2001, Ruokolainen et al. 2007, Chave 2008). Indeed, the Amazonian basin, rather than homogeneous, hosts many different plant communities. In this context, it is not surprising that the factors that influence the distribution of species are still poorly known, especially because these influences seem to be region-specific.

This dissertation also brings elements to understand the role of indigenous peoples in modeling ecosystems. Empirical studies are needed not only at large, continental scales, but also at small scales within a single culture (Pretty et al. 2009). Studying the association between human factors and differences in richness and composition of plant communities is a starting point to understand the drivers of biocultural diversity at an intracultural level.

On a methodological level, this study explores how to “bring together” social and ecological data, which have traditionally been studied separately. Although trans-disciplinary approaches are needed, there is a lack of accepted methodologies to relate biological and social systems (Pretty et al. 2008). Here, I construct a quantitative measure of acculturation, as a proxy for individual intracultural changes, and then relate this variable to measures of biodiversity within a single habitat (old-growth forest), which is communally managed.

**Literature review**

**Natural factors affecting biodiversity**

Biodiversity can be defined and estimated at genes, populations, species, or habitats levels as unity of analysis (Noss 1990). Contrary to most studies relating indigenous management practices to biodiversity, often based on landscape-scale biodiversity estimations, in this work, I focus on tree diversity at the species level and within a relatively homogeneous tropical rainforest type.

Considering species, biodiversity has traditionally been defined at several scales. *Alpha* diversity refers to the diversity at local (plot) scale, whereas *gamma* diversity is the diversity at landscape (regional) scale (Whittaker 1977). The definition of the *beta* component of diversity is more challenging because researchers have long debated if it is a multiplicative or an additive result of alpha and gamma diversity (e.g., Jost 2007). Moreover, researchers have approached the beta component of biodiversity using many different indices that do not always
relate to the same concept (Tuomisto 2010a, 2010b). In this dissertation I look at the beta component of biodiversity using species turnover, i.e. the proportion of species composition that changes among compositional units (Tuomisto 2010c).

Much has been written about the determinants of tree alpha diversity and species turnover at several scales, throughout the tropics (compiled e.g. by Leigh et al. 2004). Tree alpha diversity has been shown to depend on large and small-scale disturbances, habitat specialization, and pest pressure (Leigh et al. 2004), as well as regional biodiversity and soil properties (Laurance et al. 2010). Ter Steege et al (2003) have shown that tree alpha diversity at the Amazonian scale is modeled by climate seasonality, with some of the lowest alpha diversity values for the Bolivian Amazon.

Tree species turnover, in turn, is strongly dependent on the scale of study and seems to be also largely dependent on the region (Chave 2008). Tree species turnover changes with environmental variables, especially edaphic and climatic variables (e.g. Phillips et al. 2003, Macía et al. 2007, Ruokolainen et al. 2007). In the Bolivian lowlands, large-scale tree species turnover has been shown to be more strongly determined by a climatic gradient than by an edaphic gradient (Toledo et al. 2010). However, beyond environmental influences many studies in tropical forests report species turnover to be geographically controlled, mainly through dispersal limitation processes (e.g. Condit et al. 2002, Bohlman et al. 2008), and researchers debate the prevalence of geographical versus environmental control over species turnover.

**Indigenous people and biodiversity**

Researchers have recently started to study the role of human societies in shaping biodiversity and landscapes. Archaeological studies have highlighted a large alteration of plant species distributions and abundances due to indigenous societies’ settlement in the Amazon (Heckenberger et al. 2003, 2007). On the contrary, it has also been seen that current small-scale indigenous societies tend to overlap with areas of high biodiversity (e.g. Galvin 2001, Sunderlin et al. 2005). Nowadays, much of the debate on the association between indigenous peoples and high biodiversity has focused on their role in managing biodiversity, and has often been addressed from the perspective of the social sciences in a body of literature
known as the “noble savage” debate (Smith and Wishnie 2000, Hames 2007). On the one side, some authors have argued that indigenous people have lived in harmony with nature and that their behavior allows biodiversity conservation and even biodiversity generation (Balée 2006, Gari 2001). On the other hand, other authors have stressed that their sustainable use of natural resources is not a result of attitudes, but rather of factors such as weak demographic pressures or nomadic way of life, without any particular active willingness to conserve (Alvard 1993, Harmon 2007).

In considering the arguments of why there is an overlap between indigenous cultures and areas with well-conserved biodiversity, researchers have understudied the patterns and the pathways that drive this association. Some researchers have argued that indigenous peoples storage information on how to manage species and landscapes in their traditional ecological knowledge (TEK) system (Gari 2001). TEK refers to the holistic sum of three components: beliefs and symbolic representations, environmental knowledge, and practices or behaviors that lead to nature appropriation (Toledo 1992, Berkes 1999, Reyes-García and Martí-Sanz 2007). Many authors have underlined the role of TEK, and especially its practices for the enhancement of biodiversity (Gadgil et al. 1993, Toledo 2001, Reyes-García 2010), but few of these studies provide adequate measures of biodiversity.

Some papers suggest that indigenous people manage old-growth forest for subsistence needs. For example, numerous ethnobotanical studies document indigenous people’s uses of the vegetation, particularly in old-growth forests. In lowland Bolivia, some studies have documented the ethnobotany of the Tsimane’ (Huanca 1999, Reyes-García 2001), the Chácobo (Boom 1987), or the Tacana (DeWalt et al. 1999). However, these studies do not make a direct link between the ecological features of the species and their uses. Few studies have assessed quantitatively how uses of species by indigenous people affect biodiversity and species ecology within a single ecosystem (Phillips and Gentry 1993a, 1993b, Torre-Cuadros and Islebe 2003, Lucena et al. 2007, Thomas et al 2009).

Other studies also show that through small-scale shifting agriculture, indigenous management creates mosaics of different land uses, from primary vegetation (including agroforests and domestic forests) to secondary vegetation,
growing after the establishment of crop fields and fallows (Peters 2000, Wiersum 2004, Michon et al. 2007). Although species richness may decrease from old-growth forests to fallows and fields (Kessler et al. 2005), the overall mosaics create biodiversity in tropical environments at the landscape scale (see Scales and Marsden 2008 for a review). For example, Posey (1985) has documented how fallow forests enhance biodiversity among the Kayapo of the southern Brazilian Amazon. Diemont and Martin (2009) have stressed the maintenance of biodiversity in four successional stages and crop fields in Lacandon Maya villages in Mexico. Another study in northern Sumatra (García-Fernández et al. 2003) underlines the importance of benzoin forest gardens, as part of a mosaic landscape, for biodiversity conservation.

The idea that indigenous management of the old-growth forest and its transformation for agricultural purposes enhance biodiversity at the landscape scale, seems to fit in the non-equilibrium dynamics of biodiversity, which recognizes disturbance as a basic element maintaining diversity (Balée 2006). This hypothesis, initially developed within natural ecosystems, states that intermediate levels of disturbance, in terms of frequency or intensity, enhance different guilds of species to coexist and thus increases biodiversity (Connell 1978). Similarly, indigenous management practices may be considered as a “cultural disturbance” of intermediate-level that enhances biodiversity through this mosaic of ecosystems (Toledo 2001, Balée 2006).

Current trends among indigenous people: acculturation and integration into Western society

An important aspect on the effects of indigenous management on biodiversity in their environments, relates to changes currently affecting most indigenous cultures (Dove 2006).

In the previous section, it has been mentioned that indigenous peoples probably enhance biodiversity in tropical landscapes, especially when compared to non-indigenous peoples (Garí 2001, Toledo et al. 2003). However, the impacts of current loss of culture among indigenous peoples on biodiversity and conservation have rarely been assessed (Smith and Wishnie 2000). According to Cocks (2006), until now the theory of biocultural diversity has failed to integrate cultural changes
affecting indigenous societies. This gap is possibly due to the scale of analysis researchers have used so far to study the association between cultural and biological diversity, since a continental scale is too large to capture changes within each culture. Nevertheless, how globalization and homogenization affects biocultural diversity is a major concern of international conservation policies (UNESCO 2008).

Indigenous peoples are facing changes associated with development and population growth and include, for example, modifications of agricultural practices, settlement, or harvesting patterns (Galvin 2001). However, beyond pure development issues, the changes also encompass acculturation of indigenous peoples into national Westernized societies.

Acculturation is the process by which a group of individuals progressively lose their culture and adopt cultural values of another group, due to the contact with outsiders (Peterson 1991, Lu 2007, Thomson and Hoffmann-Goetz 2009). Among indigenous groups, acculturation and integration into the market economy are two different processes that are nevertheless associated, since people who enter the market economy acquire new attitudes and values (Godoy et al. 2005). However, acculturation encompasses individual psychological changes that do not refer to an economic system (Caplan 2007, Byron 2003). These changes may affect people’s knowledge, beliefs or practices, i.e., the basis for the knowledge system that indigenous people use to manage their landscapes (Graham 1985, Reyes-García et al. 2005, Silva et al. 2011).

Acculturation, therefore, is a process that is likely to lead to changes in biodiversity (Galvin 2001), particularly through the changes in indigenous management and practices (Reyes-García 2010). For example, by trading, opening logging roads, or prospecting for mining, outsiders have growing contact with indigenous peoples, which results in a progressive adoption of different beliefs, forest management practices, and a loss of knowledge, and therefore may have an impact on biodiversity, for example through the modification of deforestation patterns from acculturated indigenous.

Despite the importance of the topic, only few studies have assessed the impacts of changes on management practices on biodiversity (Gross 1979, Henrich 1997, Toledo et al. 2003, Cocks 2006). Previous research among the Tsimane’ have
shown a negative association between integration to market and ethnobotanical knowledge as a proxy for TEK (Reyes-García et al. 2007). The same researchers have also related a loss of TEK to a higher level of clearance in secondary forests (Reyes-García et al. 2010), whereas Vadez et al. (2008) have found an association between changes in agricultural practices (i.e., cash-cropping development) and old-growth forest clearance. These previous studies have essentially focused on market integration, without taking into account the deeper individual changes driven by acculturation. Moreover, although they address changes in biodiversity through deforestation, these studies have not used actual biodiversity measures. To my knowledge, no empirical study has looked at the role of homogenization changes, particularly acculturation, on biodiversity using actual data from plant inventories.

Case study of the Tsimane’

Summary of the ecology of the area: climate, geomorphology, and vegetation

The Tsimane’ inhabit a large territory (14°10’ – 15°40’S, 66°20’ – 67°20’W) in the south of the province of Beni, Bolivian Amazon (Fig. 1). This territory lies between the foothills of the Andes and the flooded pampas of Moxos, and its ecology is complex, due to several biogeographical influences (see below). Mean annual temperature is 25.8ºC in the main town of the area, San Borja (Navarro and Maldonado 2002). Mean annual rainfall is 1743 mm (Godoy et al. 2008) but varies largely according to topography. Seasonality of climate is strong, with an approximately four-month dry season (less than 100 mm rainfall per month) during which episodic cold winds strongly lower temperatures.

The northern and eastern parts of the territory are part of the hydrological system of Moxos, and geomorphological changes are strongly dependent on river dynamics – flooding and low water level (Navarro and Maldonado 2002). In these areas, prehistoric raised fields are found and have probably an influence on vegetation (Gullison et al. 1996). In turn, the southern and western parts correspond to the first hills of the Andes, and the Tsimane’ use the lands until approximately 1500 m. Plains formed by main rivers are a mosaic of elements
dependent on river dynamics and flooding: *terra firme* that are never flooded and floodplains (*bajuras*) that are seasonally or permanently flooded.

Vegetation in the area depends on many factors. On the whole, the Tsimane’ territory is an interface of three biogeographic provinces with different diversity levels (Navarro and Maldonado 2002). Vegetation is also strongly dependent on the geomorphological features described. Most of the territory is covered with Amazonian lowland forests with a high semi-deciduous canopy reaching 40m. In southwestern hills at higher altitudes, forests are more similar to montane forest, which are some of the most specie-rich in Bolivia (Ibisch and Merida 2004). These two broad forest types present local variation due to flooding, and a range of floodplain forests occur. In the northeastern parts of the territory, flooded savannas are predominant and some forest islands occur locally on higher terrains, probably resulting of past human settlements (Lombardo and Prümers 2010). In the present study we focus on the first type of forest, *terra firme* lowland Amazonian rainforest.

**Cultural and historical context**

The Tsimane’ are the third largest ethnic group in lowland Bolivia. Their population was in turn of 8000 people in 2001 (Censo Indígena 2001) and nowadays probably about 10-12000 according to their population growth rate (Reyes-García 2001). The Maniqui and Apere Rivers represent the core area of the Tsimane’ territory (Fig. 1). They are essentially hunters-gatherers and also practice small-scale shifting agriculture (Vadez et al. 2004), and are particularly good at fishing with different techniques (Pérez 2001). Traditionally, the Tsimane’ were semi-nomadic and used to live in households or small groups of households closely related by kinship, without any authority, mainly along rivers (Reyes-García 2001). A typical kinship feature is their tradition of cross-cousin unions (Daillant 1994), which is still largely practiced today, in spite of a tendency to exogamous unions in some villages close to towns. Tsimane’ cosmology has been described by Huanca (1999, 2008). The society strongly relied on shamans during multiple environment-related celebrations; however, today no shaman remains among the Tsimane’. Nowadays, the Tsimane’ are represented by a modern political institution: the Gran Consejo Tsimane’ (GCT), created in 1989 under the
impulsion of evangelic missionaries. The creation of the GCT officially established a hierarchy among the Tsimane’ since chiefs were designated in each village.

The modern history of the Tsimane’ has been summarized in several publications (Huanca 1999, 2008, Reyes-García 2001, Martinez-Rodriguez 2009) and is closely linked to the exploitation of resources. Briefly, the process of evangelization that occurred in the province of Beni during the 17th and 18th centuries failed to convert the Tsimane’ in Christians, and during those centuries the Tsimane’ continued to have little contact with outsiders. During the 19th century, cattle ranchers exploited indigenous people, including some Tsimane’, in a debt-based system. However, the Tsimane’, lacking a hierarchical system of authority, commonly escaped deep into the forest. In the 1950s a Catholic mission was established in a village (Misión Fátima) and Protestant missionaries also began to permanently settle with the Tsimane’. Villages were organized, clustering many households. In the 1970s several waves of government-planned Andean colonization occurred, mainly to reduce demographic pressure in the Bolivian highlands. This process continues nowadays more or less illegally. Many logging companies began in parallel to extract precious wood, in particular mahogany (Gullison 1996). From then on, the Tsimane’ have suffered incursions of loggers, reaching a tipping point in 1996 when a logging company completely destroyed sacred petroglyphs (Daillant 1997), which became a trigger for participation to an indigenous march to La Paz.

During the decades of the 1980s and 1990s, the government started a reorganization of the land system, which included the creation of two protected areas: the Beni Biological Station in 1986 as a Biosphere Reserve and the Pilón-Lajas National Park in 1992. Only in 1997, after a large indigenous movement in Bolivia, could the Tsimane’ obtain land rights on their territory by the creation of the Territorio Comunitario de Origen (TCO). In 2005, the election of Evo Morales, the first indigenous president of Bolivia, lead to several improvements of the Tsimane’ daily life but also to further Andean colonization. In 2010, the president of the GCT was elected mayor of San Borja, the main access to the market for the Tsimane’.
Territory: land tenure organization and use of natural resources

In tropical areas, it is crucial to consider land tenure systems in the study of biocultural diversity, since it is related to resource management and biodiversity (Ortega and Kral 2007). Currently there are some 100 Tsimane’ villages distributed in several types of tenure: indigenous territories, protected areas, logging concessions and private lands (Fig. 1).

Figure 1. Map of the study area showing Tsimane’ village distribution and land tenure system.
Two indigenous territories have been given to the Tsimane’ in the 1990s, covering about 750,000 hectares in total: the Chimane (or Tsimane’) Indigenous Territory (TICH) and the Multiethnic Indigenous Territory (TIM). Although lands were given more than 20 years ago, the process of land titling has not concluded yet in some parts of the territory, particularly in areas close to market towns where many conflicts take place. According to current legislation, within indigenous territories, native people have the right to make a traditional use of the lands for subsistence purposes and to log for commercial purposes provided they have the adequate certification. However, this situation is changing as the Tsimane’ get integrated into the market economy. For example, some of the wealthier Tsimane’ rely almost exclusively on wood exploitation for cash, although they generally do not have the required permits. All the villages we surveyed in this dissertation are settled in the TICH (Fig. 1).

Other villages are settled in three protected areas that overlap partially with the indigenous territories, or have a dual status (both protected area and indigenous territory). In these protected areas the Tsimane’ can make a traditional use of resource as well, but without the possibility of commercial purposes. This generates management problems in the two protected areas that have also the status of an indigenous territory (Isiboro-Séecure and Pilón-Lajas National Parks). Colonization from the Andes is an important pressure factor on these lands.

Additionally, ten logging concessions overlap with areas inhabited by the Tsimane’. In these concessions the Tsimane’ also have the right to use the land for subsistence purposes. Commonly for the Tsimane’ living in logging concessions, the main source of cash comes from logging companies. As the concessions given to logging companies officially end in 2011, violent conflicts have emerged in the last two years between Tsimane’ and Andean colons encroaching their territory. Officially, once the concessions end, the lands that were under concession should increment the land given to indigenous peoples under the form of indigenous territories. However, since 2006, a decree allows every rural people to claim for these lands, increasing dramatically the number of migrants in the area and increasing pressure over resources.
Finally, a few Tsimane’ villages are also settled within private lands (ranches) and do not have the right to use the resources. In these areas, many Tsimane’ work for cattle ranchers to compensate for the lack of access to resources.

**Structure and aims of the dissertation**

This dissertation is a crossbreed between a monograph and a thesis by articles. That is why some of the methodologies and study area descriptions are repeated. Each chapter corresponds to an article that will be submitted to JCR journals.

This dissertation has two aims. The first aim is to describe tree diversity and structure, and to quantify the determinants of species distributions in an old-growth forest. Chapter 1 and 2 address this first aim. The second aim is to bring elements to get a better understanding of how Tsimane’ cultural features relate to tree diversity in the forests they use. This second aim is addressed in chapters 3 and 4.

In Chapter 1, the focus is on tree diversity at local scale. The objective is to describe tree floristic patterns and forest structure in inventoried plots across the Tsimane’ territory. I discuss the factors leading to floristic differences across seven Tsimane’ villages. I also discuss how floristic patterns in our study area differ from other studies across the Amazon. This chapter corresponds to the article “Comparison of tree diversity across seven sites of tierra firme forest in the Tsimane’ territory, Bolivian Amazon”, which will be submitted to *Plant Ecology*.

Chapter 2 addresses the determinants of tree species turnover in the Tsimane’ territory, distributed among different tree categories (all trees, large trees, small trees, i.e. all individuals with a diameter of less than 10 cm, and small tree species, i.e. according to diameter and plant traits). The first goal is to investigate the relative influence of environmental (mostly edaphic) and geographic factors on tree species turnover. The second goal is to determine which environmental variables have more influence on floristic patterns. The third goal is to compare congruence in the determinants of species turnover in each of the tree categories. This chapter corresponds to the article “Determinants of tree species turnover in a southern Amazonian rainforest”, submitted to *Ecography*. 
Chapter 3 explores the relation between acculturation in six Tsimane’ villages, i.e. intracultural variation, and biodiversity in the old-growth forests surrounding these villages. I use multivariate analysis to model this relation, and discuss the cultural and ecological pathways that lead to the relation observed. In this chapter, I provide insights on the role of indigenous peoples in modeling ecosystems through their role as a disturbing factor, discussed in the context of the non-equilibrium hypothesis. This chapter corresponds to the article “Does tree alpha diversity in old-growth forests relate to acculturation among native Amazonians?” which will be submitted to *Conservation Biology*.

Chapter 4 provides a quantitative analysis of how the uses of 58 tree species relate to the ecological importance of these species, proxied by their importance value index (IVI). Plant uses are broken down into several categories relevant for the Tsimane’. In this chapter I test the hypothesis that the most *visible* plant species are also the more used. This chapter corresponds to the article “Does ecological importance of tree species relate to their usefulness? A case study from the Tsimane’, Bolivian Amazon”, which will be submitted to *Economic Botany*.

In chapter 5, I provide final considerations about the natural and anthropogenic factors that influence tree species composition and richness in the study area. I propose several approaches that could be use to further study the impacts of intracultural variation on biodiversity.

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Chapter 1

Comparison of tree diversity across seven sites of *terra firme* forest in the Tsimane’ territory, Bolivian Amazon

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Abstract

A floristic inventory of trees was conducted in *terra firme* forests of the Tsimane’ indigenous territory, Bolivia, to compare similarity and oligarchic patterns across sites. Three groups of sites, totaling seven sites, were considered according to topographic features and geographic position: two groups along the main river (upstream and downstream sites) and one group along a logging road. A total of 55 0.1-ha plots was inventoried for trees ≥2.5 cm diameter at breast height, resulting in a total of 9082 individuals belonging to 426 species and morphospecies. We found a relatively low diversity, with a Fisher's Alpha index ranging 6.9-44.3. Moraceae, Arecaceae, Euphorbiaceae and Fabaceae were the most important families, fitting into continental patterns of family dominance in the Amazon. Different oligarchic patterns were found across groups of sites. The upstream sites had floristic affinities with western Amazonian forests whereas the downstream site was dominated by the palm *Astrocaryum murumuru*. These differences were likely explained by biogeographic influences as well as the history of flooding in the area.

**Key words:** floristic patterns, alpha diversity, oligarchy, flooding, 0.1-ha inventories
Introduction

The Tsimane’ territory, inhabited by a native group of hunter-gatherers, has been the focus of loggers since decades due to its richness in precious woods, especially mahogany (*Swietenia macrophylla*; Gullison et al. 1996). However, although large extents of continuous old-growth forests remain, it has been understudied for plant inventories.

Although, there is a general lack of inventories in Bolivia, and particularly in the Amazonian lowlands (Ibisch and Mérida 2004), several authors have studied neighboring regions of the Tsimane’ territory, particularly the Madidi region (DeWalt 1999, Flores 2002, Araujo-Murakami et al. 2005a, 2005b, De la Quintana 2005, Quisbert and Macía 2005, Macía 2008) and the Isiboro-Sécure Indigenous territory and National Park (TIPNIS; Thomas 2009). Two studies also inventoried areas inhabited by Tsimane’ people, the Beni Biological Station (Comiskey et al. 2000) and the Pilón-Lajas National Park (Smith and Killeen 1998), but these studies relied on trees >10 cm diameter at breast height (dbh) in 1-ha plots, and then did not capture floristic composition of the understory.

Ecological inventories have generally relied either on 1-ha or 0.1-ha plots. In the present study, we focus on 0.1-ha plots, since it has been shown to be the most efficient method for floristic assessments (Phillips et al. 2003, Macía 2008). To our knowledge, this study is the first to inventory tree diversity in the Tsimane’ territory using this methodology.

In the Amazon basin, plant communities are generally dominated by a reduced set of species that account for most of the individuals, and contain many rare species with few individuals (Terborgh et al. 1996, Pitman et al. 2001, Vormisto et al. 2004, Macía and Svenning 2005). However, different oligarchic species dominate communities across regions (Vormisto et al. 2004). Moreover, oligarchic patterns may vary according to species traits, in particular if the species are canopy or understory species (Macía and Svenning 2005).

This study aims at describing floristic composition of old-growth *terra firme* forests in seven sites of the Tsimane’ territory, distributed in three site groups according to their location and topographic features. The specific objectives are 1) to quantify the oligarchic tree species across site groups, according to family and
species importance, 2) to analyze tree floristic similarity across site groups, broken down into different tree categories (all, canopy, and understory trees), and 3) to discuss the role of flooding history in explaining floristic differences.

**Methods**

**Study area**

The study was conducted in the Tsimane' Indigenous Territory (Territorio Comunitario de Origen Tsimane'), located along the Maniqui River in the south of the province of Beni, in the Bolivian Amazon. Mean annual temperature reported in the meteorological station of San Borja is 25.8°C (Navarro and Maldonado 2002) and mean annual rainfall is 1743mm (Godoy et al 2008). Climatic seasonality is strong, with four months with less than 100 mm of precipitation. Most soils are quaternary alluvial sediments of fluvial origin, particularly acrisols and ferralsols (Navarro and Maldonado 2002).

The Tsimane’ territory is located between three biogeographic regions: Amazonia, Andes and Brazilian-Paraná (Navarro and Maldonado 2002). Different broad forest types occur in the study area according to the flooding level: most areas are never flooded and covered with well-drained *terra firme* forests, but in some places seasonally or permanently flooded terrains present a range of forests with lower tree diversity and canopy height (Killeen et al. 1993, Macía 2008).

**Data collection**

We inventoried a total of 55 0.1-ha plots (50m × 20m) in seven sites of *terra firme* forests in the nearby of seven Tsimane’ villages, between March and December 2009. These sites were geographically scattered in the Tsimane’ territory and had different topographic features, although homogeneous in terms of elevation. Five of the seven sites were situated close to the Maniqui River: four upstream from the town of San Borja, with rolling topography (Cuchisama, Misión Fátima, Uvasichi, and Yaranda; in the following, upstream sites), and one downstream from San Borja, with flat topography (Campo Bello, further designated as downstream site), whose territory is limited by the Beni Biological
Station. The two other sites were situated along a logging road which also had a
flat topography (Jamanchi and Triunfo; in the following road sites) (Fig. 1, see also
Appendix 1). We established eight plots per village, except in Campo Bello where
only seven plots were inventoried. The forest structure was rather homogeneous
in the whole area. The plots were established in old-growth forests, showing
neither sign of recent human activity nor large canopy gaps, and at a minimal
distance of 500 m from the closest house, agricultural field, or fallow.

We measured all tree stems (including palms) rooted within plots and with a
diameter at breast height (dbh) ≥ 2.5 cm at 1.3 m above ground, or 20 cm above
buttresses or stilt roots. We measured multiple stems of the same tree separately
but counting them as one individual. We identified species in the field and
collected voucher specimens for all individuals that could not be precisely
identified in the field. We sorted all vouchers to species or morphospecies level
and then identified them. Family classification was kept according to traditional
system in order to facilitate comparisons with earlier studies. Duplicates of the
collections are deposited in LPB and MA, and unicates are kept in LPB. We included
all morphospecies in the following analyses.

Data analysis

We subdivided tree floristic data into three categories: 1) all trees (dbh ≥ 2.5
cm), 2) canopy trees (dbh ≥ 10 cm), and 3) understory trees (dbh < 10 cm).

We calculated species and family richness per plot for each tree category, and
then averaged per site. We calculated the Fisher’s Alpha index to estimate tree
diversity in each plot, and then averaged per site.

To characterize floristic composition in terms of families and species, we first
calculated families’ importance value index (FIVI) for each site, as the sum of their
relative density, relative dominance and relative diversity (Mori et al. 1983). The
relative density of a family is defined as the ratio between the number of
individuals of this family and the total number of individuals in each site. The
relative dominance is the ratio between the basal area of the family and the total
basal area in each site. The relative diversity is the ratio between the number of
species of the family in each site and the total number of species. We also
calculated species importance value index (IVI) for each site, as the sum of their
relative density, relative dominance and relative frequency (Curtis and McIntosh 1951). The relative frequency of a species in each site is defined as the ratio between the number of plots in which the species appears and the sum of all frequencies in each site.

To analyze the degree of floristic similarity across sites, we performed an agglomerative hierarchical clustering with average linkage (UPGMA) for each of the three tree categories, using Steinhaus index as the similarity measure. Steinhaus index is similar to Sørensen index but the first takes into account the abundances of the species whereas the second is only based on presence/absence data.

We analyzed forest structure across sites by comparing the distribution of all trees in dbh classes.

Steinhaus index computation and cluster analysis were performed using the ‘vegan’ package in R 2.13.1. (Oksanen et al. 2011).

Results

Overall tree species richness and abundance

We found a total of 9082 individuals of trees ≥2.5 cm dbh in 55 0.1-ha plots, representing 426 species distributed across 209 genera and 64 families (Table 1.1, see also Appendix 2). The five most abundant species were Iriartea deltoidea (802 individuals), Socratea exorrhiza (463), Pseudolmedia laevis (427), Astrocaryum murumuru (325) and Rinorea viridifolia (323). These five species together represented 25.8 % of all individuals. In the upstream sites, five species accounted for 31.2% of the individuals (I. deltoidea, S. exorrhiza, R. viridifolia, Iryanthera juruensis, and Otoba parvifolia), whereas in the road sites, five species accounted for 30.7% of the individuals (P. laevis, Leonia crassa, S. exorrhiza, A. murumuru, and Unonopsis floribunda). In Campo Bello five species accounted for 56.5% of the individuals (A. murumuru, Poulsenia armata, P. laevis, Celtis schippii, and Piper reticulatum).
Table 1.1. Total number of species, families and individuals in 55 0.1-ha plots at each of the seven inventoried sites, among three tree categories, in the ‘Tsimane’ indigenous territory, Bolivian Amazon. Mean plot Fisher’s Alpha diversity index is also given per site. Range values between plots are given in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>Downstream</th>
<th>Road</th>
<th>Upstream</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Campo Bello</td>
<td>Jamanchi</td>
<td>Triunfo</td>
<td></td>
</tr>
<tr>
<td>All trees (dbh ≥ 2.5 cm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>59 (18 – 27)</td>
<td>116 (43 – 58)</td>
<td>97 (30 – 49)</td>
<td>426</td>
</tr>
<tr>
<td>Families</td>
<td>29 (13 – 17)</td>
<td>42 (23 – 31)</td>
<td>38 (17 – 28)</td>
<td>64</td>
</tr>
<tr>
<td>Individuals</td>
<td>620 (64 – 106)</td>
<td>1224 (135 – 173)</td>
<td>1261 (138 – 212)</td>
<td>9082</td>
</tr>
<tr>
<td>Canopy trees (dbh &gt; 10 cm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>51 (17 – 25)</td>
<td>87 (32 – 44)</td>
<td>75 (25 – 39)</td>
<td>332</td>
</tr>
<tr>
<td>Individuals</td>
<td>561 (57 – 98)</td>
<td>961 (103 – 138)</td>
<td>1087 (116 – 164)</td>
<td>7416</td>
</tr>
<tr>
<td>Understory trees (dbh &lt; 10 cm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>8 (1 – 5)</td>
<td>29 (10 – 18)</td>
<td>22 (5 – 10)</td>
<td>94</td>
</tr>
<tr>
<td>Individuals</td>
<td>59 (2 – 27)</td>
<td>263 (13 – 56)</td>
<td>174 (12 – 48)</td>
<td>1666</td>
</tr>
<tr>
<td>Mean Fisher’s Alpha index</td>
<td>10.2 (6.9 – 13.1)</td>
<td>25.6 (21.7 – 30.6)</td>
<td>17.6 (11.4 – 23.1)</td>
<td>22.8</td>
</tr>
<tr>
<td>Number of plots</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>55</td>
</tr>
<tr>
<td>Elevation (± SD)</td>
<td>208 ± 22</td>
<td>225 ± 12</td>
<td>206 ± 12</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
There was a high variation in species richness across sites. Overall different attributes such as total species and family richness, total tree density, and Fisher's Alpha index values were consistently different across site groups. The upstream group had the highest values of total species and family richness, tree densities and Fisher’s Alpha index (with the exception of Yaranda). Fisher’s Alpha index peaked in Uvasichi but even within this site, there was a high variation (15.5 - 44.3). The road sites had lower values than the upstream sites. The downstream site (Campo Bello) had the lowest species and family richness, tree density and Fisher’s Alpha index. Total species richness in Uvasichi was almost four times the total species richness in Campo Bello.

In total, canopy trees represented 77.9 % of the species and 81.7 % of the individuals, whereas understory trees represented 22.1 % of the species and 18.3 % of the individuals. In Campo Bello, the proportion of understory individuals was the lowest, reaching only 9.5 % whereas in Uvasichi this proportion was three times higher (28 %). For all trees, the upstream sites had generally a lower ratio between the number of individuals and the number of species than the road sites and Campo Bello. In other words, the upstream sites had more species but less individuals of each species. This tendency was also true for canopy species but in the case of understory species, no clear pattern could be observed, although the greatest variation was observed across the upstream sites.

**Floristic composition across sites**

According to FIVI, the 10 most important families per site summed 21 families, and accounted for 83.7 % of all individuals (Table 1.2). Overall, the most important families were Moraceae (29 species), Arecaceae (12), Euphorbiaceae (17), and Fabaceae (43). Moraceae and Arecaceae were important in all the sites. Euphorbiaceae, Fabaceae and Annonaceae were important in six of the sites. In Campo Bello, Fabaceae was not an important family, while Meliaceae and Ulmaceae were among the five most important. Particularly, Campo Bello was the only site where Ulmaceae was an important family. Compared to other upstream sites, in Uvasichi, Euphorbiaceae and Annonaceae were not important families, but Violaceae was, which somehow sets Uvasichi apart from the other upstream sites.
In the road sites, no particular pattern could be found in terms of family composition.

Table 1.2. Comparison of the family importance value index (FIVI) of the 10 most important families (in bold) at seven sites, totaling 55 0.1-ha plots in the Tsimane’ territory, Bolivian Amazon.

<table>
<thead>
<tr>
<th>Family</th>
<th>Campo Bello</th>
<th>Cuchisama</th>
<th>Jamanchi</th>
<th>Misión Fátima</th>
<th>Triunfo</th>
<th>Uvasichi</th>
<th>Yaranda</th>
<th>All sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anacardiaceae</td>
<td>4.49</td>
<td>0.69</td>
<td>7.27</td>
<td>1.69</td>
<td>12.42</td>
<td>3.96</td>
<td>3.69</td>
<td>4.45</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>9.96</td>
<td>8.43</td>
<td>22.59</td>
<td>13.10</td>
<td>12.21</td>
<td>6.95</td>
<td>13.73</td>
<td>11.86</td>
</tr>
<tr>
<td>Areceaceae</td>
<td>51.38</td>
<td>46.50</td>
<td>19.02</td>
<td>30.25</td>
<td>33.01</td>
<td>24.81</td>
<td>53.15</td>
<td>34.00</td>
</tr>
<tr>
<td>Bombacaceae</td>
<td>6.09</td>
<td>9.50</td>
<td>1.13</td>
<td>10.82</td>
<td>4.81</td>
<td>12.63</td>
<td>13.03</td>
<td>8.59</td>
</tr>
<tr>
<td>Burseraceae</td>
<td>0.00</td>
<td>5.06</td>
<td>7.78</td>
<td>6.94</td>
<td>1.66</td>
<td>9.27</td>
<td>4.02</td>
<td>5.38</td>
</tr>
<tr>
<td>Clusiaceae</td>
<td>2.03</td>
<td>2.55</td>
<td>11.45</td>
<td>6.64</td>
<td>12.16</td>
<td>9.35</td>
<td>7.02</td>
<td>6.67</td>
</tr>
<tr>
<td>Combretaceae</td>
<td>4.29</td>
<td>8.07</td>
<td>3.49</td>
<td>4.51</td>
<td>2.46</td>
<td>4.48</td>
<td>3.28</td>
<td>4.29</td>
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<tr>
<td>Elaeocarpaceae</td>
<td>12.67</td>
<td>5.44</td>
<td>2.71</td>
<td>2.75</td>
<td>8.26</td>
<td>3.19</td>
<td>10.35</td>
<td>6.01</td>
</tr>
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<td>Euphorbiaceae</td>
<td>17.76</td>
<td>19.83</td>
<td>39.74</td>
<td>15.54</td>
<td>43.53</td>
<td>7.64</td>
<td>24.63</td>
<td>23.20</td>
</tr>
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<td>Flacourtiaceae</td>
<td>5.27</td>
<td>4.21</td>
<td>11.35</td>
<td>5.73</td>
<td>9.76</td>
<td>7.28</td>
<td>6.68</td>
<td>5.90</td>
</tr>
<tr>
<td>Lauraceae</td>
<td>11.50</td>
<td>13.30</td>
<td>3.05</td>
<td>11.55</td>
<td>5.63</td>
<td>11.09</td>
<td>3.40</td>
<td>11.79</td>
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<td>0.00</td>
<td>5.37</td>
<td>6.06</td>
<td>11.61</td>
<td>0.00</td>
<td>4.95</td>
<td>7.05</td>
<td>6.57</td>
</tr>
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<td>Melliaceae</td>
<td>14.71</td>
<td>8.58</td>
<td>7.11</td>
<td>11.39</td>
<td>14.76</td>
<td>10.47</td>
<td>6.74</td>
<td>10.21</td>
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<td>Moraceae</td>
<td>73.22</td>
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<td>52.15</td>
<td>34.50</td>
<td>41.95</td>
<td>39.16</td>
<td>36.58</td>
<td>41.34</td>
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<td>Myristicaceae</td>
<td>3.40</td>
<td>18.85</td>
<td>10.66</td>
<td>10.33</td>
<td>2.19</td>
<td>7.49</td>
<td>15.37</td>
<td>9.36</td>
</tr>
<tr>
<td>Sapindaceae</td>
<td>9.35</td>
<td>7.20</td>
<td>5.59</td>
<td>5.75</td>
<td>4.50</td>
<td>4.96</td>
<td>4.41</td>
<td>5.89</td>
</tr>
<tr>
<td>Tiliaceae</td>
<td>0.00</td>
<td>4.48</td>
<td>0.00</td>
<td>1.64</td>
<td>0.00</td>
<td>9.80</td>
<td>4.92</td>
<td>3.68</td>
</tr>
<tr>
<td>Ulmaceae</td>
<td>13.95</td>
<td>3.90</td>
<td>6.52</td>
<td>3.84</td>
<td>7.94</td>
<td>3.67</td>
<td>3.51</td>
<td>4.73</td>
</tr>
<tr>
<td>Violaceae</td>
<td>0.00</td>
<td>3.75</td>
<td>5.74</td>
<td>10.59</td>
<td>15.92</td>
<td>18.81</td>
<td>6.39</td>
<td>9.13</td>
</tr>
</tbody>
</table>

According to IVI, the 20 most important species per site summed 65 species, and accounted for 73.4 % of all individuals (Table 1.3). Out of these 65 species, only seven were understory species. We found important variation in species importance across site groups. Only one species (P. laevis) was important in all the sites, and three species (S. exorrhiza, P. armata and C. schippii) were important in six of them. I. deltoidea was the most important species in the upstream sites, and was absent in the other sites. A. murumuru had remarkably low IVI values in the upstream sites and was among the most important species in the other sites. Similarly some species, such as Clarisia racemosa and I. juruensis, were important in the upstream sites and not (or absent) in the other sites. In the road sites, the most important species was Hura crepitans, and P. armata and P. laevis were also among the five most important species.
Table 1.3. Comparison of the importance value (IVI) of the 20 most important species (in bold) at seven sites, totaling 55 0.1-ha plots in the Tsimane’ territory, Bolivian Amazon. The species with a * symbol are understory species.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Campo Bello</th>
<th>Cuchisama</th>
<th>Jamanchi</th>
<th>Missión Fátima</th>
<th>Triunfo</th>
<th>Uvasichi</th>
<th>Yaranda</th>
<th>All sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anacardiaceae</td>
<td><em>Spondias mombin</em> L.</td>
<td>4.04</td>
<td>0</td>
<td>4.62</td>
<td>0</td>
<td>5.48</td>
<td>2.50</td>
<td>2.91</td>
<td>2.65</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>Duguetia spixiana C. Martius</td>
<td>0</td>
<td>2.60</td>
<td>5.20</td>
<td>2.89</td>
<td>0</td>
<td>0.85</td>
<td>4.88</td>
<td>2.49</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>Ruizodendron ovale R.E. Fries</td>
<td>0</td>
<td>0</td>
<td>3.31</td>
<td>7.79</td>
<td>7.98</td>
<td>0.92</td>
<td>0</td>
<td>2.81</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>Unonopsis floribunda Diels</td>
<td>8.99</td>
<td>3.09</td>
<td>10.66</td>
<td>1.53</td>
<td>5.72</td>
<td>2.42</td>
<td>5.60</td>
<td>4.86</td>
</tr>
<tr>
<td>Areceae</td>
<td>Astrocaryum murumuru C. Martius</td>
<td>44.07</td>
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<td>10.64</td>
<td>1.30</td>
<td>9.42</td>
<td>1.51</td>
<td>3.43</td>
<td>7.82</td>
</tr>
<tr>
<td>Areceae</td>
<td>Attalea butyracea (Mutis ex L. f) Wess. Boer</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1.20</td>
<td>0</td>
<td>0</td>
<td>4.43</td>
<td>0.85</td>
</tr>
<tr>
<td>Areceae</td>
<td>Attalea phalerata Mart. ex Spreng</td>
<td>4.74</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.79</td>
<td>0</td>
<td>0</td>
<td>0.54</td>
</tr>
<tr>
<td>Areceae</td>
<td>*Chamaedorea angustisecta Burret</td>
<td>5.60</td>
<td>0.33</td>
<td>1.68</td>
<td>0</td>
<td>3.42</td>
<td>0</td>
<td>0</td>
<td>1.12</td>
</tr>
<tr>
<td>Areceae</td>
<td><em>Iriartea deltoidea</em> Ruiz &amp; Pavón</td>
<td>0</td>
<td>33.03</td>
<td>0</td>
<td>17.74</td>
<td>0</td>
<td>17.16</td>
<td>34.35</td>
<td>16.07</td>
</tr>
<tr>
<td>Areceae</td>
<td><em>Socratea exorrhiza</em> (C. Martius) H.A. Wendl.</td>
<td>0</td>
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<td>6.24</td>
<td>8.23</td>
<td>14.70</td>
<td>5.24</td>
<td>12.20</td>
<td>8.88</td>
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<tr>
<td>Bombacaceae</td>
<td>Ceiba pentandra (L.) Gaertn.</td>
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<td>0</td>
<td>8.20</td>
<td>2.69</td>
<td>4.64</td>
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<td>4.33</td>
</tr>
<tr>
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<td>Quararibea cf. witti K. Schum. &amp; Ulbr.</td>
<td>0</td>
<td>9.68</td>
<td>0</td>
<td>0.94</td>
<td>0</td>
<td>1.00</td>
<td>2.23</td>
<td>2.24</td>
</tr>
<tr>
<td>Burseraceae</td>
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<td>0</td>
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<td>3.37</td>
<td>3.93</td>
<td>1.25</td>
<td>4.95</td>
<td>4.39</td>
<td>3.12</td>
</tr>
<tr>
<td>Burseraceae</td>
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<td>0</td>
<td>0</td>
<td>5.71</td>
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<td>5.58</td>
<td>1.08</td>
<td>2.19</td>
</tr>
<tr>
<td>Chrysobalanaceae</td>
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<td>5.01</td>
<td>1.15</td>
<td>0.33</td>
<td>1.53</td>
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</tr>
<tr>
<td>Clusiaceae</td>
<td><em>Rhedia acuminata</em> Miers</td>
<td>0</td>
<td>0.77</td>
<td>4.89</td>
<td>2.36</td>
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<td>5.80</td>
<td>2.57</td>
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<td>2.51</td>
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<td>7.67</td>
<td>0.26</td>
<td>0.65</td>
<td>2.28</td>
</tr>
<tr>
<td>Combretaceae</td>
<td>Terminalia amazonia (Gmelin) Exell</td>
<td>0</td>
<td>4.94</td>
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<td>1.56</td>
</tr>
<tr>
<td>Combretaceae</td>
<td><em>Terminalia oblonga</em> (Ruiz &amp; Pavón) Steudel</td>
<td>4.47</td>
<td>3.20</td>
<td>2.19</td>
<td>0.68</td>
<td>2.05</td>
<td>0.27</td>
<td>2.65</td>
<td>2.05</td>
</tr>
<tr>
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<td>0.35</td>
<td>3.10</td>
<td>1.42</td>
<td>5.42</td>
<td>0.26</td>
<td>1.52</td>
<td>1.73</td>
</tr>
<tr>
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<td>Sloanea sp. (GUM483)</td>
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<td>0</td>
<td>0</td>
<td>1.45</td>
</tr>
<tr>
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<td>6.83</td>
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<td>1.11</td>
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<td>0.90</td>
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<tr>
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<td>17.11</td>
<td>13.04</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
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Within the upstream sites, there was a tendency for one or two very important species (*I. deltoidea*, and *R. viridifolia* in Uvasichi, or *I. juruensis* in Cuchisama), whereas Yaranda was slightly different from the other sites. In Yaranda, *H. crepitans* and *P. armata* were among the five most important species, which resembled the road sites, while *H. crepitans* was not important in the other upstream sites. Similarly, *U. floribunda* was not important in the upstream sites (except Yaranda) and was important in the other sites.

Lastly, Campo Bello was particularly different from the other sites. Two species had a very high IVI: *A. murumuru* and *P. armata*. *Sloanea sp.* had a high IVI and was absent from the other sites, and *Theobroma cacao*, which was important in Campo Bello, was only present in Uvasichi. Many of the most important species in the other inventoried site groups were absent in Campo Bello (e.g. *S. exorrhiza*, *Inga ruizii*, *L. crassa*, and *O. parvifolia*).

**Floristic similarity and forest structure across sites**

Cluster analysis based on Steinhaus index across sites yielded comparable results for all the tree categories (Figure 1.1). The four upstream sites were rather similar floristically for all the tree categories. Campo Bello was very different to all other sites and for all the tree groups. The road sites were similar, and either closer to the upstream sites (for canopy trees) or to Campo Bello (for all trees and canopy trees).

![Figure 1.1](image-url). Floristic similarity UPGMA dendrograms based on Steinhaus index for three types of trees at seven sites, totaling 55 0.1-ha plots, in the Tsimane’ territory, Bolivian Amazon. CB=Campo Bello; CU=Cuchisama; JA=Jamanchi; MF=Misión Fátima; TR=Triunfo; UV=Uvasichi and YA=Yaranda.
All sites had a relatively similar structure, being the trees <10 cm dbh, the most frequent category (Figure 1.2). However, in Campo Bello the structure was slightly different, since the trees with a dbh ranging 10-19.9 cm were almost as abundant as the trees with a dbh <10 cm.

Figure 1.2. Diameter class distributions of trees ≥ 2.5 cm dbh at seven sites of the Tsimane' territory, Bolivian Amazon. The dbh categories were the following: 1=2.5-9.9cm; 2=10-19.9cm; 3=20-29.9cm; 4=30-39.9cm; 5=40-49.9cm; 6=50-59.9cm; 7=more than 60cm.

**Discussion**

**Overall diversity and floristic composition**

We found a relatively low tree species richness in the Tsimane' territory. The total species found was 426, and tree species richness ranged 18-80 per plot, while Fisher’s Alpha index ranged 6.9-44.3. Other studies in the Bolivian Amazon clearly found higher values. In TIPNIS, which neighbors the Tsimane' territory, have been found 133-137 tree species per 0.1-ha transect and Fisher's Alpha index values of 124-127.7 (including lianas; Thomas et al. 2009). This study used 0.1-ha transects (500m × 20m), which include more species and individuals in the inventories due
to a longer perimeter (Macía 2008, Thomas 2009). However, several studies using 0.1-ha plots (50m × 20m) in the Bolivian lowlands have also highlighted higher richness and diversity values. For example, in the Madidi region, situated northwest of our study area, were found 47-111 woody plant species (including lianas) per plot, and a Fisher’s Alpha index ranging 21.7-71.3 in lowland forests (Araujo-Murakami et al. 2005a, 2005b, Quisbert and Macía 2005, Macía 2008).

The low richness species corresponds to a low tree density (64-254 per plot), as the two variables are associated and correlated in other studies (Macía 2008). However, it has been documented that rainfall amount and climate seasonality may play an important role in explaining differences in richness and diversity across studies (Smith and Killeen 1998, Givnish 1999, Thomas 2009). For example, Thomas (2009) explained the higher values found in the TIPNIS by a higher amount of rainfall than in Madidi. This could also fit in our study, although we lack reliable data at our scale of study, since average annual rainfall was lower than in Madidi or TIPNIS (<2000 mm). In turn, although seasonality may be important at a continental level, we do not expect it to explain differences in species richness within the Bolivian Amazon, since the Madidi region shares the same seasonality patterns as our study area.

**Family composition**

According to the FIVI, four families were particularly important in our study area (Moraceae, Arecaceae, Euphorbiaceae, and Fabaceae), which is generally consistent with earlier studies in TIPNIS and Madidi regions. The importance of families among Amazonian rainforests is highly predictable (Terborgh and Andresen 1998), particularly across studies using the same sampling (Macía 2008). Fabaceae is often the most important family in the Bolivian Amazon and other Amazonian regions, because it is also the most species-rich family (Gentry 1988, Terborgh and Andresen 1998, Nebel et al. 2001, Thomas 2009, Macía 2011). Our data support this statement, since we also found Fabaceae as the most species-rich family.

However, in our study Fabaceae was only the fourth in terms of ecological importance, consistent with other studies in Bolivia (Araujo-Murakami et al. 2005a, Macía 2008). Although we have not used the same inventory methodology,
the forests in our study area had floristic affinities with those inventoried in northern Beni (Boom 1986), in the neighboring Pilón-Lajas region (Smith and Killeen 1998), or in the Beni Biological Station (Comiskey 2000). These three studies have also reported Moraceae as the most important family. Consistency in family distribution in the Bolivian lowlands is likely explained by continental factors; the family Moraceae shows a gradient of increasing abundance from northeast to southwest Amazonia (ter Steege et al. 2007), supported by our results.

Patterns of oligarchic species across sites

Our three site groups showed different oligarchic patterns. Campo Bello was particularly different from the other sites by the following six reasons. First, Fisher’s Alpha index was the lowest of the inventory, and only five oligarchic species accounted for more than half of the individuals. Second, the understory stratum was underrepresented, accounting for only 9.5% of individuals. Third, structural differences in terms of diameter classes were well marked. Fourth, Campo Bello was the most dissimilar site of the whole inventory. Fifth, contrary to what was found in the other sites, Fabaceae was not an outstanding family whereas Ulmaceae was important, mostly due to the species C. schippii. Sixth, the forests were dominated by A. murumuru and P. armata, whereas interestingly, T. cacao was abundant, which could result of a particular human management in the area.

A floristic gradient seems to exist between the richest upstream sites, through the road sites, to the poorest in species, Campo Bello. On the one hand, this gradient is visualized in cluster analyses: the road sites (Triunfo and Jamanchi) form a group either closer to Campo Bello or to the upstream sites. On the other hand, species richness is lower in the road sites than in the upstream sites, where at the same time, there are also more rare species, and family and species importance patterns are different between the two groups. Among the five most abundant species in the two sites groups, only one (S. exorrhiza) was shared. The palm I. deltoidea was the most important species in the upstream sites and was absent of the other sites, whereas there was an increasing gradient of importance of A. murumuru from the upstream sites (not important) to Campo Bello (most
important species), being also among the five most important species in the road sites.

This floristic gradient is likely explained by the geographic position of the inventoried sites, possibly due to biogeographic affinities and differences in flooding history. Concerning biogeographic status, an example is the palm *I. deltoidea* which is restricted to upstream sites, being the most important species. This is consistent with studies in the Madidi region and in TIPNIS (Araujo-Murakami et al. 2005a, Macía 2008, Thomas 2009) which suggest that the upstream sites strongly share floristic affinities with the transition Amazonian-Andean biogeographic regions. Other studies have highlighted that this palm is characteristic in the Amazonian forests of Madidi (Fuentes 2005) and is also common in the foothills of the Andes, while absent from the Brazilian Shield region (Smith and Killeen 1998). This all suggests that the road sites and Campo Bello share more affinities with the Brazilian-Paraná biogeographic region.

Second, the gradient might be due to flooding history. Smith and Killeen (1998) hypothesize that the late establishment of lowland forests during the Holocene, and recurrent catastrophic disturbances due to flooding, might explain the low diversity of these forests. Since these factors are likely influenced by variation in topography, we argue that in more rolling terrains, as in the upstream sites, they have had less impact, leading to higher richness and diversity. The differences in abundances of *A. murumuru* likely illustrate differences in flooding history. It has been shown that this palm species is more abundant in poorly-drained terrains in Madidi, i.e. lands that are never flooded but with edaphic features that can lead to temporal stagnant water (Fuentes 2005). Other studies have shown that this species is more adapted to seasonally or permanently flooded forests (Moraes et al. 2001, Wittmann et al. 2006). However, some authors argue that *A. murumuru* occurs in *terra firme* forests (Vormisto et al. 2004) and in a wide range of habitats (Comiskey 2000). Since Fuentes (2005) stresses the difficulty of differentiating between *terra firme* and poorly-drained forestes because they share many species, and although the forests in Campo Bello are not properly temporally-flooded, we hypothesize that the history of inundations partly controls compositional and structural patterns. However, further studies must address the
importance of edaphic factors, as well as geographic distances, in explaining floristic composition across sites.

We found other minor differences within the upstream sites, especially between Yaranda, which seems closer floristically to the road sites, and Uvasichi, in which the understory stratum is important, with abundance of *R. viridifolia*. We acknowledge that sampling might partly explain these differences, since we only inventoried 0.8 hectares per site, which does not capture all tree diversity (Macía 2008). However, although *R. viridifolia* is often an important species in the Bolivian Amazon (Flores 2002, Araujo-Murakami 2005a, 2005b, Macía 2008), it is possible that these different patterns are due to human utilization of the forest, particularly because the abundance of understory trees can develop after e.g. selective logging, or even indigenous utilization.

**Acknowledgements**

We thank the Gran Consejo Tsimane’ and the Dirección General de la Biodiversidad (Bolivia) for research permits. We also thank M. Lero, E. Huasnay, D. Cari, and Tsimane’ local guides for help with the inventories; S. G. Beck, N. Paniagua-Zambrana, A. Fuentes, F. Zenteno, I. Loza and researchers from LPB for help with sample identification; and T. Huanca and E. Conde for logistical support. This research was funded by a FBBVA grant (BIOCON_06_106-07).

**Reference list**


Chapter 2

Determinants of tree species turnover in a southern Amazonian rainforest

(co-authors: Jaime Paneque-Gálvez, Ana Catarina Luz, Joan Pino, Martí Orta, Victoria Reyes-García, and Manuel J. Macía)

Abstract

The relative importance of the factors influencing the distribution of tree communities in tropical forests and the determinants of species turnover remains largely debated. Here, we quantify the relative contribution of environmental variables and geographical distances to explain the turnover of tree species, broken down into four categories: all trees (dbh ≥ 2.5 cm), large trees (dbh ≥ 10 cm), small trees sensu lato (dbh <10 cm), and small trees sensu stricto (strictly understory species, dbh <10 cm). We inventoried 55 0.1-ha plots in old-growth tierra firme forest in seven sites of the Tsimane’ indigenous territory, Bolivian Amazon. Composite soil samples from each of the plots were analysed for physical and chemical properties. Floristic differences between sites yielded significant Mantel correlations with both geographical distances and environmental variables (pH, Ca, Mg, exchangeable acidity, C/N relation, and sand content) for all tree categories. Phosphorus was correlated with floristic patterns only for small trees sensu stricto. Together, geographical distances and environmental variables explained 62% of the floristic variation for all trees. Environmental variables explained more variation for large trees than for small trees sensu stricto. Our results support the hypothesis that species distributions are driven by both geographical distances (neutral factors) and environmental variables (niche factors). In general terms, large trees and small trees sensu stricto are determined by common factors.

Key words: floristic distances, geographical distances, environmental variables, neutral, niche, lowland Bolivia
Introduction

In tropical rainforests, and particularly in the Amazon, the number of woody plant species is higher than in any other terrestrial biome (Gentry 1988, ter Steege et al. 2003, Milliken et al. 2011), and the relative importance of the factors influencing spatial patterns of these plant communities remains largely debated. Two major views have been put forward. “Niche” models explain species distribution as a result of competition for resources (Tilman 1994, Tuomisto et al. 2003a, Chave 2008), whereas “neutral” models explain species distribution through dispersal limitation and random disturbances (Bell et al. 1993, Hubbell 2001, Seidler and Plotkin 2006, Rosindell et al. 2011). Since explanations from the two models are not exclusive, recently there has been a growing tendency to take into account both models to explain floristic spatial patterns (Barot 2004, Gravel et al. 2006, Macía et al. 2007, Haegeman and Loreau 2010, Mutshinda and O’Hara 2010), particularly when considering different spatial scales. At medium and large scales, i.e. landscape and regional scales as defined by Poulsen et al. (2006), John et al. (2007) and Sesnie et al. (2009), environmental variables (resource-driven processes) seem to predominate in determining floristic patterns and species distributions (Duque et al. 2002, Phillips et al. 2003, Tuomisto et al. 2003a, Macía et al. 2007, Ruokolainen et al. 2007, Sesnie et al. 2009, Slik et al. 2010, Andersen et al. 2010). At small scales, i.e. plot size (<50 ha), floristic patterns seem to be more influenced by geographical distances (neutral processes) than by the environment (Condit et al. 2002, Bohlman et al. 2008, Legendre et al. 2009). However, this general tendency is still debated, especially because environmental variables gradients might depend on space (Ruokolainen et al. 2007). For example, some authors find evidence of environmental determinism at local scales (Poulsen et al. 2006, John et al. 2007, Laliberté et al. 2009).

The present paper aims to understand the processes that explain species turnover in southern Amazonian region. Although floristic patterns and species distributions have been studied using many different proxies (see Tuomisto 2010a, 2010b for a review), here we focus on species turnover because it affords testing of neutral predictions (Tuomisto and Ruokolainen 2006, 2008, Baselga 2010).
Species turnover quantifies the proportion of species composition that changes among compositional units (Tuomisto 2010b).

Research on species turnover in tropical forests has yielded three significant insights. First, the determinants of species turnover seem to vary from region to region (Chave 2008). Researchers have reported more geographical control of floristic distances in Central America (Condit et al. 2002, Chust et al. 2006) than in the Amazon basin (Phillips et al. 2003, Macía et al. 2007) or in Borneo (Potts et al. 2002, Paoli et al. 2006). Second, on the few studies that have directly measured soil properties from inventory plots in the Amazon, edaphic conditions have proved to be key to explain species turnover (Duque et al. 2002, Phillips et al. 2003, Tuomisto et al. 2003b, Macía et al. 2007, Ruokolainen et al. 2007, Bohlman et al. 2008). Several authors have found a consistent and strong influence of exchangeable cations (calcium, magnesium) on species turnover (e.g. Phillips et al. 2003, Honorio et al. 2009). Some studies have also highlighted the importance of texture (Tuomisto et al. 2003a), pH (Macía et al. 2007), and aluminium content (Phillips et al. 2003), whereas results for nitrogen and phosphorus are inconsistent (e.g. John et al. 2007, Bohlman et al. 2008).

Thirdly, the relative effects of neutral and environmental factors on floristic patterns may depend on the life history traits of the species in question, especially on the life form and dispersal strategies. Some authors have emphasized that understory species distribution is more dependent on the environment than canopy species distribution (Duque et al. 2002) although this apparent difference might be due to a large extent to sampling (Jones et al. 2008b). Few studies have separately analysed canopy and understory species. Some of them have studied only one or two plant groups, i.e. pteridophytes and Melastomataceae (Tuomisto et al. 2003b) or palms (Normand et al. 2006, Sesnie et al. 2009, Andersen et al. 2010). On the few studies that analysed all woody plants, in one case the distinction was done only on the basis of diameter (Duque et al. 2002) and did not include a real distinction of understory trees sensu stricto (Macía et al. 2007).

The objectives of this paper are 1) to assess the relative influence of environmental and geographical distances in explaining variation in species turnover; 2) to determine which of the studied environmental variables are more relevant in explaining patterns of species turnover; and 3) to compare congruence
in these floristic patterns between large canopy trees and two groups of small understory trees, segregated first according to diameter and second according to plant traits.

**Materials and methods**

**Study area**

We conducted the study in the Tsimane’ Indigenous Territory (Territorio Comunitario de Origen Tsimane’), located in the south of the department of Beni, in the Bolivian Amazon (Fig. 1). The Tsimane’ are one of the largest indigenous groups in the Bolivian Amazon and inhabit a densely forested area (Reyes-García et al. 2010). The study area has a mean annual temperature of 25.8 ºC, reported in the meteorological station of San Borja (Navarro and Maldonado 2002), and a mean annual rainfall of 1743 mm (Godoy et al. 2008). The region shows a strong annual seasonality with four months with less than 100 mm of precipitation. Most soils are quaternary alluvial sediments of fluvial origin, particularly acrisols and ferralsols (Navarro and Maldonado 2002). The Tsimane’ territory is covered with old-growth forest, which has been degraded by selective logging in many places (Gullison et al. 1996). Different broad forest types occur according to the flooding level history: most areas are never flooded and covered with tierra firme forests, but in some places seasonally or permanently flooded terrains present a range of bajío forests, with lower canopy height and tree diversity (Killeen et al. 1993, Macía 2008). In this study, we focus on tierra firme forests.

**Floristic sampling**

We inventoried 55 0.1-ha plots (50 m×20 m) in tierra firme forests within the territory of seven Tsimane’ villages, between March and December 2009. The villages are settled along the Maniqui River in a north-south gradient or along logging roads (Fig. 1). We set up eight plots per village, except in one village, in which there were only seven plots. The forest structure and topography in the studied area were generally homogeneous. We established plots in old-growth forests showing neither sign of recent human activity nor large canopy gaps, and at a minimal distance of 500 m from the closest house or agricultural field.
We measured all tree stems rooted within plots and with a diameter at breast height (dbh) ≥ 2.5 cm at 1.3 m above ground. We measured multiple stems of the same tree separately but counting them as one individual. We collected voucher specimens for all individuals that we could not identify in the field. We sorted all vouchers to species or morphospecies level and identified them. Duplicates of the collections are deposited in LPB and MA herbaria, and unicates are kept in LPB. We included all morphospecies in the following analyses.

**Environmental variables**

We collected a composite superficial (0 – 15 cm) soil sample in each plot. Each composite soil sample was composed by five subsamples collected in the four corners and in the centre of each plot, and then mixed to obtain a unique sample to analyze. Soil samples were air-dried and transported to the Laboratory of Environmental Quality (Universidad Mayor de San Andrés, La Paz, Bolivia) for physico-chemical analyses. Samples were then sieved in a 2 mm sieve. Soil properties were determined following ISRIC protocols (van Reeuwijk 2002). Soil pH was measured in a 1:2.5 soil: 1M KCl suspension. Exchangeable bases (Ca, Mg, Na, and K) were extracted with 1M ammonium acetate solution, and exchangeable acidity was extracted with 1M KCl solution. Exchangeable acidity contains the exchangeable fraction of aluminium. Total organic carbon and organic matter contents were determined following the Walkley and Black procedure, total nitrogen following the semi-micro Kjeldahl procedure, and available phosphorus with the Bray I method (colorimetry with blue ammonium molybdate). Texture was determined using the three-fraction method (van Reeuwijk 2002).

We recorded GPS coordinates in the centre of each plot. For each plot position, we obtained a set of average annual values of all environmental variables (30 arc-seconds resolution) from the WORLDCLIM database (http://www.worldclim.org). Since the different variables showed high Pearson correlation coefficients and almost inexistent variability at our scale of study, we retained only rainfall (BIO12) for further analyses, since it showed the highest variability between plots.
**Data analysis**

For all analyses, we subdivided floristic data into four tree categories: i) all trees (dbh≥2.5 cm), ii) large trees (dbh≥10 cm), iii) small trees sensu lato (s.l., dbh<10 cm), i.e. including juvenile stems of the large tree species, and iv) small trees sensu stricto (s.s., dbh <10 cm), i.e. excluding stems of the species that were included in the large trees category.

We calculated three groups of distance matrices: i) tree floristic distances, ii) environmental distances, and iii) geographical distances. First, we calculated the Jaccard similarity index between plots for each of the tree categories and computed floristic distance matrices for each group as 1−Jaccard index (Legendre and Legendre 1998). The Jaccard index is based on presence-absence data and allows conclusions on proportional species turnover (Tuomisto 2010c). Second, for all environmental variables, we calculated Euclidean distance matrices. Previously, we transformed exchangeable cations concentrations values to their natural logarithms because plants are likely to be more responsive to differences in resources when resources are scarce (Jones et al. 2008b). Third, we calculated a geographical distances matrix as Euclidean distances. We applied a previous ln-transformation to make neutral hypotheses testable, as the theory predicts that floristic distance between two sites decreases approximately linearly along with the logarithm of geographical distance between these sites (Hubbell 2001, Tuomisto et al. 2003b).

To assess the role of the different environmental variables and geographical distances in explaining floristic patterns, we performed Mantel tests (rM). Specifically, for each of the tree categories, we used Mantel tests to analyse correlations between 1) floristic and environmental distance matrices, and 2) floristic and geographical distance matrices. To assess statistical significance at the P<0.001 level, we run 999 permutations in all cases. If floristic distances correlated significantly with environmental distances, we also performed partial Mantel tests partialling out geographical distances, to verify whether the correlation remained significant after the effect of geographical distances had been taken into account. To visualize floristic patterns among the inventory sites, we performed non-metric multidimensional scaling (NMDS) ordinations.
To disentangle the relative contribution of environmental and geographical distances, i.e. to distinguish between pure environmental variation, spatial autocorrelation, and the intercorrelation of both, we used variation partitioning analyses for each of the tree categories. Variation partitioning is a method that quantifies the relative influence of different groups of variables over another (Borcard et al. 1992, Tuomisto and Ruokolainen 2006). In our study, we based variation partitioning analyses on multiple regressions on distance matrices, a method similar to multiple regression analysis but that works on an unfolded distance matrix (Lichstein 2007, Goslee 2010, Smith and Lundholm 2010). For each of the four tree categories, we selected the significant environmental variables explaining the floristic patterns through a backward elimination procedure (removal criterion P>0.1). We used three different models for variation partitioning. Model 1 includes matrices of environmental variables only, capturing environmental variation and environmental - geographical interactions. Model 2 includes ln-transformed geographical distances only, capturing geographical variation and environmental - geographical interactions. Model 3 includes environmental variables and ln-transformed geographical distances, capturing environmental variation, geographical variation and environmental - geographical interactions. The residuals of the most inclusive model (3) give the variation unexplained by environmental variables or geographical distances. We calculated the four fractions of variation in floristic distances by subtraction, using the R2 of each regression (Legendre and Legendre 1998) as follows:

\[a\] = variation explained by environment = \(R^2(3) - R^2(2)\);

\[b\] = variation explained by interactions environment-space = \(R^2(1) + R^2(2) - R^2(3)\);

\[c\] = variation explained by geographical distance = \(R^2(3) - R^2(1)\);

\[d\] = variation unexplained = 1 - \(R^2(3)\).

As the fractions are subtractions, their significance could not be tested statistically (Legendre and Legendre 1998).

We run all statistical analyses in R 2.11.1, except backward elimination procedure based on distance matrices that was performed using Permute! (http://www.bio.umontreal.ca/casgrain/en/lab0/permute/index.html). We used the ‘vegan’ package (Oksanen et al. 2011) for the Mantel and partial Mantel analyses, the ‘ecodist’ package (Goslee and Urban 2007) for multiple regressions in
variation partitioning, and the ‘labdsrv’ package (Roberts 2010) for NMDS ordination.

**Results**

**Floristic variation**

We measured and identified a total of 9082 tree individuals ≥2.5 cm dbh, representing 427 species and morphospecies in 55 0.1-ha tierra firme plots (Table 2.1). We observed consistent differences in species richness and abundance in the four tree categories across the studied sites. We found the highest species richness in Uvasichi plots and the lowest values in Campo Bello plots, where the total richness accounted for only 36.5% of the total richness in Uvasichi.

Large trees represented 36.4% of total individuals and 63.4% of total species (Table 2.1). Juvenile individuals of canopy species represented most of the trees found in the understory strata, and therefore the values of the group small trees s.l. were very close to those of the category all trees. Small trees s.s. were less diverse than the other tree categories, reaching an average of 2 – 13 species per plot, and representing 10.6% of total individuals and 34.0% of total species. The sum of large tree species and small trees s.s. species did not equal the total number of species because some individuals <10 cm dbh belonged to the large tree species category but were not found in our inventory. These sum 24 species that were excluded of the small trees s.s. category.

**Table 2.1.** Mean ± standard deviation number of species and individuals in four tree categories at eight study sites, as recorded in 55 0.1-ha plots in the lowland forests of the Tsimane' territory, Bolivian Amazon.

<table>
<thead>
<tr>
<th>Study sites</th>
<th>Number of plots</th>
<th>All trees (dbh≥2.5cm)</th>
<th>Large trees (dbh≥10cm)</th>
<th>Small trees sensu lato (dbh&lt;10cm)</th>
<th>Small trees sensu stricto (dbh&lt;10cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>species</td>
<td>individuals</td>
<td>species</td>
<td>individuals</td>
</tr>
<tr>
<td>Campo Bello</td>
<td>7</td>
<td>23±3</td>
<td>89±14</td>
<td>13±3</td>
<td>50±7</td>
</tr>
<tr>
<td>Cuchisama</td>
<td>8</td>
<td>47±9</td>
<td>190±40</td>
<td>24±6</td>
<td>71±9</td>
</tr>
<tr>
<td>Jamanchi</td>
<td>8</td>
<td>50±5</td>
<td>153±15</td>
<td>22±2</td>
<td>51±6</td>
</tr>
<tr>
<td>Misión Fátima</td>
<td>8</td>
<td>55±7</td>
<td>188±23</td>
<td>29±6</td>
<td>64±17</td>
</tr>
<tr>
<td>Triunfo</td>
<td>8</td>
<td>40±6</td>
<td>158±24</td>
<td>22±3</td>
<td>57±10</td>
</tr>
<tr>
<td>Uvasichi</td>
<td>8</td>
<td>63±14</td>
<td>208±41</td>
<td>28±5</td>
<td>60±10</td>
</tr>
<tr>
<td>Yaranda</td>
<td>8</td>
<td>50±11</td>
<td>162±19</td>
<td>25±4</td>
<td>68±10</td>
</tr>
<tr>
<td>Total</td>
<td>55</td>
<td>427</td>
<td>9082</td>
<td>258</td>
<td>3306</td>
</tr>
</tbody>
</table>
In the NMDS ordinations, the position of plots showed a clear floristic separation between Campo Bello and the other sites for all floristic groups (Fig. 2.1). Triunfo and Jamanchi formed a consistent group that segregated from the other sites, but Cuchisama and Misión Fátima plots were widespread throughout the graphs. This pattern was relatively consistent among three floristic groups (Fig. 2.1a, 2.1b, 2.1c) but not for the group of small trees s.s. (Fig. 2.1d). We performed a Mantel test between the floristic distance matrices of the two independent tree categories (large trees and small trees s.s.), which was highly significant ($r_M=0.46$, $P<0.001$).

**Figure 2.1.** Non-metric multidimensional scaling (NMDS) site scores for 55 0.1-h plots in lowland forest in the Tsimane' territory, Bolivian Amazon; a=all trees (dbh≥2.5cm); b=large trees (dbh≥10 cm); c=small trees *sensu lato* (dbh<10 cm); d=small trees *sensu stricto* (dbh<10 cm).
Environmental data and study sites

Soils showed clear differences between sites (Table 2.2). All soils were acidic with an average pH ranging 3.86 – 5.11. We found the highest amount of all exchangeable cations (except sodium) in Triunfo and the lowest in Misión Fátima. Contrarily, Misión Fátima had the highest exchangeable acidity values and Triunfo the lowest. In all sites, calcium accounted for the largest part of the four principal exchangeable bases. The amount of available phosphorus was relatively homogenous among sites. For organic carbon, total nitrogen and organic matter, Triunfo had also the highest values. Yet, we observed the highest value of the relation C/N in Misión Fátima. Concerning soil textural properties, Misión Fátima had the highest sand proportion and the lowest proportion of silt and clay. In contrast, Triunfo showed the highest clay proportion and the lowest sand proportion.

Table 2.2. Mean ± standard deviation data for the environmental variables recorded in 55 0.1-ha plots at seven sites in the lowland forests of the Tsimane’ territory, Bolivian Amazon.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Campo Bello</th>
<th>Cuchisama</th>
<th>Jamanchi</th>
<th>Misión Fátima</th>
<th>Triunfo</th>
<th>Uvasichi</th>
<th>Yaranda</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH (in KCl)</td>
<td>5.11±0.96</td>
<td>4.21±0.58</td>
<td>4.56±0.47</td>
<td>3.86±0.20</td>
<td>4.91±0.39</td>
<td>4.61±0.76</td>
<td>4.14±0.55</td>
</tr>
<tr>
<td>Ca (cmol, kg⁻¹)</td>
<td>6.04±2.41</td>
<td>4.15±4.51</td>
<td>4.65±2.78</td>
<td>2.01±2.54</td>
<td>9.83±1.65</td>
<td>2.99±1.62</td>
<td>3.08±2.36</td>
</tr>
<tr>
<td>Mg (cmol, kg⁻¹)</td>
<td>1.64±0.57</td>
<td>0.85±0.83</td>
<td>1.55±0.96</td>
<td>0.71±0.76</td>
<td>2.29±0.46</td>
<td>0.97±0.12</td>
<td>1.57±1.15</td>
</tr>
<tr>
<td>Na (cmol, kg⁻¹)</td>
<td>0.03±0.01</td>
<td>0.05±0.05</td>
<td>0.04±0.01</td>
<td>0.03±0.01</td>
<td>0.05±0.01</td>
<td>0.03±0.01</td>
<td>0.07±0.08</td>
</tr>
<tr>
<td>K (cmol, kg⁻¹)</td>
<td>0.20±0.04</td>
<td>0.23±0.18</td>
<td>0.15±0.11</td>
<td>0.10±0.06</td>
<td>0.30±0.12</td>
<td>0.14±0.05</td>
<td>0.19±0.08</td>
</tr>
<tr>
<td>Exchangeable acidity (cmol, kg⁻¹)</td>
<td>0.14±0.19</td>
<td>1.20±0.93</td>
<td>0.53±0.64</td>
<td>2.25±1.42</td>
<td>0.12±0.09</td>
<td>0.38±0.41</td>
<td>1.22±1.05</td>
</tr>
<tr>
<td>Sum of Ca, Mg, Na, K</td>
<td>7.91±2.47</td>
<td>5.28±5.45</td>
<td>6.39±3.78</td>
<td>2.86±3.25</td>
<td>12.46±2.04</td>
<td>4.13±1.65</td>
<td>4.92±3.00</td>
</tr>
<tr>
<td>Available P (mg kg⁻¹)</td>
<td>5.46±1.25</td>
<td>10.63±5.90</td>
<td>3.53±1.69</td>
<td>4.00±1.40</td>
<td>7.33±3.64</td>
<td>4.90±1.95</td>
<td>4.65±1.40</td>
</tr>
<tr>
<td>Total N (%)</td>
<td>0.11±0.01</td>
<td>0.15±0.05</td>
<td>0.10±0.05</td>
<td>0.11±0.04</td>
<td>0.22±0.04</td>
<td>0.11±0.03</td>
<td>0.15±0.05</td>
</tr>
<tr>
<td>Organic C (%)</td>
<td>0.98±0.18</td>
<td>1.47±0.35</td>
<td>0.77±0.30</td>
<td>1.13±0.39</td>
<td>1.52±0.44</td>
<td>1.16±0.29</td>
<td>1.16±0.39</td>
</tr>
<tr>
<td>Organic Matter (%)</td>
<td>1.66±0.30</td>
<td>2.55±0.60</td>
<td>1.31±0.49</td>
<td>1.69±0.29</td>
<td>2.63±0.74</td>
<td>1.99±0.50</td>
<td>1.99±0.68</td>
</tr>
<tr>
<td>C/N</td>
<td>8.60±0.87</td>
<td>10.08±2.16</td>
<td>7.80±0.99</td>
<td>11.35±4.10</td>
<td>6.99±1.07</td>
<td>10.78±1.80</td>
<td>8.04±2.22</td>
</tr>
<tr>
<td>Sand (%)</td>
<td>24.3±9.9</td>
<td>43.4±21.3</td>
<td>31.0±13.7</td>
<td>49.8±17.9</td>
<td>17.6±8.7</td>
<td>43.1±17.2</td>
<td>25.3±18.5</td>
</tr>
<tr>
<td>Silt (%)</td>
<td>37.9±7.4</td>
<td>21.4±9.2</td>
<td>25.0±9.9</td>
<td>18.5±11.3</td>
<td>21.5±13.9</td>
<td>20.9±8.7</td>
<td>24.9±10.1</td>
</tr>
<tr>
<td>Clay (%)</td>
<td>37.7±13.0</td>
<td>35.4±17.3</td>
<td>43.8±20.5</td>
<td>31.8±9.8</td>
<td>59.5±13.6</td>
<td>36.0±11.9</td>
<td>49.8±20.4</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>208±22</td>
<td>265±13</td>
<td>225±12</td>
<td>276±37</td>
<td>206±12</td>
<td>245±16</td>
<td>248±11</td>
</tr>
<tr>
<td>Precipitation (mm)</td>
<td>1763±5</td>
<td>2092±10</td>
<td>1868±3</td>
<td>1985±13</td>
<td>1828±6</td>
<td>1835±25</td>
<td>1902±5</td>
</tr>
</tbody>
</table>
Average rainfall WORLDCLIM values were not markedly different among sites, ranging from 1763 mm in Campo Bello to 2092 mm in Cuchisama (Table 2.2).

**Determinants of floristic variation**

All floristic groups showed strongly significant Mantel correlations for five environmental variables: two exchangeable cations (Ca, Mg), exchangeable acidity, relation C/N, and sand content (Table 2.3). The correlations were also significant although weaker for exchangeable potassium.

**Table 2.3.** Mantel correlations between floristic and environmental differences along with their partial Mantel correlations with the effect of geographical distances (GD) partialled out for significant variables, between 55 0.1-ha plots in lowland forests in the Tsimane’ territory, Bolivian Amazon. Statistical significance was calculated with a Monte Carlo permutation test using 999 permutations. *=P<0.05; **=P<0.01; ***=P<0.001.

<table>
<thead>
<tr>
<th>Environmental variables</th>
<th>All trees (dbh≥2.5cm)</th>
<th>Large trees (dbh≥10cm)</th>
<th>Small trees <em>sensu lato</em> (dbh&lt;10cm)</th>
<th>Small trees <em>sensu stricto</em> (dbh&lt;10cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH (in KCl)</td>
<td>0.22**</td>
<td>0.13</td>
<td>0.22**</td>
<td>0.18***</td>
</tr>
<tr>
<td>pH, GD partialled out</td>
<td>0.14*</td>
<td>0.05</td>
<td>0.14*</td>
<td>0.11*</td>
</tr>
<tr>
<td>Ca</td>
<td>0.53***</td>
<td>0.48***</td>
<td>0.46***</td>
<td>0.25***</td>
</tr>
<tr>
<td>Ca, GD partialled out</td>
<td>0.56***</td>
<td>0.47***</td>
<td>0.47***</td>
<td>0.19**</td>
</tr>
<tr>
<td>Mg</td>
<td>0.51***</td>
<td>0.47***</td>
<td>0.45***</td>
<td>0.25***</td>
</tr>
<tr>
<td>Mg, GD partialled out</td>
<td>0.54***</td>
<td>0.46***</td>
<td>0.46***</td>
<td>0.21**</td>
</tr>
<tr>
<td>Na</td>
<td>−0.01</td>
<td>0.02</td>
<td>0.01</td>
<td>0.04</td>
</tr>
<tr>
<td>K</td>
<td>0.15*</td>
<td>0.14*</td>
<td>0.12*</td>
<td>0.09*</td>
</tr>
<tr>
<td>K, GD partialled out</td>
<td>0.17*</td>
<td>0.14*</td>
<td>0.13*</td>
<td>0.08*</td>
</tr>
<tr>
<td>Acidity</td>
<td>0.30***</td>
<td>0.22***</td>
<td>0.27***</td>
<td>0.25***</td>
</tr>
<tr>
<td>Acidity, GD partialled out</td>
<td>0.18***</td>
<td>0.11**</td>
<td>0.15**</td>
<td>0.15***</td>
</tr>
<tr>
<td>Sum of Ca, Mg, Na, K,</td>
<td>0.25***</td>
<td>0.18**</td>
<td>0.22***</td>
<td>0.14***</td>
</tr>
<tr>
<td>Sum, GD partialled out</td>
<td>0.17***</td>
<td>0.10*</td>
<td>0.13*</td>
<td>0.06</td>
</tr>
<tr>
<td>Available P, GD partialled out</td>
<td>−0.15</td>
<td>−0.17</td>
<td>−0.13</td>
<td>0.14*</td>
</tr>
<tr>
<td>Total N</td>
<td>−0.02</td>
<td>−0.06</td>
<td>−0.01</td>
<td>−0.01</td>
</tr>
<tr>
<td>Organic C</td>
<td>−0.11</td>
<td>−0.13</td>
<td>−0.11</td>
<td>−0.06</td>
</tr>
<tr>
<td>Organic matter</td>
<td>−0.12</td>
<td>−0.15</td>
<td>−0.12</td>
<td>−0.03</td>
</tr>
<tr>
<td>C/N</td>
<td>0.25**</td>
<td>0.26**</td>
<td>0.24**</td>
<td>0.15**</td>
</tr>
<tr>
<td>C/N, GD partialled out</td>
<td>0.29***</td>
<td>0.25**</td>
<td>0.23**</td>
<td>0.11*</td>
</tr>
<tr>
<td>Sand</td>
<td>0.32***</td>
<td>0.31***</td>
<td>0.29**</td>
<td>0.21***</td>
</tr>
<tr>
<td>Sand, GD partialled out</td>
<td>0.33***</td>
<td>0.30***</td>
<td>0.29***</td>
<td>0.18**</td>
</tr>
<tr>
<td>Silt</td>
<td>0.14*</td>
<td>0.07</td>
<td>0.14**</td>
<td>0.12**</td>
</tr>
<tr>
<td>Silt, GD partialled out</td>
<td>0.12*</td>
<td>0.03</td>
<td>0.12*</td>
<td>0.10*</td>
</tr>
</tbody>
</table>
Additionally, soil pH and silt content yielded significant Mantel correlations with all groups except large trees. The sum of exchangeable cations yielded significant correlations with all groups except small trees s.s. Nevertheless, we did not use this latter variable for further analyses because Ca and Mg contents accounted for most of the sum value, and significantly explained floristic patterns. Available P yielded a significant Mantel correlation only for small trees s.s. Soil Na content, total N, organic C, organic matter and clay amount showed no statistically significant Mantel correlations with any group of trees.

All tree groups showed strong statistically significant Mantel correlations with ln-geographical distances (Table 2.3). The five most important environmental variables remained significant when the effect of geographical distances was partialled out, and the correlations remained mostly unchanged, regardless of partialling out ln-geographical distances or not. Similarly, for small trees s.s., the partial Mantel correlation for available phosphorus remained significant.

Concerning precipitation, the Mantel correlations were highly significant for all groups (P<0.001) (Table 2.3). However, partialling out geographical distances strongly affected both coefficients and significance. For large trees and small trees s.s., partial Mantel correlations were no longer significant. Therefore, we removed precipitation data for further analysis.

The stepwise selection procedure for environmental variables in multiple regression analyses, showed that soil sand content and exchangeable acidity significantly explained the floristic patterns of all four tree groups (Table 2.4). However, calcium was most strongly significant (P<0.001) to explain the floristic patterns for all tree categories with the exception of small trees s.s., best explained by exchangeable magnesium.
Table 2.4. Multiple regression coefficients between floristic distance matrices and environmental and geographical distance matrices. *=P<0.05; **=P<0.01; ***=P<0.001. n.s.= non significant coefficients.

<table>
<thead>
<tr>
<th></th>
<th>All trees (dbh≥2.5cm)</th>
<th>Large trees (dbh≥10cm)</th>
<th>Small trees sensu lato (dbh&lt;10cm)</th>
<th>Small trees sensu stricto (dbh&lt;10cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ca</td>
<td>0.43***</td>
<td>0.40***</td>
<td>0.42***</td>
<td>n.s.</td>
</tr>
<tr>
<td>Sand</td>
<td>0.11*</td>
<td>0.12*</td>
<td>0.14*</td>
<td>0.12*</td>
</tr>
<tr>
<td>Acidity</td>
<td>0.17*</td>
<td>0.11*</td>
<td>0.15**</td>
<td>0.22***</td>
</tr>
<tr>
<td>Mg</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>0.15*</td>
</tr>
<tr>
<td>K</td>
<td>n.s.</td>
<td>n.s.</td>
<td>-0.13*</td>
<td>n.s.</td>
</tr>
<tr>
<td>R²</td>
<td>0.31***</td>
<td>0.25***</td>
<td>0.26***</td>
<td>0.12***</td>
</tr>
</tbody>
</table>

Variation partitioning analyses showed differences regarding the determinants of floristic patterns among tree groups and geographical distances explained the main amount of variation for all groups. However, for large trees a major amount of relative variation (36.2%) was explained by environmental variables with respect to the other tree groups. The group small trees s.s. showed reversed patterns as environmental distances accounted for a small part (17.1%) of explained variation (Fig. 2.2B). For the four groups the interaction component was also important (6.8 – 13.3% of total variation; Fig. 2.2A). A large part of the total variation remained unexplained (38.3% for all trees and 71.0% for small trees s.s.; Fig. 2.2A). The unexplained component increased as the sample size decreased: small trees s.s. had the smallest number of individuals and showed the highest unexplained variation.
Figure 2.2. Relative contribution of environment variables, geographical distances, and the interaction of both for explaining floristic patterns between 55 0.1-ha plots among four tree categories in lowland forest of the Tsimane’ territory, Bolivian Amazon. A: Percentages of total variation. B: Percentages of explained variation only. Each bar represents a floristic group: a= All trees (dbh≥2.5 cm); b= Large trees (dbh≥10 cm); c= Small trees sensu lato (dbh<10 cm); d= Small trees sensu strict (dbh<10 cm).

Discussion

Determinants of species turnover: environmental vs. geographical distances

Our results support the hypothesis that environmental distances, particularly edaphic variables, and geographical distances are both important to understand tree floristic patterns in southern Amazonian tierra firme forests by the following points. First, the highest Mantel correlation coefficients are obtained for geographical distances, but the coefficients for two exchangeable cations (Ca and Mg) are comparable to those. Three other edaphic variables (exchangeable acidity, C/N relation and sand content) also contribute to explain floristic patterns for all tree categories. Second, partial Mantel tests show that the contribution of edaphic variables remains significant and even increases when geographical distances are taken into account, suggesting that the contribution of edaphic variables to explain floristic patterns is not due to spatial autocorrelation. Third, in variation partitioning analyses for all tree categories, both geographical and environmental distances explain independently sizable parts of the total variation. Therefore, our
results are consistent with other studies that found both significant contributions of environmental and geographical factors on floristic patterns at comparable scales (Phillips et al. 2003, Tuomisto et al. 2003a, Vormisto et al. 2004, Macía et al. 2007, Duque et al. 2009, Sesnie et al. 2009, Andersen et al. 2010).

Our results suggest that neutral theory alone cannot explain the observed floristic patterns, although previous studies had also suggested that spatial random processes is the dominant driver of species distributions at our scale (Chust et al. 2006, Bohlman et al. 2008). Therefore, our data seem to support the continuum hypothesis proposed by Gravel et al. (2006) which maintains that observed differences between floristic patterns are the result of differences in the relative influence of combined neutral processes and environmental selection.

However, two main biases challenge the interpretation of our results. First, the pure spatial fraction of explained variation is not necessarily due to seed dispersal, but may have an environmental component related to temporal variation that we did not capture (Jones et al. 2008a). Second, the choice of the method used to model space is susceptible to modify the relative contribution of geography and environment, although it has been suggested that the predictions of the neutral theory can only be tested using a distance approach (see Legendre et al. 2008 and Tuomisto and Ruokolainen 2008, debate between distance-based and canonical analysis). Furthermore, a large part of floristic variation remains unexplained in our models, suggesting either a bias due to sample size, or that other factors could help explain tree floristic patterns. Such factors include historical natural events and stochastic disturbance processes (Svenning et al. 2004, Svenning and Skov 2005, Cardinale et al. 2006, Hoorn et al. 2010), historical land use with varying degree of intensity that may have influenced the distribution of some species (Heckenberger et al. 2003, Macía 2008), or other unmeasured environmental variables, such as drainage, water availability in soils or depth of water table (Sollins 1998, Duque et al. 2002, Phillips et al. 2003, Tuomisto et al. 2003a, Brenes-Arguedas et al. 2011). It would be interesting to take into account all these factors in future analyses.
Environmental variables that contribute to explain floristic patterns

Differences in soil nutrient contents and texture between plots explain a large part of the differences in floristic patterns in the study area. Consistent with other studies in the Amazon (Phillips et al. 2003, Macía et al. 2007, Ruokolainen et al. 2007) and throughout the humid tropics (e.g., Potts et al. 2002, Paoli et al. 2006), the strongest correlations with floristic patterns were for calcium and magnesium. These nutrients are likely to play an important role in the distribution of species since they are essential elements for cell processes (Honorio et al. 2009). We found exchangeable aluminium content to be also strongly related to floristic patterns. It has been suggested that aluminium toxicity at low pH controls species distributions (Sollins 1998), since aluminium inhibits cellular growth and elongation (e.g. Kochian 1995).

Phosphorus is a limiting nutrient for plant growth in lowland tropical forests (Sollins 1998) but our results do not support this hypothesis since available phosphorus was not significantly related to the floristic patterns except for small trees s.s. This result is consistent with other studies finding no relation between phosphorus and floristic patterns in the Neotropics (Phillips et al. 2003, Poulsen et al. 2006, John et al. 2007, Macía et al. 2007) but in Asian Paleotropics the opposite was found (Baillie et al. 1987, Paoli et al. 2006). Future studies are needed to clarify the significance of total and available phosphorus in plant-soil relationships.

Some studies have found nitrogen to be significant in explaining floristic patterns (Andersen et al. 2010 for understory palms). However, in most of the studies nitrogen was relatively insignificant (e.g. Macía et al. 2007), probably because nitrogen is not limiting in lowland tropical rainforests soils (Sollins 1998, John et al. 2007). In our study, consistent with the results of Bohlman et al. (2008), total nitrogen had no influence on floristic patterns, although C/N relation was strongly related to it.

Studies which analysed pH have found contrasting results regarding its influence on floristic patterns (Baillie et al. 1987, Tuomisto et al. 2003a, Macía et al. 2007, Bohlman et al. 2008). In our study, pH was significant to explain floristic patterns for all groups, except for large trees. It seems likely that pH does not play an important role in the establishment of large tree species, whereas small tree (understory species) distribution is influenced by pH. Bohlman et al. (2008)
emphasized that the role of pH may be limited to some regions or taxa. It is also possible that pH affects floristic patterns indirectly, through modifying cation concentrations in soils (John et al. 2007).

Consistent with the results of earlier papers in the Neotropics (Poulsen et al. 2006, Bohlman et al. 2008, Sesnie et al. 2009), in our study sand content was important in explaining floristic patterns. Many studies have also found soil textural properties significantly associated to floristic distances (Duque et al. 2002, Phillips et al. 2003, Tuomisto et al. 2003a). It has been emphasized that soil texture is related to nutrient gradients and water availability (Phillips et al. 2003).

Concerning rainfall, simple Mantel correlations with floristic distances were strong, but these correlations decreased when geographical distances were partialled out, suggesting a strong spatial autocorrelation of the data (Jones et al. 2008b). Since WOLRDCLIM data are estimates obtained by interpolation, it is likely that the data are not accurate at our small scale of study (Slik et al. 2010). Moreover, the significance of the correlations might be affected by the fact that the resolution of climatic variables is lower than the resolution of variables recorded in the field. At landscape and regional scales, many other studies in the Bolivian lowlands and elsewhere have found measured climatic variables such as rainfall amount and seasonality to explain floristic patterns (e.g. Chust et al. 2006, Sesnie et al. 2009, Toledo et al. 2010), suggesting that more efforts are needed in gathering of in situ climatic data in our study area.

Our results confirm tendencies observed in other studies to explain floristic patterns and need to be interpreted keeping in mind that variability in soil variables (and statistical likelihood) might depend on geographical distances between plots.

**Congruence between canopy and understory tree species**

Our results show a general congruence between tree categories. This is highlighted by the significant Mantel test between large trees and small trees s.s., suggesting that they are determined by common factors. We found that the categories all trees and small trees s.l. show rather similar spatial patterns, which may be explained by the fact that most individuals of the category small trees s.l. are juveniles of canopy species. This finding implies that segregating tree
understory individuals based solely on the criterion of diameter (i.e., without considering the species to which they belong) is not sufficient to explain differences between canopy trees and understory trees (Duque et al. 2002, but see Macía et al. 2007).

Despite the general congruence observed, several differences are put forward in the floristic determinants of large trees and small trees s.s. First, large trees floristic patterns were explained more by environmental variables and small trees s.s. floristic patterns by geographical distances. Second, available phosphorus was significant only for small trees s.s. As phosphorus is principally present at top 30 cm soil depth, it is possible that phosphorus acquisition is more efficient for understory species than for canopy species (Liu et al. 2010), e.g. through differences in the root system or different seed sizes (e.g. Hanley et al. 2007). Third, the NMDS ordination for small trees s.s. show a different spatial pattern than for each of the other tree categories. Fourth, the R2 in variables selection for small trees s.s. was the lowest, and the results were qualitatively different as different variables were selected. The differences observed between large trees and small trees s.s., however, could be due to a large extent to sample size, since small trees s.s. contained less individuals than the other categories (see also Macía et al. 2007). This contrasts with the study of Jones et al. (2008b) who focused on Pteridophytes with a larger numbers of herbaceous individuals. Although we agree with Macía et al. (2007), who emphasize that the small sample size of small trees s.s. is probably responsible for the patterns observed, our study is consistent with the results of Paoli et al. (2006) who found an increasing importance of niche processes when increasing tree diameter class. One explanation for the significance of edaphic conditions on large trees is that geographical distances influence juvenile distribution through dispersion, and then edaphic conditions limit growth and select juveniles. For small trees s.s., these mechanisms are probably not involved, since the individuals measured in this group are potentially adults. Why the distribution of understory trees depends more on environmental factors than does that of large trees should be tested by studying species life history (e.g. physiological) traits, particularly their abilities to remove soil phosphorus.
Acknowledgements

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References


Chapter 3

Does tree alpha diversity in old-growth forests relate to acculturation among native Amazonians?

(co-authors: Ana Catarina Luz, Jaime Paneque-Gálvez, Manuel J. Macía, Martí Orta, Joan Pino, Victoria Reyes-García)

Abstract

The understanding of indigenous management practices and its association with biodiversity requires to address changes in indigenous’ way of life through the study of intracultural variation. This paper explores the relation between acculturation at village level among a Bolivian Amazonian indigenous group, the Tsimane’, and tree diversity surrounding their villages. We inventoried tree species in 55 0.1-ha plots in old-growth forests distributed in six villages and we interviewed 86 informants in the same villages to obtain diversity and acculturation values. We used multivariate models to relate diversity (Fisher’s Alpha index) and structure (tree density) to acculturation. We found an inverse U-shaped significant association between diversity and acculturation but no relation for forest structure. We hypothesize that acculturation constitute a cultural disturbance impacting tree diversity through modifications in traditional ecological knowledge and practices. We propose that management pathways used in old-growth forests are harmless enough no to affect forest structure.

Key words: Tsimane’, Bolivia, intracultural diversity, anthropogenic impact, biodiversity, rainforest
Introduction

The effects of local human populations on tropical biodiversity have generated much debate (Chazdon 2009). In the Amazon, there is growing evidence that the landscapes and biodiversity that we currently observe result not only from natural phenomena, but are also shaped by centuries of indigenous management (Denevan 1966, Heckenberger et al. 2003, Lombardo et al. 2011). Although in neotropical forests some researchers report only natural influences on forest composition (White and Hood 2004, Espinosa et al. 2011), the effects of past human disturbances are often reflected in current forest vegetation (Chazdon 2003, Macía 2008). For example, anthropogenic black earths in central Amazonia are a key determinant of plant diversity, and result of intense pre-Colombian farming practices, including slash-and-burn agriculture (Willis et al. 2004, Freire 2007, Paz-Rivera and Putz 2009). Similarly, forest islands in lowland Bolivia have been shown to grow on ancient fields raised for agricultural purposes (Denevan 1966, Gullison et al. 1996, Lombardo and Prümers 2010).

Furthermore, researchers recognize that contemporary indigenous peoples living in small-scale societies have managed rain forest to keep a large forest cover, enhancing biodiversity (Garí 2001, Zent and Zent 2002). Probably, and in part as a consequence of this type of management, nowadays many indigenous territories overlap with areas of high biodiversity (Toledo 2001, Sunderlin et al. 2005).

The overlap between high biodiversity and native peoples’ management contrasts with the harmful effects of non-indigenous people on the same type of environment (Fearnside 2005, Armenteras 2006, Turton 2008). For example, while it has been argued that the slash-and-burn agricultural system, as practiced by small-scale societies, can lead to an increase in landscape biodiversity through the creation of a mosaic of different habitats (Peters 2000, Wiersum 2004), the large-scale shifting cultivation system, with increased plot size, or intensive agriculture practiced by non-indigenous peoples results in deforestation increase and a loss of biodiversity (Toledo et al. 2003, Donald 2004).

Although this general picture is largely accepted, the current trends in market integration and acculturation among Amazonian groups (Godoy et al. 2005a) has led some authors to question the current effects of indigenous peoples on biodiversity as
they adopt the modes and forms of Western society (Gross 1979, Henrich 1997, Reyes-García et al. 2010a). We define acculturation as the process by which a group of individuals progressively adopt the modes of another cultural group (Peterson 1991, Lu 2007, Thomson and Hoffmann-Goetz 2009). Acculturation processes are linked, but distinct to those of integration into market economy, as they do not refer only to an economic system (Byron 2003). Rather, acculturation encompasses a wide range of social and psychological changes (Caplan 2007) and includes processes that result in a loss of cultural distinctiveness by the acculturated group (Peterson 1991, Berry 2008). While integration to the market economy certainly affects forest management (Reyes-García et al. 2010a), it is probable that acculturation also relates to biodiversity, as it reflects deep cultural changes associated to management practices. In a review of the causes of deforestation, Geist and Lambin (2002) have underlined the role of cultural factors as an underlying factor leading to deforestation in tropical areas. However, most of the studies focus on the sociopolitical context rather than deep cultural changes, and to date, we know of no study that has addressed the effects on biodiversity of the process of acculturation of an indigenous society.

This study has two goals. First, we analyze the relation between the acculturation patterns of a native Amazonian society and tree diversity in old-growth forests surrounding their villages. We focus on tree diversity, since trees are the most important structural organisms of forests and provide a reliable estimation of overall biodiversity (Macía 2008). Second, we explore the pathways through which acculturation and tree diversity may be associated, and how these pathways relate to ecological processes. According to previous research, biodiversity is expected to decrease as the impact of acculturated indigenous people on the environment grows (Sunderlin et al. 2005, Reyes-García et al. 2007a). Therefore, we hypothesized that acculturation would be negatively associated to tree diversity in the forests managed by one village.

To our knowledge, the present study will be the first to empirically analyze the relation between acculturation within an indigenous group and tree diversity, measured through field quantitative inventories.
Materials and methods

Study area – The Tsimane’ and their lands

We conducted our research in the Tsimane’ territory, in the Amazonian province of Beni, Bolivia. The area extends in a densely forested region between the foothills of the Andes and the savannas of Moxos (14°10’– 15°40’S, 66°20’– 67°20’W). The Tsimane’ typically live within altitudinal ranges of 150-300m. Annual mean temperature is 25.8°C (Navarro and Maldonado 2002) and annual mean precipitation is 1743mm (Godoy et al. 2008). Climate shows a marked dry season of four months with less than 100mm of rainfall. Different broad forest types occur in the area; the most spread is a lowland forest lacking some typical Amazonian species, due to the rather high seasonality of climate, including sporadic strong cold winds from the south during the dry season. Most forests are terra firme forests, although some areas are covered with inundated or seasonally-flooded forests due to geomorphology and highly variable micro-topography. In many places of the Tsimane’ territory, precious woods such as mahogany (*Swietenia macrophylla*) have been selectively logged since the 1980s (Gullison et al. 1996).

The Tsimane’ are one of the largest ethnic groups in the Bolivian Amazon. As other Amazonian groups (Henrich 1997, Zent and Zent 2002), the Tsimane’ population is increasing, growing at an annual rate of 4.86% during 1971-2002 (Reyes-García 2001). The latest census estimated Tsimane’ population at around 8000 people (Censo Indígena 2001). They are traditional semi-nomadic hunters-gatherers and also practice slash-and-burn agriculture and fishing (Vadez et al. 2004). They also often sell or barter the leaves of a thatch palm, locally known as *jatata* (*Geonoma deversa*). The Tsimane’ used to live in households mainly along the Maniqui and Apere River and their tributaries, which represent the core area of their territory (Fig. 1), but recent changes have pushed them to aggregate in villages closer to communication axes, such as logging roads (Ringhofer 2010).

Tsimane’ villages present a strong gradient of acculturation as they experiment different levels of contact with outsiders. Several historical, social, and geographical factors (i.e. remoteness from main towns) have led to this gradient. First, cattle ranching in the open lands of the Tsimane’ territory (*pampas*) has been practiced for centuries,
but has intensified in the last decades (Jones 1980, 1991), thus influencing Tsimane’ life in villages close to pampas. Second, despite previous failures in evangelizing the Tsimane’, Christian missionaries have been present permanently in the area since the 1950s (Martinez-Rodriguez 2009). Despite their remote location, some missions, such as Misión Fátima (Fig. 1) have more contact with other sectors of the Bolivian society than surrounding villages. Third, after a reorganization of the Bolivian land tenure system by the government in the 1970s, several waves of Andean colonization have affected the Tsimane’ territory (Reyes-García 2001), a process that continues nowadays in spite of the recent acquisition of land rights by the Tsimane’. Andean colonists often illegally encroach on Tsimane’ lands for agriculture, cattle ranching or speculation. Fourth, nowadays traders reach the majority of Tsimane’ villages. The closest villages to market towns are visited on an almost daily basis whereas remote villages receive the eventual visit of traders on a monthly basis. In the remotest parts of the territory it is still common that traders deceive people into contracting debts. Fifth, selective logging activities have taken place even in the most remote Tsimane’ areas for decades since the region is an ecological optimum of mahogany in Bolivia (Navarro and Maldonado 2002). Nowadays, mahogany trees do not exist anymore in the area, and logging companies often employ Tsimane’ to extract some other valuable tree species mainly for construction purposes.

Today, in most remote villages people still practice traditional activities (e.g., subsistence slash-and-burn agriculture, hunting, and fishing with bow and arrow) and hold traditional beliefs. On the contrary, in villages closer to market towns, people typically work for logging companies, illegal loggers or cattle ranchers, and sell cash crops rather than practicing subsistence agriculture (Vadez et al. 2008). In these villages, people generally no longer hold traditional beliefs and taboos and tend to adopt outsiders’ beliefs and behaviors.

**Data collection**

**Village sampling**

We followed a purposive sampling strategy and selected six Tsimane’ villages on the basis of 1) homogeneity in their old-growth forest cover; 2) variability in the level of
acculturation and market integration; and 3) similar population size. Based on visual analysis of recent Landsat satellite images, we identified villages that displayed a continuous forest cover at rather small distance of the village, without large extents of natural pampas or pastures. Of these, we selected villages with different acculturation levels and similar population, based on a previous survey in 25 Tsimane’ villages (about 25% of the total number of Tsimane’ villages; Reyes-García et al. 2011). For each village, we calculated the average schooling (number of years) of male household heads and the average share of rice sold (out of total rice harvested) as proxies of acculturation and market integration (Godoy 1998). We ranked the villages according to the value of those indices and then selected a total of six villages. Two of them displayed a high average level of schooling and market integration, two an intermediate level, and two displayed low levels.

Ecological data

Between March – December 2009, we established 48 0.1-ha plots (50 × 20 m) in terra firme forests within the territory of six Tsimane’ villages (i.e., eight plots per village). We placed the plots in old-growth forests apparently not recently modified by human activity, at a minimum distance of 500m from the last agricultural field or fallow, and avoiding large canopy gaps. We retrieved the location of the centre of each plot using a hand-held GPS. All tree stems with a diameter at breast height (dbh) ≥ 2.5 cm were inventoried and voucher specimens were collected for all individuals that could not be fully identified. Duplicates of the vouchers are deposited in LPB and MA and unicates are kept in LPB.

To obtain edaphic variables, one composite superficial (0 – 15 cm) soil sample was collected in each plot. After being air-dried and 2-mm sieved, soil samples were analyzed for the following variables: pH in KCl, organic carbon, total nitrogen, available phosphorus, exchangeable cations (Ca, Mg, Na, K), exchangeable acidity (Al + H), and texture (sand, silt, and clay). Further details on soil analyses can be found in chapter 2 of this dissertation. We have no accurate data for rainfall, as the study area has only one meteorological station in the town of San Borja (see Fig. 1) and estimations of climatic variables yield highly auto-correlated data at the scale of our study (chapter 2), so rainfall variability is not included in our analysis.
We also obtained measures for plot disturbance, as disturbances are one of the main factors driving alpha diversity (Leigh et al. 2004, Nesheim et al. 2010). Thus, to capture the influence of logging on vegetal diversity, we estimated distances from each plot to logging areas and to the closest village (see further details in Reyes-García et al. 2011). We also measured the distance from the plot to the closest village. In addition, early-growth and degraded forest cover was used as a proxy for landscape heterogeneity. To calculate the proportion of these forests, we used the best land cover classification obtained by Paneque-Gálvez et al. (2011) for the year 2009, and applied a 6-km circular buffer (including all the inventoried plots) to the centre of each of the six villages surveyed.

Social data

To collect data on acculturation, we surveyed each of the six Tsimane’ villages during field campaigns in 2008 – 2009. Upon arrival to a village we interviewed one authority (e.g., headman or professor) to get the general characteristics of the village, such as actual number of households and number of people. Then, we interviewed 10 male household heads chosen at random, or 25 % of the household heads if the village had more than 40 families. A total of 86 informants were interviewed with an average of 14.3 interviews per village.

Individual interviews had two sections. First, we asked about general socio-economic characteristics of the person, such as schooling level, abilities in speaking Spanish – the national language –, and number of times the person visited the closest market-town. Second, to obtain an individual level of acculturation per se we presented to each subject nine questions about Tsimane’ habits, traditions, rituals, and beliefs. These questions encompass important features of the Tsimane’ culture (Huanca 2008) and constitute an especially-designed scale to measure individual self-perceived attachment to Tsimane’ traditional values (Table 3.1). To capture variability in this measure of acculturation, we presented to the subjects the picture of a five-step ladder with two poles: a “traditional” scene representing a Tsimane’ wearing traditional clothes in a traditional house and a “modern” scene representing Tsimane’ people in a town, using bicycles. We asked informants to position their finger on the grade of the scale corresponding to their perception (ranging from 0 to 4). For example, “Tsimane’
grandfathers used to work a lot in their fields, and modern Tsimane’ tend to prefer working for loggers. Where do you place yourself in the scale?” The direction of the ladder was randomized before the interview.

<table>
<thead>
<tr>
<th>Question</th>
<th>Topic</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>Importance of traditional cross-cousin union</td>
</tr>
<tr>
<td>2</td>
<td>Importance of traditional fishing using toxic plants</td>
</tr>
<tr>
<td>3</td>
<td>Importance of small-scale agriculture (versus nontraditional activities)</td>
</tr>
<tr>
<td>4</td>
<td>Importance of a belief concerning cassava sowing</td>
</tr>
<tr>
<td>5</td>
<td>Importance of a spiritual ritual before cutting big trees</td>
</tr>
<tr>
<td>6</td>
<td>Importance of a calendar ritual concerning the fruits of a palm (Bactris gasipaes)</td>
</tr>
<tr>
<td>7</td>
<td>Belief concerning bad luck brought by breaking a bow</td>
</tr>
<tr>
<td>8</td>
<td>Nature of medicines used in case of disease: plants versus allopathic medicines</td>
</tr>
<tr>
<td>9</td>
<td>Attitude towards outsiders: passivity versus conflict</td>
</tr>
</tbody>
</table>

Data analysis

To explore the relation between acculturation and forest tree diversity we used multiple linear regressions with our measure of tree diversity as outcome variable and our index of acculturation as main explanatory variable. Since the measure of diversity in one village is based on the average of eight 0.1-ha plots, analyzing the relation between acculturation and tree diversity at the village level with a correct number of villages would require inventories of hundreds of plots. Therefore, we did analyses at the plot level, repeating for each plot the values of average village acculturation.

We calculated our outcome variable, vegetal diversity, using plot data. Specifically, we calculated the Fisher’s Alpha diversity index of each plot, which provides a reliable estimation of the whole alpha diversity in plots (i.e., relates to species richness) and is not dependent on the plot size (Macía 2011). Fisher’s alpha calculations for each plot were done using R 2.12.0.

Our explanatory variable, acculturation, was constructed using data from the ladder questions. First, we summed the values of all questions to obtain an index for each individual ranging from 0 to 36, with 36 indicating the highest acculturation level. Then, for each village, we calculated the average value of acculturation.
Control variables to our regression model included 1) village-level variables, i.e., schooling and market integration, and 2) plot-level variables, i.e., edaphic variables and distances to human activities. All values of social variables were averaged at the village level as the mean of informants’ values, except for village size that was a single value per village. We used the amounts of total nitrogen and available phosphorus in the main models since they are two of the limiting edaphic factors for plant growth and have shown an association with alpha diversity in the Amazon (Laurance et al. 2010).

Regressions were run for Fisher’s alpha in the 48 plots (outcome variable), using repeated village average values of explanatory and control variables. A scatterplot of Fisher’s Alpha versus acculturation showed a polynomial shape; therefore the main models were run with a quadratic term of acculturation using Ordinary Least Squares (OLS) regressions with robust standard errors, clustered by village. All regressions were performed using Stata 11.1.

Results

Table 2 shows descriptive statistics of the variables used in the analyses. Mean Fisher’s Alpha index in the 48 plots was 24.69, displaying great variation within and across villages. For example, the maximum Fisher’s Alpha value was observed for a plot in Uvasichi (α=44.30), but one plot in the same village had one of the lowest values of all plots (α=15.98). The lowest mean Fisher’s Alpha values were found in plots placed around the village of Triunfo (17.58 ± 1.21).
Table 3.2. Definition and descriptive statistics of the variables used in the regression analysis.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>N</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Outcome variables (plots’ attributes)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fisher’s Alpha index</td>
<td>Fisher’s logseries index</td>
<td>48</td>
<td>24.69</td>
<td>7.88</td>
</tr>
<tr>
<td>Shannon</td>
<td>Shannon index</td>
<td>48</td>
<td>3.31</td>
<td>0.33</td>
</tr>
<tr>
<td>Basal area</td>
<td>Overall basal area of all tree species per plot (sqm ha⁻¹)</td>
<td>48</td>
<td>47.65</td>
<td>13.89</td>
</tr>
<tr>
<td>Tree density</td>
<td>Number of trees (diameter ≥ 2.5 cm) per plot</td>
<td>48</td>
<td>175.6</td>
<td>33.8</td>
</tr>
<tr>
<td><strong>Explanatory variable (villages’ attribute)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acculturation</td>
<td>Village average acculturation level, measured with an index that ranges from 0 (minimum acculturation) to 36 (maximum acculturation). Index calculated based on the answers of 86 informants</td>
<td>6</td>
<td>9.69</td>
<td>5.13</td>
</tr>
<tr>
<td><strong>Control variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot-level (edaphic)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C/N</td>
<td>Ratio between total organic carbon and total nitrogen content of the plot</td>
<td>48</td>
<td>9.17</td>
<td>2.73</td>
</tr>
<tr>
<td>N</td>
<td>Total nitrogen content (%)</td>
<td>48</td>
<td>0.14</td>
<td>0.06</td>
</tr>
<tr>
<td>P</td>
<td>Available phosphorus content (mg kg⁻¹)</td>
<td>48</td>
<td>5.84</td>
<td>3.86</td>
</tr>
<tr>
<td>Sand</td>
<td>Sand proportion (%) in a three-fraction texture (sand, silt, and clay)</td>
<td>48</td>
<td>35.02</td>
<td>19.51</td>
</tr>
<tr>
<td>Sum of cations</td>
<td>Sum of exchangeable calcium, magnesium, sodium and potassium (cmolc kg⁻¹)</td>
<td>48</td>
<td>6.96</td>
<td>4.03</td>
</tr>
<tr>
<td>pH</td>
<td>Soil acidity measured with pH</td>
<td>48</td>
<td>4.38</td>
<td>0.60</td>
</tr>
<tr>
<td><strong>Plot-level (geographic)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance to logging</td>
<td>Linear distance from the plot to the closest currently used or recently abandoned logging camp (km)</td>
<td>48</td>
<td>1.49</td>
<td>0.89</td>
</tr>
<tr>
<td>Distance to village</td>
<td>Linear distance from the plot to the closest Tsimane’ village (km)</td>
<td>48</td>
<td>2.71</td>
<td>1.06</td>
</tr>
<tr>
<td><strong>Village-level</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Village size</td>
<td>Number of households in the village</td>
<td>6</td>
<td>47.83</td>
<td>21.63</td>
</tr>
<tr>
<td>Schooling</td>
<td>Average of the highest school grade reached by the surveyed individuals of each village (ranges from 0 to 13). Average of the answers of 86 people</td>
<td>6</td>
<td>2.51</td>
<td>2.91</td>
</tr>
<tr>
<td>Travel to market</td>
<td>Average number of times informants traveled to the closest market town in the 12 months before the interview. Average of the answers of 86 people</td>
<td>6</td>
<td>9.53</td>
<td>11.70</td>
</tr>
<tr>
<td>Early-growth and degraded forest cover</td>
<td>Percentage of early-growth and degraded forest (including early-growth secondary forest, small agricultural plots with fruit trees and remnant scattered trees, and selectively logged forest areas) in a 6-km radius around the village</td>
<td>6</td>
<td>14.99</td>
<td>9.43</td>
</tr>
</tbody>
</table>

Mean value of acculturation for all villages was 9.69 (± 5.13), which is rather low on the scale we defined (0 to 36). There were differences in the range of individual acculturation values within each village. For example, acculturation values in the village of Misión Fátima ranged from 3 to 25 (the highest value in our sample), but in the village of Cuchisama only ranged from 0 to 11.

To give a more intuitive explanation of the values of acculturation, the village with the highest level of acculturation, Triunfo, is about 40km away from the closest market...
town, but is only 12km away from a major national road (Fig. 1), and one out of three interviewed subjects is fluent in Spanish. In turn, the village with the lowest level of acculturation, Cuchisama, is about 123km away from the closest market town, is accessible only by canoe, and has no fluent Spanish speakers.

Figure 3.1 offers a visual representation of the Fisher’s Alpha index ranked by average acculturation value, which resembles an inverted U. Fisher’s Alpha increases when acculturation increases, reaching a maximum in the village of Uvasichi; beyond this maximum Fisher’s Alpha decreases while acculturation increases.

![Figure 3.1](image)

**Figure 3.1.** Boxplot of Fisher’s Alpha index in six Tsimane’ villages, ranked by the acculturation level (from left to right, increasing acculturation).

Table 3.3 shows the results of the multivariate regressions for Fisher’s Alpha. The different columns in Table 3.3 include different sets of controls in different regressions because of our small sample size. In column [1] we included only edaphic control variables, in column [2] only geographic control variables, and in column [3] only village-level control variables. In column [4] we included one edaphic (nitrogen amount), one geographic (distance to village), and one village-level control variable (degraded forest cover). The main result of Table 3.3 is that Fisher’s Alpha index in plots
in the village commons is significantly associated with a quadratic term of the average level of acculturation in a village. The coefficients in column [4] imply that if the average level of acculturation in a village increased there would be an increase in the Fisher’s Alpha of plots around that village. The increase, however, would reach an inflexion point for an average acculturation value of 8.84. Only one village has an acculturation value below 8.84 (Cuchisama). Beyond this inflexion point, an increase of the average level of acculturation would be associated with a decrease in Fisher’s Alpha. The relation between Fisher’s Alpha and acculturation remains robust independently of the controls used in the model.

Table 3.3. Multivariate OLS regression results between Fisher’s Alpha in 0.1-ha plots (outcome), acculturation (explanatory), and control variables in Tsimane’ villages, Bolivian Amazon (N=48).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Acculturation</td>
<td>20.64*</td>
<td>29.29*</td>
<td>16.31***</td>
<td>21.04*</td>
</tr>
<tr>
<td></td>
<td>(7.86)</td>
<td>(9.78)</td>
<td>(0.00)</td>
<td>(7.03)</td>
</tr>
<tr>
<td>Acculturation²</td>
<td>-1.12*</td>
<td>-1.62*</td>
<td>-0.91***</td>
<td>-1.19*</td>
</tr>
<tr>
<td></td>
<td>(0.43)</td>
<td>(0.56)</td>
<td>(0.00)</td>
<td>(0.41)</td>
</tr>
<tr>
<td>Plot-level controls (edaphic)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>-29.61</td>
<td>^</td>
<td>^</td>
<td>-29.27</td>
</tr>
<tr>
<td></td>
<td>(23.57)</td>
<td></td>
<td></td>
<td>(15.97)</td>
</tr>
<tr>
<td>P</td>
<td>-0.04</td>
<td>^</td>
<td>^</td>
<td>^</td>
</tr>
<tr>
<td></td>
<td>(0.36)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot-level controls (geographic)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance to village</td>
<td>^</td>
<td>0.0003</td>
<td>^</td>
<td>0.0007</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.001)</td>
<td></td>
<td>(0.0009)</td>
</tr>
<tr>
<td>Distance to logging</td>
<td>^</td>
<td>^</td>
<td></td>
<td>^</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-0.001</td>
<td></td>
<td>^</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Village-level controls</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early-growth and degraded forest</td>
<td>^</td>
<td>^</td>
<td>0.50***</td>
<td>0.17 (0.17)</td>
</tr>
<tr>
<td>cover</td>
<td></td>
<td></td>
<td>(0.00)</td>
<td></td>
</tr>
<tr>
<td>Travel to market</td>
<td>^</td>
<td>^</td>
<td>-1.12***</td>
<td>^</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.00)</td>
<td>^</td>
</tr>
<tr>
<td>Village size</td>
<td>^</td>
<td>^</td>
<td>-0.08***</td>
<td>^</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.00)</td>
<td>^</td>
</tr>
<tr>
<td>Constant</td>
<td>-63.04</td>
<td>-101.83</td>
<td>-38.49***</td>
<td>-65.20</td>
</tr>
<tr>
<td></td>
<td>(34.32)</td>
<td>(42.11)</td>
<td>(0.00)</td>
<td>(29.75)</td>
</tr>
<tr>
<td>R²</td>
<td>0.23**</td>
<td>0.23</td>
<td>0.34</td>
<td>0.26**</td>
</tr>
</tbody>
</table>

Notes: Robust standard errors with clustering by villages in parenthesis. Significance levels: *=5%; **=1% and ***=0.1%. ^= variables intentionally left out.
In Table 3.4 we performed other regressions to test for the robustness of the results presented in Table 3.3. These robustness regressions were similar to the main models. In column [1] we included the C/N ratio and the sum of cations, and in column [2] we included the sand amount and the pH as edaphic control variables. In column [3], we used average village schooling rather than average acculturation as a proxy for acculturation and main explanatory variable. From columns [4] to [6], we used different measures of forest tree diversity and structure, i.e. Shannon index (column [4]), overall basal area (column [5]) and tree density (columns [6]).

Table 3.4. Robustness analysis: multivariate OLS regression results between diversity and structure measured as different indices (dependent variables) and environmental and cultural variables.

<table>
<thead>
<tr>
<th>Outcome variable</th>
<th>Same models with other edaphic controls</th>
<th>Other proxy of acculturation</th>
<th>Other proxies of biodiversity and forest structure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Explanatory</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acculturation</td>
<td>22.19** (4.51)</td>
<td>26.03* (7.52)</td>
<td>^</td>
</tr>
<tr>
<td>Acculturation²</td>
<td>-1.19** (0.26)</td>
<td>-1.41* (0.43)</td>
<td>^</td>
</tr>
<tr>
<td>Schooling</td>
<td>^</td>
<td>-12.72 (8.22)</td>
<td>^</td>
</tr>
<tr>
<td>Schooling²</td>
<td>^</td>
<td>3.15 (1.90)</td>
<td>^</td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C/N</td>
<td>0.02 (0.51)</td>
<td>^</td>
<td>^</td>
</tr>
<tr>
<td>Sum of cations</td>
<td>-0.56 (0.26)</td>
<td>^</td>
<td>^</td>
</tr>
<tr>
<td>Sand</td>
<td>^</td>
<td>0.07 (0.08)</td>
<td>^</td>
</tr>
<tr>
<td>pH</td>
<td>^</td>
<td>-0.46 (1.22)</td>
<td>^</td>
</tr>
<tr>
<td>N</td>
<td>^</td>
<td>^</td>
<td>-51.07* (13.41)</td>
</tr>
<tr>
<td>Distance to</td>
<td>^</td>
<td>^</td>
<td>0.0009 (0.007)</td>
</tr>
<tr>
<td>village</td>
<td>^</td>
<td>^</td>
<td></td>
</tr>
<tr>
<td>Degraded forest</td>
<td>^</td>
<td>^</td>
<td>0.006* (0.003)</td>
</tr>
<tr>
<td>cover</td>
<td>^</td>
<td>^</td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>-71.53* (20.16)</td>
<td>-92.80* (33.06)</td>
<td>32.01*** (4.07)</td>
</tr>
<tr>
<td>R²</td>
<td>0.27** (no P value)</td>
<td>0.23* (no P value)</td>
<td>0.28 (no P value)</td>
</tr>
</tbody>
</table>

Notes: Robust standard errors with clustering by village in parenthesis. N=48. Significance levels: *=5%; **=1% and ***=0.1%. ^ = variables intentionally left out.
Robustness regressions in Table 3.4 provide three main results. First, the relation between Fisher’s Alpha and acculturation is robust to changes in the controls for edaphic conditions. In the two models with different edaphic controls, Fisher’s Alpha remains significantly associated with acculturation (columns [1] and [2]). Second, Fisher’s Alpha is not significantly associated with acculturation when acculturation is proxied by the average level of schooling in a village (column [3]). Third, acculturation is associated with diversity indices but not with proxies of forest structure. A model using Shannon index as the outcome variable yielded a significant association with a quadratic term of acculturation (column [4]). In turn, the two models using proxies of forest structure (basal area and total tree density) as the outcome variables yielded no significant association with acculturation.

Discussion

Caveats: challenges to relate human individual factors and biodiversity

The main caveat of the present study relates to the dissimilar samplings of ecological and social variables. These dissimilar samplings reflect the challenge to relate individual acculturation measures to measures of biodiversity in a forest that is commonly managed. Since –for an area commonly managed– it does not make sense to measure the individual effects on biodiversity, the analysis should ideally be done at the village level. However, obtaining a reliable measure of tree diversity in one village requires a great sampling effort. Therefore, we based our regression analyses at the plot level, although we acknowledge a lack of statistical power and a simplification of the acculturation process. Moreover, it is challenging to estimate tree diversity of a region with only 0.8 hectares per village or study site (Macía 2008, Sheil 2010). A partial solution to this is to use a less time-consuming proxy of diversity, e.g. using indicator species or families, as suggested by Ruokolainen et al. (2007).

Another important caveat of our study relates to the distinction between acculturation and market integration. As mentioned in the introduction, those two processes are different but linked (Godoy et al. 2005b). Data obtained in this study does not allow testing the separate effects of market integration on biodiversity, and it is
possible that, to some extent, our measure of acculturation reflects market integration as well. Moreover, it is possible that our control variable capturing market integration (frequency of travel to market town) fails to reflect real economic changes. Therefore, the data presented here does not allow us to run out the possibility that market integration is more strongly associated to tree alpha diversity than acculturation, and that our measure of acculturation does in fact reflect integration into market economy.

A further limitation of this study is our lack of control for biogeographical influences that could have occurred in the area. Fisher's Alpha is dependent on the region studied, particularly regional species richness (ter Steege et al. 2000, Leigh et al. 2004). Since the Tsimane’ territory is situated at the transition between three biogeographical regions (Navarro and Maldonado 2002), the villages in which we inventoried forest plots could display different levels of overall species richness. Then, the relation between alpha diversity and acculturation might disappear once controlling for these potential biogeographical differences across villages. For example, it is possible that the high values of Fisher's Alpha observed in Uvasichi or Misión Fátima (Fig. 1) are due to higher values of overall species richness in these areas.

**Acculturation, management practices and tree diversity**

We found a statistically significant association between acculturation and tree species richness proxied by Fisher's Alpha index. The relation is significant independently of other factors, particularly living in a larger village or travelling more to market towns. In other words, our results suggest that the degree by which people feel attached to Tsimane’ traditional values across villages relates to tree alpha diversity in the forest surrounding the village where they live. Furthermore, we found that the average education level of people in a village is not significantly associated with Fisher's Alpha, suggesting that what is associated to alpha diversity is specifically acculturation, rather than formal schooling. Although schooling has been reported to be a measure of acculturation (Godoy et al. 2005b), it is possible that it does not capture profound changes in the Tsimane’ life and thus does not relate to practices involved in managing the forest. In a study among Mexican Americans, Graham (1985) underlined that schooling is an acculturating factor particularly if classes take place outside the culture;
in Tsimane’ villages in turn, classes are often bilingual and given by Tsimane’ teachers. Reyes-García et al. (2010b) found that, due to this school contextualization among the Tsimane’, schooling was weakly associated with a loss of knowledge.

This finding opens up the interesting question of the pathways that explain how acculturation might be related to biodiversity. We offer explanations of two pathways.

First, tree diversity might be affected by management practices. Practices are one of the three components of traditional ecological knowledge (TEK), forming a knowledge – practice – belief complex (Berkes 1999). Acculturation may affect the three components of this system. For example, in a study among the Tsimane’, Reyes-García et al. (2007b) have found that acculturation affects ethnobotanical skills, which in turn is associated with deforestation (Reyes-García et al. 2007a). Therefore, acculturation might also likely affect management practices that would have an impact on tree diversity.

Second, taboos and rituals are strong social mechanisms that govern traditional management practices and behaviors (Berkes et al. 2000). As Tsimane’ engage in activities with outsiders, such as loggers or cattle ranchers, they are more exposed to different ideas and values from the Bolivian society. Examples of how acculturation may affect beliefs in a way that might end up affecting tree diversity can be found in the ethnographic context of the Tsimane’. We provide two examples. First, the Tsimane’ used to pray the spirit inhabiting big trees before cutting them, to keep the spirit peaceful. The Tsimane’ believe that failure to do so would result in illness (Huanca 1999). Acculturation and contact with non-Tsimane’, who do not pray the trees, might have induced the idea on the Tsimane’ that there is no real relation between cutting trees and praying, which would ease the logging practiced by Tsimane’ people, resulting in a change in tree diversity. Second, Tsimane’ sacred groves are areas of the forest that remain untouched, and often unvisited, due to the presence of spirits. Due to contact with outsiders, some Tsimane’ no longer fear spirits inhabiting sacred groves, resulting in the modification of management practices. Some sacred groves directly relate to tree diversity as they are often taboo trees (Wiersum 1997); emergent tree species such as vojshina (Ceiba pentandra) or cotison (Terminalia oblonga) were protected because they were the shelter of masters (Huanca 1999). Berkes (2001) stresses that a high biodiversity is often found in sacred groves. It seems likely that changes in these beliefs
due to acculturation, would affect tree diversity through the way sacred groves are managed.

**Can acculturation relate to disturbance?**

We found an inverse U-shaped relation between Fisher's Alpha and acculturation. Although the finding does not confirm our hypothesis of a linear relation, it finds support in the intermediate disturbance hypothesis (IDH), which relates to the levels of species richness observed in ecosystems. According to the IDH, intermediate levels of disturbance, either in intensity, frequency or time of recovery after disturbance, allow the cohabitation of several guilds of species, i.e. both pioneer and shade-tolerant, which increases species richness or diversity in the system (Connell 1978, Molino and Sabatier 2001, Shea et al. 2004). Intermediately-disturbed systems are then more species-rich than few- or highly-disturbed systems.

Anthropogenic disturbances are an important type of disturbance, modeling most current ecosystems (e.g. Kessler 2001). Balée (2006) proposed that indigenous management, through burning, settlement, or tree cultivation, generates intermediate disturbance levels with respect to the gradient between no management and “industrial” management systems. Our results suggest that this hypothesis is even applicable at a lower scale of analysis, i.e., within a cultural system. We suggest that changes in indigenous management as a result of acculturation modify old-growth forests by increasing the level of disturbance, and thus modify species richness. In intermediately acculturated villages, the co-occurrence of several guilds of species would increase species richness. In not very acculturated villages, anthropogenic disturbance is too weak to result in this co-occurrence, whereas in much acculturated villages, species richness decreases with acculturation, suggesting that the management becomes closer to a non-indigenous management type.

This effect of intracultural variation on diversity finds support in two studies. Lefevre et al. (2011) showed that even low-level human disturbances can have an impact on plant and bird communities. Moreover, Bongers et al. (2009) have reported that in forests with semi-deciduous canopy, as in our study, the level of disturbance required to make diversity peak is lower than in evergreen forests. These two studies
provide arguments for the likelihood of a subtle, small-scale intracultural relation between humans and biodiversity.

Our regression models show that degraded forest cover (early successional stages) does not affect the relation between Fisher’s Alpha and acculturation. Therefore, if the IDH applies to our system, it is not through the influence of landscape heterogeneity on undisturbed forest, but rather by non-destructive modification of the forest itself. Moreover, our results show that variables capturing forest structure are not significantly associated with acculturation, contrary to proxies for tree diversity. This suggests that the changes in alpha diversity as a result of acculturation are subtle enough to affect only species richness, but not forest structure (Wiersum 2004). Our inventoried forests, then, would fit one of the transitional systems between natural forests and agroforests defined by Wiersum (2004). An explanation of this result can be found in the way people manage the forest (Wiersum 1997). As other indigenous groups, the Tsimane’ might modify species richness through a management that does not affect structure but rather seed dispersion, e.g. through enrichment planting (Peña-Claros et al. 2002), or management of non-timber forest products (Takasaki et al. 2001, Lawrence et al. 2005, Byg et al. 2007). It is also possible that different levels of hunting pressure affect dispersion of animal-dispersed species seeds (Bennett and Robinson 2000).

The present study helps improving our understanding of how biodiversity is shaped both by human and ecological factors (Byg et al. 2007) and of how acculturation of indigenous peoples relates to changes on ecological processes (Lu 2007). The results of this study also provide important insights for the debate on indigenous management and biocultural diversity conservation (Smith and Wishnie 2000, Hames 2007), especially in regions where biodiversity peaks, like western Amazonia. Our data suggest that intermediately acculturated indigenous villages, through different levels of indigenous management, enhance tree diversity, likely by allowing cohabitation of different taxa adapted to different levels of disturbance. Since community-based managed areas seem to have a great potential for biocultural diversity conservation, and since indigenous people fail to obtain land rights over many developing countries, our results are important in order to take into account both human and ecological factors.
when delimiting protection areas. Managed forests, until a certain threshold, seem to be a viable strategy to support biodiversity conservation.

Acknowledgements

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References


Chapter 4

Does ecological importance of tree species relate to their usefulness? A case study from the Tsimane’, Bolivian Amazon

(co-authors: Ana Catarina Luz, Jaime Paneque-Gálvez, Manuel J. Macía, Martí Orta, Joan Pino, and Victoria Reyes-García)

Abstract

Researchers have recently argued that local people use more the most apparent plant species, particularly medicinal species; however the patterns of association between ecological importance of the species and their usefulness remain unclear. Here, we quantify this association for six use categories (firewood, canoe construction, house building, edible, medicinal and other uses) in the Tsimane’ territory, Bolivian Amazon. We collected data of uses of 58 tree species, reported by 93 informants in 22 villages, and we matched these data to ecological importance of the species calculated by their importance value index (IVI) in 55 0.1-ha plots established in old-growth forests. We found a positive relation between the IVI of the species and their overall use value (UV), as well as with their UV for house building and other uses. We found a negative relation between IVI and UV for medicinal and edible uses, and no clear pattern for the other categories. We discuss the differences observed according to the substitutability of the species involved.

Key words: importance value index (IVI), use value (UV), species visibility, indigenous, rainforest
Introduction

The ethnobotanical knowledge of people living in tropical rainforests has been increasingly well-documented in the last decades (Bennett 1992, Albuquerque and Lucena 2005). However, little is known about why people use some species more than others, and particularly whether distribution patterns of species relate to patterns of use. To address this question, ethnobotanists have applied the ecological apparency hypothesis to study plant uses (Phillips and Gentry 1993a, 1993b; Lucena et al. 2007). The hypothesis, first developed to explain the relation plants-herbivores, considers that the visibility of the plant, together with its chemical composition, will influence herbivores’ behaviour. When the hypothesis is applied to humans as consumers, it is expected that most apparent species (i.e. most frequent and abundant) will have more uses (use value, sensu Phillips and Gentry 1993a) because they are readily available.

Some studies have tested this hypothesis, relating human uses to species apparency proxied by different ecological measures. For example, some authors have related the overall use value of the species to their density, dominance, and frequency (Phillips and Gentry 1993b, Galeano 2000, Lawrence et al. 2005) or to the importance value index (IVI) of the species (Torre-Cuadros and Islebe 2003, Lucena et al. 2007, Thomas et al. 2009a). Particularly, the IVI of a species seems to be a good indicator of apparency, because it provides data of basal area, abundances and therefore to the salience of the species (Thomas et al. 2009a). Other studies have related use value to length in the case of lianas (Paz y Miño et al. 1995) or to the accessibility of plant communities (Thomas et al. 2009b). In all these studies, the visibility of the species tends to be positively associated to its number of uses, thus giving support to the ecological apparency hypothesis.

Focusing on medicinal uses and based on the frequency of species collection by botanists, Berlin (2003) found that among Highland Mayas in Mexico, common species are more commonly used as medicines than rare species. Stepp and Moerman (2001) have stressed that weeds, i.e., common species, are the most frequently found life form in the pharmacopeia of the Mayas, since people implicitly look for highly bioactive compounds, commonly found in weeds. Voeks (2004) also reports the importance of secondary vegetation for traditional
medicines. Findings from these studies are important for ethnopharmacological research because they challenge the traditional understanding that people obtain medicinal species from “unique and inaccessible habitats of tropical rain forests” (Berlin 2003, p. 2). However, these studies are not based on ecological inventories.

Results from studies measuring ecological apparency based on inventories in natural vegetation, yield ambiguous results. For example, studies among rural people in caatinga vegetation in Brazil, found a negative association between medicinal importance (an index related to use value) and density and frequency of the species (Silva and Albuquerque 2005), whereas others found a positive association between medicinal use values and frequency of the species in the same environment (Lucena et al. 2007). A study among indigenous groups of Bolivia found a positive correlation between medicinal use values and the IVI of the species (Thomas et al. 2009a), whereas a study among mestizos in the Peruvian Amazon reported no association between medicinal use values and density, dominance or frequency of the species (Phillips and Gentry 1993b).

The overall objective of this study is to analyze the relation between tree species’ usefulness and their ecological importance in the territory used by a lowland Bolivian indigenous group, the Tsimane’. Specifically, our goals are to 1) describe the association between the usefulness of a species, proxied by its use value, and its importance value index, and to 2) analyze different patterns of association across different uses. As predicted by the ecological apparency hypothesis, we expect that the higher the IVI of a species, the more uses it has. The ecological importance of a species could drive its number of uses because people have different opportunities to learn about visible species.

Materials and methods

The Tsimane’: lands and knowledge

The Tsimane’ are one of the largest ethnic groups in the lowlands of Bolivia (Censo Indígena 2001). Their territory lies between the foothills of the Andes and an extent area of flooded savannas, the Moxos savannas (Fig. 1). Annual mean temperature is 25.8ºC (Navarro and Maldonado 2002) and annual mean
precipitation is 1743mm (Godoy et al. 2008). There is an important inter-annual climatic variation due to El Niño events. Climate presents a strong seasonality with four months with less than 100mm rainfall and the presence of episodic southern cold winds. Soils are quaternary alluvial sediments of fluvial origin, mostly acrisols and ferralsols (Navarro and Maldonado 2002).

The territory of the Tsimane’ is situated at the interface between three biogeographic regions: Amazonia, Andes, and Brazilian-Paraná. Most of the territory is covered with well-drained upland terra firme rainforest. In some places, different types of flooded forests occur according to the history of inundation. The north-eastern part of the territory coincides with the edge of the Moxos savannas, with gallery forests and forest islands that seem to have an anthropogenic origin (Denevan 1966, Lombardo et al. 2011).

Traditionally, the Tsimane’ were semi-nomadic hunters-gatherers who practiced slash and burn agriculture. They have deep traditional knowledge of wild plants. For example, Reyes-García (2001) reported uses of 410 plant species. Traditional ecological knowledge (TEK) is also strongly shared by all the community members (Reyes-García et al. 2003). Tsimane’ villages are settled in different ecosystems, such as savannas or partially flooded forests, and people from distant villages have different levels of knowledge (Reyes-García et al. 2005). In the present study we focus on villages settled within large extents of terra firme forests. TEK has important consequences for Tsimane’ daily life, as higher TEK is associated with less deforestation and more diversity in agricultural fields (Reyes-García et al. 2007a, 2008). Nowadays, although they still rely greatly on forest resources for their livelihood, the Tsimane’ experience different levels of integration to the market economy, acculturation, and encroachment, which in turn affect their knowledge and their use of the forest (Reyes-García et al. 2007b). Activities that drive Tsimane’ to leave their village are associated with a lower TEK whereas activities that keep them in the forest contribute to the maintenance of this form of knowledge (Reyes-García et al. 2007b).

Data collection

Since we want to study the relationship between species usefulness and ecological importance, our data collection strategy includes methods that come
from cultural anthropology and methods that come from ecology. The analysis focuses on trees (including palms) because they are well-known for most Tsimane' and some species are known for an only local name (see below, personal observation).

_Ecological data_

To obtain ecological importance values we established 48 0.1-ha plots in the territory of six Tsimane’ villages (eight plots per village) (Fig. 4.1). We selected villages on the basis of homogeneity in 1) forest types and topography, visually analyzing Landscape images and 2) village characteristics, such as the number of households. We used data obtained from an ecological description of the forest with edaphic factors (see chapters 1 and 2). Within each village, we established plots in old-growth _terra firme_ forest with no apparent sign of recent human activities, at a minimal distance of 500 meters from any agricultural field or fallow, and avoiding large canopy gaps. In each plot, we inventoried all trees with a diameter at breast height (dbh) ≥ 2.5cm. We counted multiple stems rooting in the same place as one individual. We measured the dbh of each individual, at 1.30m from the ground. Palms were also included in the analyses because they are among the most useful species (Macía et al. 2011) and ecologically resemble trees, although they are not properly. We collected voucher specimens for all individuals that could not be identified in the field. Duplicates of the vouchers are deposited in LPB (Herbario Nacional de Bolivia, La Paz) and MA (Real Jardín Botánico, Madrid, Spain) and unicates are kept in LPB.

From all tree species inventoried, we selected 58 useful species following these criteria: 1) usefulness of the plant reported by at least two local guides while measuring trees in plots, and 2) unique correspondence between the local name and the scientific name of the species, based both on the names reported by local guides and on two databases on Tsimane’ ethnobotany (Huanca 1999, Reyes-García 2001).
Figure 4.1. Map of the study area, showing the 6 inventoried villages along with the buffer areas, including 22 villages where data of plant uses were collected (green lines).
Cultural data

After plot inventories and during ex situ interviews we collected data on tree species uses using local names. Specifically, we gathered ethnobotanical information of the 58 selected tree species in 22 Tsimane' villages displaying relatively similar ecological characteristics. In each village, we asked participants to identify the two men and two women most knowledgeable about plant uses. Since some villages are small and our survey was only conducted with the consent of the people, in some of them we could not obtain four expert informants, whereas in other villages we were able to survey more than four.

To keep the interviews to a reasonable duration, we randomly split the list of 58 species into two lists of the same length. In each village we used one list to interview half of the informants (one man and one woman when possible) and the other list to interview the rest of the informants. The interview consisted of asking each informant “Do you know the species X (local name of the species)?” “Can you tell me all the possible uses?” We wrote down verbatim all the uses reported by the informants.

Data analysis

To hunt, fish, and collect non-timber forest products, the Tsimane’ use the forest close to their houses, but also a large common territory, considered the territory of neighbouring villages. Therefore, the uses reported by respondents would reflect species’ ecological importance at landscape scale. To capture this extensive use of the territory, we defined buffer areas of forest around the six villages for which we had plot data to include the 22 villages where ethnobotanical data were gathered. Buffer areas included the closest villages to the inventoried plots (3-5 villages per buffer area; Fig. 4.1) and the distance between the centre of a village (school) and a plot ranged between 4.9 (±3.4) and 8.0 (±3.4) km.

The relation between usefulness and apparenty is specific for each of the species in one buffer area, but this might change across villages. Therefore, we chose tree species per buffer area as unit of analysis, relating the reported uses of one species in one buffer area to the ecological importance of this species in one buffer area. Thus, the same ethnobotanical information was not used several times.
To analyze this association, we use a multivariate model that explains the use value of a species (UV) as a function of its IVI per buffer area. We calculated the IVI of a species in the inventoried plots per buffer area, as the sum of its relative density, relative dominance, and relative frequency (Curtis & Macintosh 1951).

We defined the UV of a species as the average number of uses reported per plant per buffer area (Phillips and Gentry 1993a). We interviewed each informant once for each species. Then, we calculated the total UV regardless the category of use. Tsimane’ ethnobotanical knowledge has been shown to be mostly distributed in five representative use categories: canoe construction, firewood, edible, house building, and medicinal (Reyes-García 2001). Another category (“other uses”) was also considered to include uses, such as dye, hunting-fishing tools, or fishing toxins, with a reduced number of species in each case. We calculated the UV of the species for each of the six categories. We counted each single use reported, even if several uses were reported in the same category. For example, we counted all medicinal uses of a species mentioned, because the fact that a species has more medicinal uses is an indicator of its usefulness and could be related to its density or frequency.

We studied the relation between the total or categorical UV and the IVI of the species per buffer area using ordinary least square (OLS) regressions. When the outcome variable had more than 15% of zero values, we used tobit regressions. Both OLS and tobit models were run with robust standard errors and clustered by buffer area. We included two controls in the models: one set of dummies for buffer areas and one set of dummies for the life form of the species (large tree, small tree or palm). The dummies for buffer areas (not shown in the tables) capture fixed effects of the villages such as population size or proximity to towns. We attributed the life form of each species on the basis of diameter in plots, verifying reported life forms in Killeen et al (1993). Small trees, i.e., understory species, were defined as all the species that never reached 10cm dbh (referred as small trees sensu stricto in chapter 2). We performed all statistical analyses with Stata version 11 for Windows.
Results

We surveyed a total of 93 people, representing an average of 3.2 people per village. Overall, the average number of informants per species was 1.6 in each village, i.e. 35.2 responses per species in all the dataset.

On the 58 useful species, 33 had were ecologically important with an IVI>1 (Table 4.1). Several species showed both high IVI and UV values. The four most ecologically important species, *Iriartea deltoidea* (Arecaceae), *Hura crepitans* (Euphorbiaceae), *Poulsenia armata* (Moraceae), and *Socratea exorrhiza* (Arecaceae) showed a high UV. The three most useful species were *Attalea phalerata* (Arecaceae), *Swietenia macrophylla* (Meliaceae) and *Clarisia biflora* (Moraceae) but only this last species showed a high IVI. *A. phalerata* and *S. macrophylla* were some of the less ecologically important species.

Of the 58 species, 54 were used for firewood and 55 for other uses, whereas only 26 species were used for canoe. Some patterns arise when we examine the association between IVI and use values by categories. All the species that showed a higher UV for the house building category belonged to the Arecaceae family (e.g. *I. deltoidea, Astrocaryum murumuru*). The species with higher UV in the medicinal category had low IVI, indicating that medicinal species in our list were rare species (e.g. *Aniba canelilla, Galipea longiflora*). This tendency was also observed in a lesser extent for edible uses, whereas for firewood uses no tendency could be brought out. For canoe construction the most useful species had either high IVI (*H. crepitans, Otoba parvifolia*) or low IVI (*Cedrela odorata, Calophyllum brasiliensis, S. macrophylla*).
Table 4.1. Importance value index (IVI), and use value (UV) of 58 tree species used in six Tsimane' villages, Bolivian Amazon, ranked by average IVI. The five species with highest UV in each of the use categories are shown in bold.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Family</th>
<th>Tsimane' name</th>
<th>Mean IVI</th>
<th>UV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Food</td>
</tr>
<tr>
<td>All species mean</td>
<td></td>
<td></td>
<td>2.44</td>
<td>0.44</td>
</tr>
<tr>
<td>Iriartea deltoidea</td>
<td>Arecales</td>
<td>ojdo'</td>
<td>17.05</td>
<td>0.46</td>
</tr>
<tr>
<td>Hura crepitans L.</td>
<td>Euphorbiaceae</td>
<td>conofoto</td>
<td>13.80</td>
<td>0</td>
</tr>
<tr>
<td>Poulsenia armata</td>
<td>Moraceae</td>
<td>asha'ba</td>
<td>10.65</td>
<td>0.73</td>
</tr>
<tr>
<td>Socratea exorrhiza</td>
<td>Arecales</td>
<td>vijri</td>
<td>9.78</td>
<td>0</td>
</tr>
<tr>
<td>Leonia crassa L.B. Sm. &amp; A. Fernández</td>
<td>Violaceae</td>
<td>rojro</td>
<td>6.51</td>
<td>0.07</td>
</tr>
<tr>
<td>Otoba parvifolia</td>
<td>Myristicaceae</td>
<td>cam</td>
<td>5.35</td>
<td>0</td>
</tr>
<tr>
<td>Astrocaryum murumuru</td>
<td>Arecales</td>
<td>shibo'</td>
<td>4.90</td>
<td>0.49</td>
</tr>
<tr>
<td>Unonopsis floribunda</td>
<td>Annonaceae</td>
<td>veja</td>
<td>4.84</td>
<td>0</td>
</tr>
<tr>
<td>Celtis schippii Standl.</td>
<td>Ulmaceae</td>
<td>ñove</td>
<td>4.72</td>
<td>0</td>
</tr>
<tr>
<td>Clarisia racemosa Ruiz &amp; Pav.</td>
<td>Moraceae</td>
<td>vávaij</td>
<td>4.66</td>
<td>0</td>
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<td>Iryanthera juruensis</td>
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<tr>
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<td>0</td>
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<tr>
<td>Clarisia biflora Ruiz &amp; Pav.</td>
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<td>mu'suru</td>
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<td>0.88</td>
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<tr>
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<td>pî'serej</td>
<td>2.74</td>
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<td>Rheedia acuminata</td>
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<td>tsocon</td>
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<td>1.00</td>
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<tr>
<td>Rheedia gardneriana</td>
<td>Clusiaceae</td>
<td>ibijquie</td>
<td>2.68</td>
<td>0.96</td>
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<tr>
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<td>Clusiaceae</td>
<td>púñupuson</td>
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<td>0</td>
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<tr>
<td>Dipteryx odorata</td>
<td>Fabaceae</td>
<td>cojma</td>
<td>2.65</td>
<td>1.00</td>
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<td>Spondias momib L.</td>
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<td>moco'</td>
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<td>1.13</td>
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<tr>
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<td>na'fa</td>
<td>2.42</td>
<td>0.98</td>
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<tr>
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<td>viñaj</td>
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<td>1.04</td>
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<td>Siparuna bifida (Poeppig &amp; Endl.) A. DC.</td>
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<td>vatason</td>
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<td>0.03</td>
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<tr>
<td>Guarea gomma Pullu</td>
<td>Meliaceae</td>
<td>rosion</td>
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<td>0</td>
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<tr>
<td>Terminalia oblonga (Ruiz &amp; Pav.) Steudel</td>
<td>Combretaceae</td>
<td>cotison</td>
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<td>0</td>
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<tr>
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<td>Moraceae</td>
<td>movaij</td>
<td>1.79</td>
<td>1.00</td>
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<td>tayei</td>
<td>1.72</td>
<td>1.00</td>
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<td>cavaquis</td>
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<td>Elaeocarpaceae</td>
<td>shoshenera</td>
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<tr>
<td>Abuta grandifolia</td>
<td>Menispermaeae</td>
<td>odo' odo'</td>
<td>1.39</td>
<td>0.98</td>
</tr>
<tr>
<td>Scientific name</td>
<td>Family</td>
<td>Tsimane' name</td>
<td>Mean IVI</td>
<td>UV</td>
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<td>----------------------------------------------</td>
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<td>ajmo</td>
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<td>ji'iyi</td>
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<td>cop'o'tare</td>
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<td><strong>Attalea butyracea</strong> (Muts ex L. f.) Wess. Boer</td>
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<td>0</td>
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<td>shishibutuj</td>
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<td><strong>Borooja claviflor</strong> (K. Schum.) Cuatrec.</td>
<td>Rubiaceae</td>
<td>vuvi'ri</td>
<td>0.22</td>
<td>0</td>
</tr>
<tr>
<td><strong>Cedrela odorata</strong> L.</td>
<td>Meliaceae</td>
<td>sijamo</td>
<td>0.20</td>
<td>0</td>
</tr>
<tr>
<td><strong>Calophyllum brasiliense</strong> Cambess.</td>
<td>Clusiaceae</td>
<td>yàjdyâ' ìyâ</td>
<td>0.20</td>
<td>0</td>
</tr>
<tr>
<td><strong>Calophyllum spruceanum</strong> (Benth.)</td>
<td>Rubiaceae</td>
<td>tunenes</td>
<td>0.19</td>
<td>0</td>
</tr>
<tr>
<td><strong>Hoek f. ex Schumann</strong></td>
<td>Meliaceae</td>
<td>chura'</td>
<td>0.17</td>
<td>0</td>
</tr>
<tr>
<td><strong>Attalea phalerata</strong> Mart. ex Spreng</td>
<td>Areceae</td>
<td>mana'i</td>
<td>0.13</td>
<td>0</td>
</tr>
<tr>
<td><strong>Chrysophyllum venezuelanense</strong> (Pierre) Penn.</td>
<td>Sapotaceae</td>
<td>ejtere'</td>
<td>0.12</td>
<td>0</td>
</tr>
<tr>
<td><strong>Helicocarpus americanus</strong> L.</td>
<td>Tiliaceae</td>
<td>mu'</td>
<td>0.11</td>
<td>0</td>
</tr>
<tr>
<td><strong>Cariniana estrellensis</strong> (Raddi) Kunzke</td>
<td>Lecythidaceae</td>
<td>cocoma</td>
<td>0.08</td>
<td>0</td>
</tr>
<tr>
<td><strong>Protium aracuainchi</strong> (Aublet) Marchand</td>
<td>Burseraceae</td>
<td>vi'si</td>
<td>0.08</td>
<td>0</td>
</tr>
<tr>
<td><strong>Aniba canellia</strong> (H.B.K.) Mez</td>
<td>Lauraceae</td>
<td>chorecho</td>
<td>0.06</td>
<td>0</td>
</tr>
<tr>
<td><strong>Alphanes aculeata</strong> Willd.</td>
<td>Areceae</td>
<td>cajna</td>
<td>0.04</td>
<td>0</td>
</tr>
<tr>
<td><strong>Genipa americana</strong> L.</td>
<td>Rubiaceae</td>
<td>ty'i</td>
<td>0.04</td>
<td>0</td>
</tr>
</tbody>
</table>
There was a linear relation between the total UV of the species and their IVI (Fig. 4.2). However, outliers (*I. deltoidea* and *H. crepitans* in two buffer areas) with high IVI values (>27), averaged upward the regression line.

**Figure 4.2.** Scatter plot of the average use value (UV) against importance value index (IVI) of 58 useful species in six Tsimane’ villages, Bolivian Amazon. Each point represents the use value of one species in one village (n=348).

The regression analyses for the total UV of a species against its IVI stand out three important results (Table 4.2). First, a bivariate regression without controls (column [1]) suggests a positive and statistically significant, although weak, association between total UV and IVI. The coefficient in column [1] implies that if the IVI of a species increases by one point, its total UV would increase by 0.0269 (P=0.000). Second, when we control for life form and for village fixed-effect (column [2]), the association between UV and IVI found in column [1] remained significant, although it was weaker. Third, the analysis segregating between “rare” species (IVI ≤1, column [3]) and “common” species (IVI>1, column [4]) yielded only a significant positive association (P=0.004) between UV and IVI when IVI>1.
The number of observations is only 293 because some species were missing in two buffer areas.

Table 4.2. Results of ordinary least-square bivariate and multiple regressions of overall use value (UV) of 58 tree species against importance value index (IVI) with robust standard errors and clustering by buffer area.

<table>
<thead>
<tr>
<th></th>
<th>Total</th>
<th>IVI≤1</th>
<th>IVI&gt;1</th>
</tr>
</thead>
<tbody>
<tr>
<td>IVI</td>
<td>0.027***</td>
<td>0.019***</td>
<td>-0.328</td>
</tr>
<tr>
<td>Life form (palms: excluded category)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small trees</td>
<td>^</td>
<td>-0.825***</td>
<td>^</td>
</tr>
<tr>
<td>Trees</td>
<td>^</td>
<td>-0.367*</td>
<td>^</td>
</tr>
<tr>
<td>Constant</td>
<td>1.92***</td>
<td>2.395***</td>
<td>2.056***</td>
</tr>
<tr>
<td>N</td>
<td>293</td>
<td>293</td>
<td>161</td>
</tr>
<tr>
<td>R²</td>
<td>0.032***</td>
<td>0.170</td>
<td>0.014</td>
</tr>
<tr>
<td>Village dummy</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
</tbody>
</table>

Notes: In column [2] six dummy variables were included for village. Significance levels: *=5%; **=1% and ***=0.1%. ^= variable intentionally omitted. Total N=293 because of missing species in two buffer areas.

To give a more intuitive interpretation of the results presented above, we took the natural logarithm of the outcome variable and the IVI and re-estimated the regressions in columns [1], [2] and [4]. When taking the natural logarithm of the total UV, we added 1 to the value of the outcome to avoid producing missing values when no uses were reported. The results of the regressions (not shown) suggest that if the IVI value doubles, the total UV of a species would increase by 5.1% (P=0.065), in the regression without controls, and by 3.7% (P=0.109) when controlling for village fixed effects and life form. The differences in the association between rare and common species were more evident when taking logarithms. Thus, for the subsample of species with IVI≤1, when the IVI value doubles, the total UV decreases by 16.4% (P=0.302) whereas for the subsample of species with IVI>1 the total UV increases by 18.1% (P=0.007).

The association between the usefulness of a species within different use categories and its ecological importance reported different patterns. The UV in the categories house building and other uses showed a positive linear relation with the IVI, indicating that most species used were common species (Fig. 4.3). However,
food and medicinal UV showed a negative linear relation with IVI, indicating less ecological importance for these species. Last, we do not find a clear relation between IVI and UV for species that were used for canoe building or firewood.

Figure 4.3. Scatter plot of the average use value (UV) per ethnobotanical categories, against importance value index (IVI) of 58 useful species in six Tsimane’ villages, Bolivian Amazon. Each point represents one species in one village (n=348).

To further explain the different patterns observed between IVI and different categories of uses, in Table 4.3 we ran bivariate and multivariate regressions similar to regressions in Table 4.2, but using only the average number of uses in a given category. It produced three main results. First, the canoe UV and firewood UV showed no association with IVI in bivariate models (columns [1] and [2]). We report bivariate regressions results only for these two categories because they were the only two categories where the regression without controls was not statistically significant. Thus, the significant association observed for those categories in multivariate analysis, i.e. when including controls for life form and village fixed effects (columns [3] and [4]), is probably an interaction effect between explanatory and control variables. Second, after controlling for village fixed-effects
and life form of the species, we found a positive but weak association between IVI and UV in the categories house building (column [6]) and others (column [8]). Third, when including the controls, we found a negative association between IVI and UV in the categories food (column [5]) and medicinal (column [7]).

Table 4.3. Results of tobit bivariate and multiple regressions of categorical use value (UV) of fifty-eight tree species against their importance value index (IVI), with left-censoring, robust standard errors and clustering by buffer area.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>IVI</td>
<td></td>
<td>0.0113</td>
<td>-0.0020</td>
<td></td>
<td>0.0207***</td>
<td>0.0059***</td>
<td>-0.0193***</td>
<td>0.0229**</td>
<td>-0.0406**</td>
</tr>
<tr>
<td>Life form (palm: excluded category)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small trees</td>
<td>^</td>
<td></td>
<td></td>
<td>0.0422</td>
<td>0.4857***</td>
<td>-0.2860***</td>
<td>-0.7103***</td>
<td>0.5450***</td>
<td>-1.0040***</td>
</tr>
<tr>
<td>Trees</td>
<td>^</td>
<td></td>
<td></td>
<td>1.1595***</td>
<td>0.6870***</td>
<td>-0.7217***</td>
<td>-0.5153***</td>
<td>0.4478***</td>
<td>-0.4110***</td>
</tr>
<tr>
<td>Constant</td>
<td>-0.4607***</td>
<td>0.3503***</td>
<td></td>
<td>-1.4872***</td>
<td>-0.3086***</td>
<td>0.7576***</td>
<td>0.5918***</td>
<td>-0.0865</td>
<td>0.8321***</td>
</tr>
<tr>
<td>Pseudo-R²</td>
<td>0.0033</td>
<td>0.0009</td>
<td></td>
<td>0.1707</td>
<td>0.8132</td>
<td>0.0578</td>
<td>0.2469</td>
<td>0.0584</td>
<td>0.1775</td>
</tr>
</tbody>
</table>

Notes: N=293. In columns 3 to 8 a set of dummy variables controlling for village fixed effect was included. Significance levels: *=5%; **=1% and ***=0.1%. ^= variable intentionally omitted.

Discussion

Use value and ecological importance of the species

In general terms, we found that the more ecologically important is a tree species, the more uses it has. Our finding is consistent with other studies that have related species uses and IVI (Torre-Cuadros and Islebe 2003, Lucena et al. 2007, Thomas et al. 2009a) and with studies that have related species uses to their apparency estimated with indicators other than IVI (Paz y Miño et al. 1995, Galeano 2000). Thus, our finding provides additional support to the hypothesis that people use more the most visible species in the forest.

This result must be taken with caution, though, for at least four reasons. First, part of the variation in the results is probably due to sampling. Ecological values are likely biased for small samples and vary depending on the diameter classes included in the study (Macía 2008). In our study, although we included all trees ≥ 2.5cm dbh, which represents a rather accurate ecological sampling, we inventoried only 0.8 hectares of forest per buffer area, which does not capture all existing tree.
Second, the IVI of the species would have to vary considerably (by 100%) to result in a small change (5.1%) in its use value. Thirdly, much of the variation in usefulness is captured by the life form of the species. This is consistent with studies that found that the family the species belongs is more important than its apparency when explaining its uses (Phillips et al. 1993b, Thomas et al. 2009a). Here, palms are the most useful life form for the Tsimane’ regardless of the ecological characteristics of the species. A simple explanation is that palms are among the most easily identifiable species, and the most useful family in the Amazon (Byg et al. 2006, Macía et al. 2011). And fourth, when dividing the sample into ecologically important and less important species (IVI≤1), the relation tends to be negative for some of the less important species which have more uses. However, some rare species in our study, such as *Genipa americana*, are often planted around the houses in home gardens (personal observation; also see Paz Y Miño 1995). Therefore, the pattern observed for rare species could be due, to some extent, to species that are well-known among the Tsimane’ regardless of their ecological characteristics. Indeed, we proxied the usefulness of a species with its use value (i.e. knowledge), but other measures, such as actual frequencies of use, might yield different results (Albuquerque 2006, Reyes-García et al. 2006, Albuquerque and Hanazaki 2009).

The ecological apparency hypothesis implies causality: the resource is the driver of consumer behaviour. Researchers have often rejected the alternative hypothesis that management and use of the species influence their ecological importance (but see Thomas et al. 2009a) because of a high dynamism of the ecosystem and because the areas studied were protected areas or areas in which young people had no interest to learn about plant uses (Phillips and Gentry 1993b, Lucena et al. 2007). However, this hypothesis might not be rejected in our study area for two reasons. First, our study area seems to have been inhabited for a long time and the actual floristic composition could have been influenced by indigenous management (Denevan 1966, Lombardo and Prümers 2010, Lombardo et al. 2011) and the effects of anthropogenic perturbation or management on composition and abundances might persist even for centuries (Macía 2008). Second, some of the most useful species have suffered intensive exploitation. For example, mahogany (*S. macrophylla*) and Spanish cedar (*C. odorata*) are the most useful species for
canoe construction and have been selectively logged in the last decades (Gullsion et al. 1996) and *A. phalerata* is intensely used by local populations for construction and food. Thus, it is likely that the IVI of these species has decreased as a consequence of species usefulness. A plausible scheme, as suggested by Lawrence et al. (2005), is a negative feedback between apparency and uses, i.e. the apparency of the species increases its use value, leading to a negative effect on its abundance.

### Categorical use values and ecological importance of the species

We found a positive relation between IVI and UV in the categories house building and other uses. This is consistent with the positive association found in other studies between construction uses and relative dominance (Lucena et al. 2007, Thomas et al. 2009a), and with the results of Phillips and Gentry (1993b), which stress a positive association between species’ relative density and frequency and their UV for construction and technology. We also found a negative association between the medicinal and food UV and the IVI of the species, consistent with some earlier studies (Silva and Albuquerque 2005), but not with others (Phillips and Gentry 1993b, Lucena et al. 2007, Thomas et al. 2009a).

These inconsistencies might be in part due to the fact that authors not always include the same uses in the same categories, particularly between indigenous and non-indigenous populations (Galeano 2000, Schwantes and Felfili 2001, Lawrence et al. 2005). For example, firewood is sometimes included in a “technology” category (Phillips and Gentry 1993a) and sometimes considered apart (Galeano 2000, Macía et al. 2011, this study). For indigenous people, firewood is a vital resource that justifies a single category, whereas for non-indigenous people it might not be so important. In our study we used use categories recognized by the Tsimane’ (Reyes-García 2001), where the category “other uses” had much more importance. Thus, it is likely that the association between usefulness and ecological importance is strongly specific of the area and people studied.

What would explain the different associations between IVI and different categories of uses? We hypothesize that the physical properties of the species, useful for canoe or tool construction, are more easily substitutable than their chemical properties, more important in medicinal and food uses. On the one hand, good physical properties, such as mechanical resistance or durability, are likely to
be shared by many species, such as palms species or common construction tree species. The Tsimane’ have a large choice of species that explains the positive relation between IVI and use values in the categories house construction and other uses: if many species have good properties for these uses, they tend to use the most visible species. On the other hand, specific chemical properties, such as those responsible for edibility, taste, or chemical compounds used for medicinal purpose, are likely to be less substitutable and in our case found in rare species. This would explain the negative association between IVI and use values in the categories medicinal and food. Stepp (2004) argues that common weedy species invest in mobile compounds such as alkaloids, cardiac glycosides and terpenoids as a defence against herbivory; these compounds are valued as medicines, which emphasizes the role of weeds (i.e., common plants) as medicinal plants. Although we do not challenge this finding, we argue that the traits associated with the production of such compounds -short-lived leaves and fast-growing capacity- can also be found in species of old-growth areas as our study area, especially in understory species and deciduous large tree species. For example, deciduous canopy trees such as Calycophyllum spruceanum have been reported to have medicinal uses in Brazil (Costa et al. 2011). Moreover, leaves are not always the most useful part of medicinal plants, but rather other parts, such as barks, roots or even saplings. Furthermore, our explanation finds support in the study of Paz y Miño et al. (1995) among indigenous people in Ecuador, which reported that people cultivate rare lianas used for their chemical compounds close to their houses.

Aknowledgements

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researchers kindly provided comments on earlier drafts. Research was funded by a FBBVA grant (BIOCON_06_106-07).

References


General conclusions

This dissertation is the result of a multidisciplinary approach linking ecology and social sciences which brings out results that are intrinsically needed to the study of biocultural diversity (UNESCO 2008, Pretty et al. 2009).

In the first part of the thesis, I have shown a gradient of floristic composition and tree species richness from the northeastern to the southwestern parts of the Tsimane’ territory. This gradient can be explained by natural factors, including the history of flooding and the particular biogeography of the region. In summary, the geographical position of the studied sites plays an important role in determining the floristic patterns of the region.

The second chapter deals with analysis to explain species turnover across inventoried sites. This is mainly influenced by geographical distances between plots and several key environmental factors, such as the amounts of calcium and magnesium in soils. Additionally, breaking down tree species into different tree categories allowed me to underline the importance of phosphorus in explaining understory species distribution.

In the following two chapters, I have also emphasized an association between indigenous people (through cultural factors) and tree diversity and composition.

In chapter 3, I have shown that, although the inventoried forests are commonly managed, acculturation processes are associated to tree diversity. In villages with intermediate levels of acculturation, tree diversity is higher, suggesting that indigenous management practices can be seen as a disturbance in the context of the non-equilibrium hypothesis. However, acculturation is not associated with proxies for forest structure and tree diversity is also influenced by patterns of traditional knowledge.

In chapter 4, I have put forward different patterns of association between indigenous uses of tree species and their ecological importance. These patterns could be the result of the impact of species’ ecological importance on their uses. However, I believe that the associations found also come from the impacts of indigenous uses on the ecology of the species. Particularly, this finds support in
previous researches in the area, which have emphasized a landscape modeled by centuries of indigenous management.

In sum, although tree floristic composition and richness seem to be more strongly controlled by natural factors, the forests inventoried here as old-growth forests seem to constitute one of the intermediate systems between natural forests and agroforests, *sensu* Wiersum (2004). Tsimane’ management within *terra firme* old-growth forests is probably not as strong as we can expect in the case of gardened forests, but our results suggest that their system of traditional ecological knowledge can lead to compositional and richness modifications. Considering past land-use of the forests likely to have occurred in the area (Denevan 1966, Gullison 1996, Lombardo et al. 2011), as well as Tsimane’ current ways of managing lands, it seems impossible to think of a system that would solely be shaped by natural factors.

However, since acculturation is associated with tree diversity, quickly increasing acculturation will probably change the patterns highlighted in this dissertation. For instance, it is likely that in villages closer to towns, indigenous management will resemble a non-indigenous one in a few years, with increased levels of deforestation to allow the establishment of agricultural systems.

The results of this thesis are particularly interesting in the light of the need to study biocultural diversity at small scales. I suggest that biocultural diversity patterns change at an intracultural level, through an association between indigenous culture -knowledge and practices system - and biodiversity.

On the methodological level, it is challenging to empirically relate cultural changes to biodiversity, unless biodiversity is measured at the same level than cultural changes, i.e., at an individual level. This is possible when studying the association between acculturation and agricultural management practices, because one individual manages his own field, where crop diversity, for instance, can easily be measured. However, when studying communally-managed areas, an individual measure of biodiversity could be done through interviews, such as the quantification of individual management pathways, or the observation of one’s actual management in the forest. Biodiversity could also be proxied by other
measures than vegetal diversity, such as individual patterns of hunting, which would relate to animal diversity.

This thesis gives way to many interesting future researches. First, in explaining species turnover with natural factors, future studies are needed to reduce the unexplained component of floristic variation. For instance, including reliable rainfall data at site level and variables related to water availability in soils would be a first step to reduce it. Second, to disentangle the role of indigenous people in managing biodiversity in commonly-managed forests, future studies need to compare biodiversity inventories with data of each pathway of traditional indigenous management, especially those having potentially no direct impact on forest structure or resemble natural disturbances, such as enrichment planting, small-scale selective clearing for fruit harvesting and honey collection, or hunting patterns. To further capture the current changes affecting indigenous peoples and to understand their association with biodiversity, such studies must focus on systems managed under different levels of acculturation, and must include controls for no management and non-indigenous management. However, one of the challenges is to study such differences in ecosystems or landscapes that are ecologically similar, with no important biogeographic differences that would impact overall biodiversity; this would be possible studying neighboring villages or sites. Another approach would be to study the dynamics of the association between biodiversity and indigenous changes on a temporal scale.

The results of this dissertation have also important policy implications. It seems obvious that conservation strategies have to give more weight to local people, especially to indigenous people. However, as researchers and local actors (e.g., NGOs) debate on how to make the most of community based management (Porter-Bolland et al. 2011, Nelson and Chomitz 2011), little is known of how actual indigenous practices relate to biodiversity, and how acculturation affects this relation. Here, since an intermediate level of acculturation seems to enhance biodiversity, community-based planning is needed in the territory of these villages to help give more power to indigenous people living there, and then to protect remaining biodiversity against encroachers. Such planning is based on scientific
studies of biodiversity. However, it is intrinsically dependent on indigenous willingness to protect their lands, as in the case of the creation of Municipal Protected Areas in Bolivia (Oller et al. 2008). Since it is irrelevant to avoid acculturation among indigenous peoples, the creation and the implementation of national parks would also be needed to avoid a loss of biodiversity when drastic changes affect local people’s way of life.

References


Appendix 1. Location and features of 55 0.1-ha plots inventoried in *terra firme* forests in seven sites of the Tsimane’ territory, Bolivian Amazon. CB= Campo Bello; CU= Cuchisama; JA= Jamanchi; MF= Misión Fátima; TR= Triunfo; UV= Uvasichi; YA= Yaranda.

<table>
<thead>
<tr>
<th>Plot name</th>
<th>Topography</th>
<th>Elevation (m)</th>
<th>Geographic coordinates</th>
<th>Number of stems</th>
<th>Number of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>CB1</td>
<td>Flat</td>
<td>183</td>
<td>14°47'36&quot;S; 66°37'21&quot;W</td>
<td>89</td>
<td>22</td>
</tr>
<tr>
<td>CB2</td>
<td>Flat</td>
<td>239</td>
<td>14°48'4&quot;4&quot;S; 66°37'11&quot;W</td>
<td>106</td>
<td>23</td>
</tr>
<tr>
<td>CB3</td>
<td>Flat</td>
<td>204</td>
<td>14°48'3&quot;3&quot;S; 66°37'22&quot;W</td>
<td>86</td>
<td>18</td>
</tr>
<tr>
<td>CB4</td>
<td>Flat</td>
<td>218</td>
<td>14°47'8&quot;8&quot;S; 66°37'33&quot;W</td>
<td>94</td>
<td>23</td>
</tr>
<tr>
<td>CB5</td>
<td>Flat</td>
<td>224</td>
<td>14°46'5&quot;6&quot;S; 66°37'16&quot;W</td>
<td>64</td>
<td>21</td>
</tr>
<tr>
<td>CB6</td>
<td>Flat</td>
<td>208</td>
<td>14°46'4&quot;4&quot;S; 66°37'38&quot;W</td>
<td>82</td>
<td>26</td>
</tr>
<tr>
<td>CB7</td>
<td>Flat</td>
<td>179</td>
<td>14°46'2&quot;9&quot;S; 66°37'27&quot;W</td>
<td>99</td>
<td>27</td>
</tr>
<tr>
<td>CU1</td>
<td>Flat</td>
<td>265</td>
<td>15°32'5&quot;3&quot;S; 66°36'45&quot;W</td>
<td>153</td>
<td>41</td>
</tr>
<tr>
<td>CU2</td>
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<td>258</td>
<td>15°32'1&quot;3&quot;S; 66°36'53&quot;W</td>
<td>223</td>
<td>67</td>
</tr>
<tr>
<td>CU3</td>
<td>Flat</td>
<td>268</td>
<td>15°32'8&quot;S; 66°36'26&quot;W</td>
<td>155</td>
<td>41</td>
</tr>
<tr>
<td>CU4</td>
<td>Flat</td>
<td>293</td>
<td>15°34'0&quot;0&quot;S; 66°37'22&quot;W</td>
<td>222</td>
<td>50</td>
</tr>
<tr>
<td>CU5</td>
<td>Flat</td>
<td>266</td>
<td>15°33'5&quot;8&quot;S; 66°37'4&quot;W</td>
<td>256</td>
<td>47</td>
</tr>
<tr>
<td>CU6</td>
<td>Flat</td>
<td>262</td>
<td>15°34'4&quot;4&quot;S; 66°36'32&quot;W</td>
<td>149</td>
<td>48</td>
</tr>
<tr>
<td>CU7</td>
<td>Flat</td>
<td>250</td>
<td>15°32'15&quot;S; 66°37'30&quot;W</td>
<td>175</td>
<td>39</td>
</tr>
<tr>
<td>CU8</td>
<td>Flat</td>
<td>256</td>
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### Appendix 2. List of species and morphospecies inventoried in 55 0.1-ha plots of terra firme forest of the Tsimane’ territory, Bolivian Amazon. CB= Campo Bello; CU= Cuchisama; JA= Jamanchi; MF= Misión Fátima; TR= Triunfo; UV= Uvasichi; YA= Yaranda.

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<td><em>Rinoreocarpus ulei</em> (Melchior) Ducke</td>
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