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RESEARCH ARTICLE

Implications of forest type and land tenure diversity for the sustainability of ecosystem services provided by northern Amazonia's multiple-use tree species

Anthony R. Cummings · Jane M. Read · Jose M. V. Fragoso

Abstract

Context As global landscapes continue to change, the sustainability of the ecosystem services they support are increasingly coming into question. In the rapidly changing neotropics, multiple-use plants epitomize sources of ecosystem services. To sustain the relationship that exists between such plants and human populations, a sound understanding of their well-being is required.

Objectives Density data on multiple-use plants were compared across forest types and land tenure classes to understand the implications of these two spatial frames of reference for landscape sustainability.

Methods The density of an aggregate sample of seventeen multiple-use and a sub-sample of five species were examined relative to forest type and land tenure class across fourteen Rupununi, Southern Guyana, study sites. The examination of plant density based on the two sample sizes was used to make inferences on how the two frames of reference may impact landscape sustainability.

Results The mean density of the aggregate sample was highest in three of six forest types, but showed no statistical difference across land tenure classes. When individual species were considered mean densities showed no statistical difference across land tenure classes, but differences were observed for three species across forest types. Mean densities were highest in forest types within which swidden agriculture occurs and in the protected area where logging is prohibited.

Conclusions Our findings suggested that in changing tropical landscapes plant species distribution can be predicted by forest types, but land tenure classes may provide clearer signals as to where a species well-being and hence ecosystem services may be compromised.

Keywords Multiple-use plants · Ecosystem services · Forest type · Land tenure · Landscape diversity · Landscape sustainability · Tropical landscapes

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Introduction

Global biodiversity continues to face severe threats from human activities. As biodiversity levels decline, increased efforts are being made to protect landscapes or Earth's life-support systems (Wu 2013a; Kates et al.

2001) to safeguard human well-being. At the core of landscape protection efforts are ecosystem services (ES) that are indispensable to the existence of human societies, such as indigenous peoples. Because of the wide variety of ES derived from within them and the threats posed by land-use and land-cover change (LUCC), Amazonian landscapes are among the most important to protect. Within Amazonian landscapes, various plant species are the sources of important ES for indigenous peoples and the wildlife they hunt (see Cummings 2013) and the survivability of such plants may be threatened by landscape fragmentation.

Amazonia's indigenous peoples-influenced landscapes are often fragmented by a diversity of land tenure types. Invariably, indigenous properties are distributed side-by-side with properties dedicated to resource extraction, such as gold mining and commercial logging (see Colchester 1997). Such heterogeneous landscapes exhibit what Stocks (2005) described as the *archipelago syndrome* with the possibility of different land owners having different motivations for resource use on their land. Recently, a large body of work has emerged in the landscape ecology community focussed on landscape sustainability (see Musacchio 2009; Cumming 2010) and the implications of landscape heterogeneity on ES sustainability (see Turner et al. 2013; Ferraz et al. 2014). Yet, the impact of land tenure arrangements and their resulting LUCC influence on plant distributions and the sustainability of ES within tropical landscapes remain highly underexplored.

Legally-recognized indigenous territories in Amazonia occupy tens of millions of ha of intact forest ecosystems (Zimmerman et al. 2001). In fact, Peres (1994) noted that indigenous territories accounted for 248 of all 459 officially designated conservation areas in nine South American countries or 52% of the area that receives some form of protection. In the Brazilian Amazon, for example, such protected areas account for more than 100 million ha, of which 29 were larger than 1 million ha (WCMC 1992) and these areas have been identified as having enormous potential for biodiversity protection (Zimmerman et al. 2001). Human population densities on indigenous territory are often low (< 0.5 people/km^2) with subsistence activities dominating, resulting in reduced rates of natural resource depletion (Zimmerman et al. 2001). In fact, despite the large area occupied by indigenous territories and protected areas, only 17% of

deforestation occurred within their boundaries compared to 87% outside (Environmental Defense Fund et al. 2017).

Land tenure, is defined as the form of rights or title under which property is held and determines how an individual or group may use, share, sell, lease, inherit, or otherwise control property and resources (Brandon et al. 1998; Naughton-Treves and Wendland 2013). Early studies in the legal Amazon, for example, showed that land ownership by small farmers, medium and large ranchers, were the main drivers for deforestation (e.g. Fearnside 1993). In other settings, the impacts of land tenure have been examined by other scholars with Damnyag et al. (2012) finding that tenure insecurity in Ghana led to increased deforestation. Abdulai et al. (2011) reported that land ownership resulted in greater investment in resource protection while McCune et al. (2017) noted that while protected areas are important in biodiversity protection, private lands also have a role to play. Across Amazonia, such land holdings give rise to indigenous peoples-influenced landscapes hosting generally wide and varied land tenure arrangements, including indigenous titled lands, private lands, protected areas and state-owned lands. Each land tenure class may present a different reality for resource use and hence may influence landscape pattern and configuration. For example, a group of indigenous peoples owning land in Guyana has all rights over all forest resources, including permitting logging within their forests (Amerindian Act 2006). However, communities have little say over the types of resource extraction activities that may occur adjacent to their lands.

A diversity of land tenure arrangements or spatially heterogeneous landscapes (Turner et al. 2013) within indigenous peoples-influenced landscapes can predispose them to change due to disturbance and have implications ES sustainability. In fact, Wu (2013a) put forward "ecosystem services in changing landscapes" as one of the ten pressing questions in landscape ecology. Further, Turner et al. (2013) noted that changes in key drivers, including disturbance regimes and land use, will impact the sustainability of landscapes. Within Amazonia, changing landscapes have implications for plant distribution, in particular plants that provide more than one ES. To date, most studies examining plant distribution in Amazonia (e.g. Menton et al. 2009; Klimas et al. 2012b) have either been limited in geographical scope, e.g. to a protected area (e.g. Klimas et al. 2007) or a logging area

(Menton et al. 2009). As a consequence the realities of fragmented indigenous-peoples landscapes, with multiple land tenure arrangements, have been rarely considered. In addition, within the tropics studies that have focussed on ES associated with plants, have considered a single well-known species (e.g. Klimas et al. 2007 but see Cummings and Read 2016 who worked with a larger group) with little attention to multiple-use plants.

Multiple-use plant species (see Cummings and Read 2016; Sivasailam and Cummings 2017) provide food for wildlife (supporting ES), non-timber forest products (NTFPs) for indigenous peoples (provisioning and cultural ES, e.g. Forte 1996; Byron and Arnold 1999; Ticktin 2004; Cummings 2013; Cummings and Read 2016), may be commercially logged (provisioning ES, Klimas et al. 2007; 2012a, b), and are the core of Amazonian landscapes. Traditionally, when scholars have examined the distribution patterns of multiple-use plants, habitat type, or its synonym forest type (Peters 1996; Keith et al. 2013), has been the primary spatial frame of reference utilized (Peters 1996; Klimas et al. 2007). Yet, using forest type to describe species distribution can be problematic from two main perspectives. First, forest type is often difficult to define, especially within tropical settings (see for example Prance 1979; de Granville 1988; Hamilton 1991). In Amazonia, for example, Prance (1979) noted that scholars in limnology and botany may refer to the same forest type with different terms. de Granville (1988) noted that in the Guianas, the upland moist forests are the equivalent of lowland tropical moist forests of Prance (1979), the lowland rain forests of Richards (1952) and the rainforest of Fanshawe (1952). Secondly, de Granville (1988) suggested that defining the spatial extent of forest types and their associated environmental parameters is difficult, with the elevation of some forest types ranging from sea level to above 1000 m. Using forest type solely, therefore, to define the distribution of multiple-use plants and, by extension, examine where within a landscape the sustainability of ES may be threatened, can lead to a skewed view of a landscape's reality.

With the foregoing in mind, this paper's overarching goal was to examine how two frames of reference, land tenure classes and forest types, impact the distribution of multiple-use plants. Given the call for work to examine the implications of changing landscapes on ES (see Wu 2013b), and the impacts of spatial heterogeneity on ES sustainability (e.g. Turner et al. 2013), the overarching hypothesis of this paper is that land tenure classes add spatial heterogeneity to tropical landscapes and by examining plant distributions through this frame of reference, insights into where a plant species may face human–induced pressure and hence compromise the sustainability of ES may be gained. To examine this hypothesis, a sample of multiple-use plants were obtained from Guyana, South America, to advance two objectives. First, the density of an aggregated sample of seventeen multiple-use plant species were compared between land tenure classes and forest types and used to assess implications for landscape sustainability. Secondly, using a smaller sub-sample of the five most abundant species in our sample, their distribution by land tenure classes and forest types were compared to determine implications for species management and landscape sustainability.

Methods

Overview

This study examined the distribution and density of multiple-use plant species across two frames of reference—land tenure classes and forest types. Abundance (count) data for seventeen multiple-use plant species were collected from transects that covered four land tenure classes and six forest types and used to compute density by the areas sampled in the two frames of reference. Density comparisons were made for the aggregated sample of seventeen species, in addition to the top five most abundant species in our sample, across the two frames of reference.

Study Area

This study was completed in the forest and savannah biome of the Rupununi, Southern Guyana located between $1°59'$–$4°50'$ N and $58°23'$–$59°43'$ W (Fig. 1). The Rupununi lies around 350 km southwest of Guyana's capital, Georgetown (Fig. 1) and is the homeland of the Makushi and Wapishiana Amerindians. The Rupununi landscape, both forested and savannah, is intricately tied to the subsistence activities of the area's Amerindian peoples, supporting hunting, fishing, swidden agriculture and gathering activities (David et al. 2006; Read et al. 2010). The
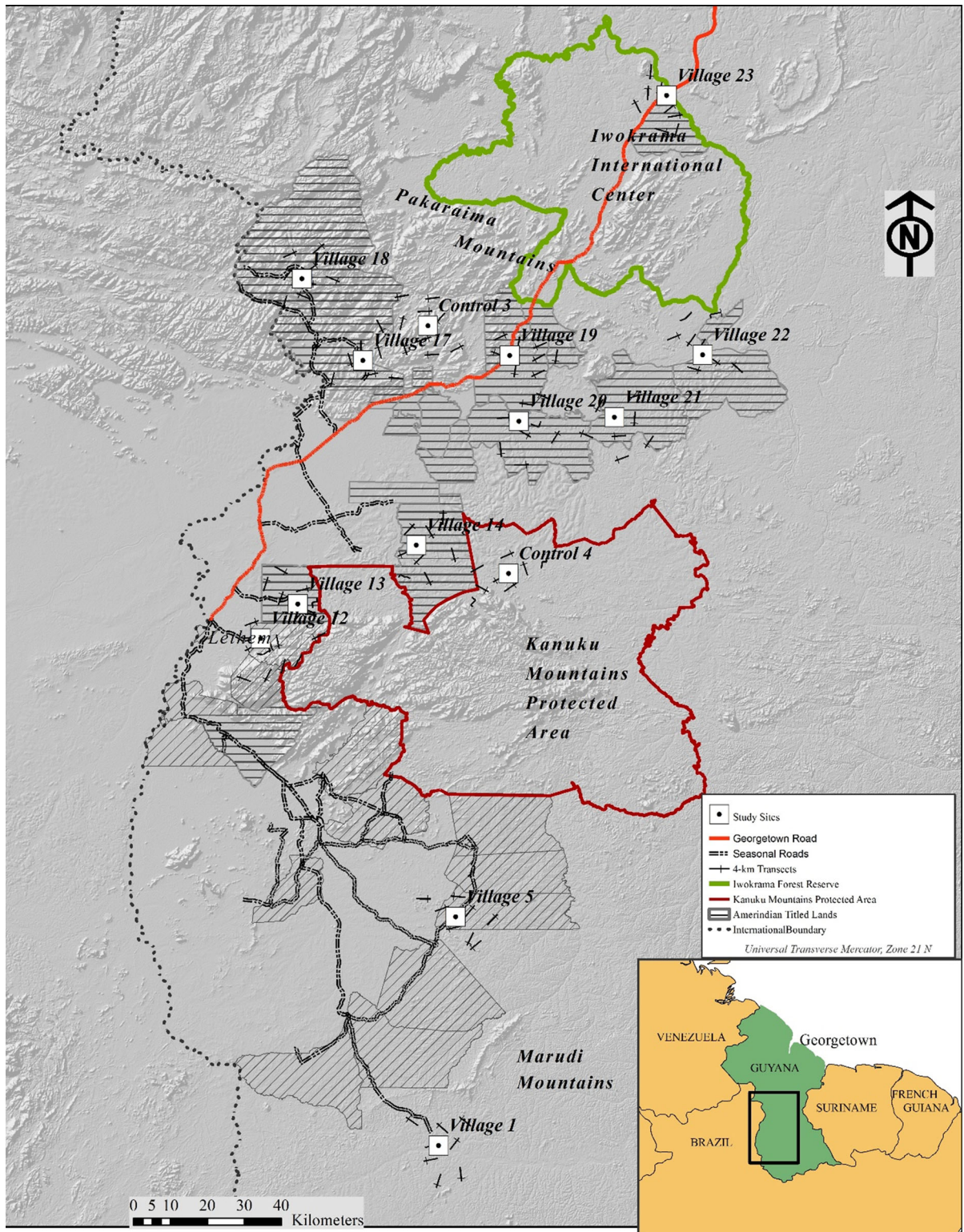
Fig. 1 **a** Study area with land tenure classes and sampling locations depicted. **b** Study area with forest types and sampling locations depicted
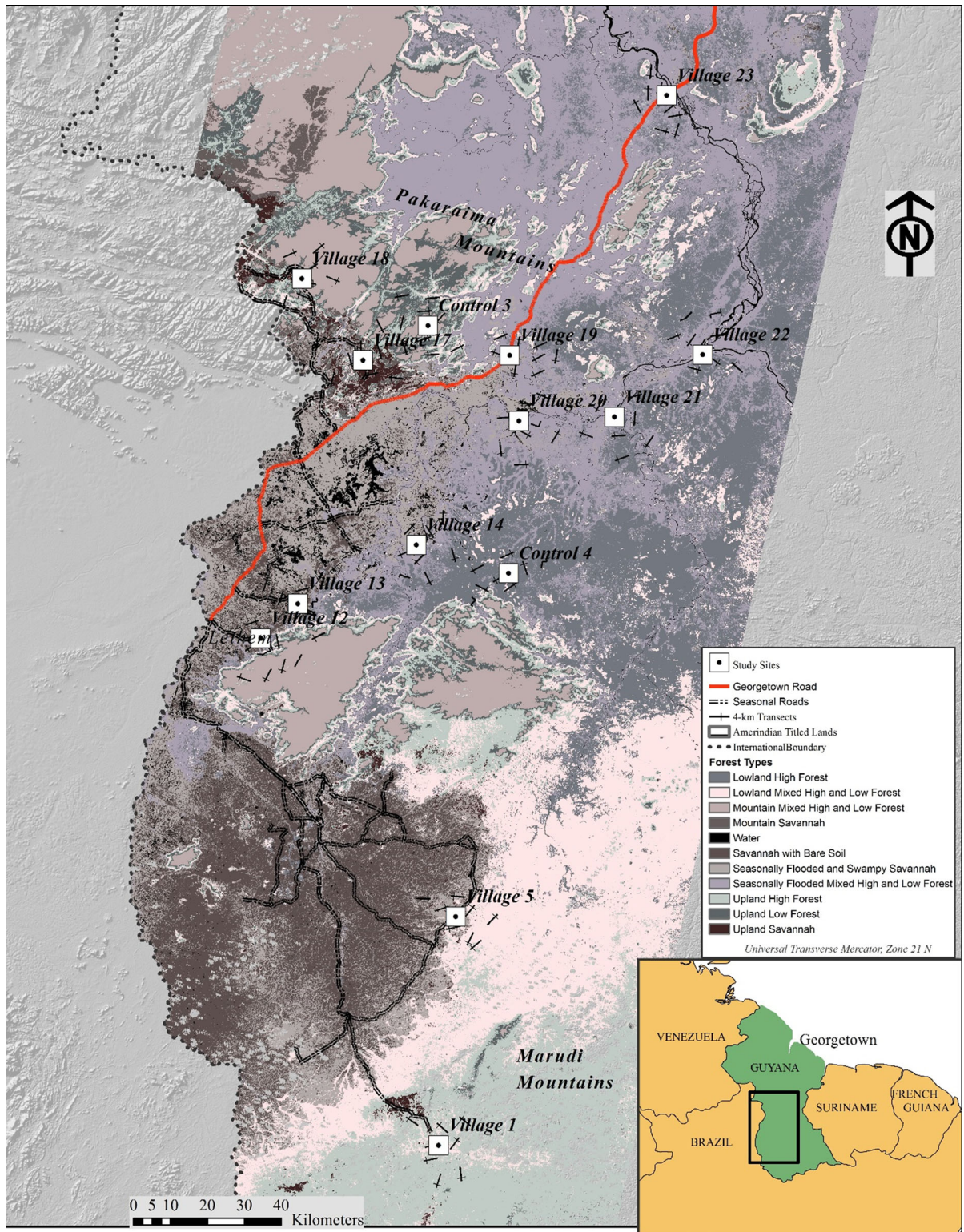
Fig. 1 continued

Rupununi has a diverse landscape configuration with four (4) main land tenure classes: titled Amerindian villages, protected areas, state-owned lands, and a small number of private properties. The area's Amerindians hold tenure to 25 legally-titled[1] villages. In Guyana, tenure is granted to a group of Amerindians numbering more than 150 individuals that have occupied an area for more than 25 years (Amerindian Act 2006). As a legal instrument, tenure gives villages all authority over above-surface resources and control of access to their lands by non-village members (Amerindian Act 2006).

There are two protected areas in the study area: Iwokrama International Center for Rainforest Conservation and Development (IIC) and the Kanuku Mountains Protected Area (KMPA); Fig. 1). The 371,000 ha IIC was established in 1996 to demonstrate that tropical forests can be sustainably utilized. The IIC has two zones: the Sustainable Utilization Area (SUA) where commercial logging is permitted and ongoing (began in 2007), and the Wilderness Preserve (WP) where commercial logging is not permitted but indigenous traditional activities are allowed (Iwokrama Act 1996). Tree distribution data for this study were obtained from within the SUA. The KMPA was officially gazetted as a protected area in 2012, and like the IIC, indigenous peoples living adjacent to its boundaries may continue traditional activities here. The KMPA is listed as a category six protected area under the International Union for the Conservation of Nature (IUCN) classification system (EPA 2009), which prohibits commercial resource extraction. State-owned lands are those properties to which the national government maintains management control.

Some private land holdings are also found in the Guyana-Brazil border town of Lethem. These holdings are relatively small and are located in the savannah regions and away from forests. There are also settlements, with sizeable non-Amerindian populations from coastal Guyana, living on state lease holdings within the vicinity of Villages 14 and 19 (Fig. 1). Further, the savannah region of the study area hosts various cattle ranches and commercial farms. For this analysis, only Amerindian titled lands, state-owned lands, and protected areas are considered. We contrasted the two protected areas (IIC and KMPA) based on the occurrence of logging activity within their boundaries. The IIC is referred to as "Protected Area (logging permitted)," and the KMPA as "Protected Area (no logging)" in this paper.

Sampling multiple-use tree species by forest types and land tenure classes

Count data for seventeen (17) multiple-use plant species were used to compute the density and examine distribution patterns across land tenure classes and forest types. The species used in this analysis were drawn from a larger sample (see Cummings 2013; Cumming and Read 2016) and selected based on two criteria. The first, each plant needed to have an abundance greater than 50 individuals across the study area. Secondly, each of the seventeen species needed to belong to the multiple-use class of plants *commercial timber, wildlife food, and traditional uses* (see Sivasailam and Cummings 2017). Species in this multiple-use class provide NTFPs for indigenous and forest-dependent peoples, food for hunted and unhunted wildlife, and their stems are commercially logged (see Cummings 2013). By considering this large number of species, trophy species alone would not be included in our analysis. The typology of ES derived from each plant species is presented in Table 1, and we focused here on the supporting and provisioning ES. Count data for each species were obtained from fourteen study sites, twelve Amerindian villages and two non-village locations, distributed across the study area (Fig. 1). At each study site, eight randomly-located 4-km long transects, cut through the forest at a random bearing, were established (see Read et al. 2010 for more details on the establishment of study sites) for sampling. Transects were located at a minimum of 3 km apart and were established within a 12 km buffer relative to the center of Amerindian villages and the control site. Despite using the center

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[1] The Amerindian Act 2006 defines an Amerindian village as a group of Amerindians occupying a portion of land to which they have been granted village lands (title) by the state. In this sense, the count of villages in the study area only includes legal communities and does not account for those functional communities that occupy state lands or satellite communities that fall under the purview of a village but is away from village lands. Culturally, satellite villages start as farming areas or as a group of people moving away to maintain the customary sparse housing patterns observed in communities, but generally remain connected to their mother communities. In this regard the Rupununi landscape consists of many more than twenty-five groups of people living in communal arrangements.

Table 1 The seventeen multiple-use plant species and the typology of ecosystem services with which they are associated

Species/common name (number of plants in sample in parenthesis)	Supporting ES (eaten by)	Provisioning ES (non-timber forest products)
Catostemma commune Sandwith/ Baromalli (1653)	Agouti, deer, tapir, howler[a] and spider monkeys[a], bats[a]	Fuelwood and building materials
Pachira aquatica Aubl./ Kanahia (795)	Scatter-hoarding rodents, such as agoutis and acouchis	Fuelwood
Protium decandrum (Aubl.) Marchand/ Kurokai (358)	Agouti, marudi, powis (black curassow), deer, capuchin[a]	Fuelwood
Licania alba (Bernouli) Cuatrec. and *L. majuscula* Harvey ex Gomont/ Kautaballi (312)	Agouti	Fuelwood and building materials
Parinari campestris Aubl./ Burada (1196)	Macaws[a], saki monkeys[a]	Fuelwood and building materials
Humiria balsamifera (Aubl.) A. St.-Hil./ Tauroniro (344)	Deer, peccaries, powis, marudi, tortoise, foxes[a], macaws[a], other birds[a] and monkeys*	Fuelwood and building materials; fruits may be eaten
Chlorocardium rodiei (Schomb.) Rohwer, H.G.Richt. & van der Werff/ Greenheart (361)	Agouti, labba, and white lipped peccaries	Seeds used to treat parasitic worms and skin diseases
Lecythis zabucajo Aubl./ Monkey Pot (278)	Labba	Lashing material
Hymenaea courbaril L./ Locust (104)	Agouti, labba, tapir, peccaries, monkeys[a] (saki, capuchin)	Fuelwood and building materials; fruits eaten
Mora excelsa Benth./ Mora (2193)	Peccaries, deer and tapir graze newly germinated seedlings	Fuelwood and building materials
Inga alba (Sw.) Willd./ Maporakon (414)	Agouti, labba, tapir, deer, powis, marudi, peccaries, parrots[a], capuchin[a] and spider[a] monkeys	Fuelwood and building materials; fruits eaten
Carapa guianensis Aubl., *C. procera* DC/ Crabwood (248)	Agouti, labba, peccaries	Therapeutic oil from seeds
Bagassa guianensis Aubl./ Cowwood (431)	Tapir, deer, peccaries, labba, agouti	Fuelwood and building materials; fruits eaten
Manilkara bidentata (A.DC.) Chev./ Bulletwood (1091)	Peccaries, tapir, deer, tortoise, labba, agouti, spider[a] and howler monkeys[a], macaws[a]	Gum used to make utensils for storing water and beverages, figurines and toys
Pouteria cuspidata (A.DC.) Baehni/ Kokoritiballi (312)	Agouti, red brocket deer, labba, monkeys[a]	Fuelwood and building materials
Pouteria guianensis Aubl./ Asepoko (381)	Agouti, red brocket deer, labba, spider[a] and howler monkies[a], capuchins[a]	Fuelwood and building materials; fruits eaten

[a]Species not hunted—data from traditional knowledge and Roosmalen (1985)

Data on supporting services from traditional knowledge, Roosmalen (1985) and Forget and Hammond (2005). Data on provisioning services from traditional knowledge, Forte (1996), and van Andel (2000)

Laba or paca (*Agouti paca*), agouti (*Dasyprocta leporina*), white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), red brocket deer (*Mazama americana*), white-tailed deer (*Odocoileus virginianus*), nine-banded armadillo (*Dasypus novemcinctus*) and red footed tortoise (*Chelonoidis carbonaria*), howler monkey (*Alouatta seniculus*), spider monkey (*Ateles paniscus*), white saki (*Pithecia pithecia*), bats (*Artibeus lituratus* among other species), black saki (*Chiropotes satanas*), capuchin (*Cebus paella*, *C. olivaceus*), toucans (*Ramphastos toco, R. vitellinus*), macaws (*Ara ararauna, A. macao, A. nobilis*)

Table 2 A description of the six main forest types associated with the distribution of the seventeen plant species

Forest Type	Description
Seasonally flooded mixed high and low forest (SFM)	Vegetation that are seasonally flooded (low bush and high bush) and the area where most swidden agriculture plots are located
Lowland high forest (LHF)	Forests at slightly higher elevation that the seasonally flooded mixed high and low forest. Trees tend to be larger trees, and wide some seasonal flooding may occur here, this vegetation is generally located away from rivers and creeks. Some swidden agriculture also occurs here
Lowland mixed high and low forest (LMH)	Forests located on slightly higher elevation than the lowland high forests but the plant species present here are similar to those in lowland high forests
Upland high forest (UHF)	High density forests of the South Rupununi, located at higher elevations than the North and is the area in which most swidden agriculture occurs
Upland low forest (ULF)	Smaller trees and shrubs and lower density that those found in the upland high forests
Mountain mixed high and low forest (MMF)	Forests found at the highest elevation in the Rupununi, mainly on the Pakaraima and Kanuku Mountain ranges. Swidden agriculture also takes place in these forests

See Fig. 1b for the distribution of these forest types

of Amerindian villages to establish transects, their final locations allowed for all four land tenure classes and six main forest types to be sampled.

The distributions of the seventeen plant species relative to forest types were assessed using a vegetation map developed with descriptions of vegetation obtained by Makushi and Wapishiana hunters (Table 2; Cummings et al. 2015). Indigenous hunters' descriptions of vegetation were used to train the classification and accuracy assessment of a combined mosaic of Landsat and ASTER DEM data (ASTER Global Digital Elevation Model (GDEM).[2] We utilized the vegetation map developed by Cummings et al. (2015), rather than a state-produced map, as it was prepared within the context of the study area, and accuracy assessment of the classification was available (see Cummings et al. 2015).

On each transect established at the individual study sites, all trees > 25 cm diameter-at-breast-height (dbh) within a 10-m belt (5 m on either side of the transect's imaginary center line) were sampled. For each tree, data on its location along a transect were collected to determine its location relative to the two main frames of reference. At the time of sampling the common name of each plant was recorded and used to determine a species botanical name. Post sampling, each plant's common name was referenced to a botanical name (species or genus; see Cummings

2013; Cummings and Read 2016) using traditional knowledge (TK; Posey 1992; Parrotta and Trosper 2012) of the Makushi and Wapishiana Amerindians and the literature (Roosmalen 1985; Forte 1996; van Andel 2000). Once a species common and botanical names were established, the literature and TK were used to determine the ES derived from that species. The inventory of trees was mapped in a geographic information system (GIS) and intersected with the four land tenure classes and six forest types. The intersection of the plant distribution across the four land tenure classes and six forest types allowed us to determine the length of each transect in the two frames of reference. The area sampled by the each frame of reference was computed along with the number of trees present in each.

Significance of forest type and land tenure classes in tree distributions

Density comparison of multiple-use plants were completed at two levels. First, all count data for the seventeen multiple-use plants were aggregated and compared across the two frames of reference. Mean species densities were computed based on the area sampled by the respective land tenure classes and forest types and used to determine whether statistical differences in species distribution existed relative to these two frames of reference. Secondly, the density of the five most abundant species (*Manilkara bidentata*

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[2] ASTER GDEM is a product of METI and NASA.

(A.DC.) Chev., *Catostemma commune* Sandwith, *Licania alba* (Bernouli) Cuatrec., *Parinari campestri*s Aubl. and *Carapa guianensis* Aubl.) were compared across the two spatial frames of reference. The densities of the five species were ranked across land tenure classes and forest types to determine whether there were differences between the two main frames of reference. To compare species distribution characteristics across the two frames of reference, histograms and Shapiro–Wilk tests were used to determine whether the data conformed to the assumptions of a normal distribution. The normality tests indicated that the data failed to conform to the assumptions of normality, and a subsequent log transformation failed to meet the assumptions of normality. Therefore, Kruskal–Wallis tests, completed using the *pgirmess* package in R for Windows version 3.3.2 (The R Foundation for Statistical Computing 2016), were used to compare mean densities of plants across land tenure classes and forest types at the 0.05 significance level for both the aggregate sample and individual species.

Results

The location of transects within the forested Rupununi landscape allowed for data to be collected from 92 transects across the study area. While eight transects were established at each study site, the nature of the landscape meant that 20 were location in savannah regions and hence did not allow access to trees. The analysis of mean density across forest types and land tenure classes showed differences for the aggregated sample of plants (seventeen species). Similarly, differences in mean density were also observed for the five most abundant plant species across land tenure classes and forest types. It should be noted that the area sampled by each forest type and land tenure class varied across the study area as determined through GIS computations (see Tables 3, 4). Nevertheless, the sampling strategy allowed for all forest types present within the study area to be represented in our analysis (see Table 2; Fig. 1) as were land tenure classes. Three forest types—SFM, LHF, and UHF—dominated the area sampled (Table 3) while ULF occupied the smallest area, accounting for less than 16 ha. The area sampled by land tenure classes varied, with Amerindian Titled Lands the largest area, followed by State-Owned Lands (see Table 4). The influence of the area sampled by forest types and land tenure classes on the aggregate sample and the five select species is described below.

Density of the aggregate sample by forest types and land tenure classes forest type

When the mean densities of plants for the aggregate sample of seventeen species were examined, variations were observed across the six forest types. The highest density was observed in the LHF forest type (Table 3), with 37.7 trees/ha. The SFM and MMF forest types had mean densities of 34 and 35 trees per ha, respectively. Statistically, the density of trees in the SFM and MMF forest types were similar ($p > 0.50$), but densities for both of these forest types were significantly lower than that observed in the LHF forest type ($p < 0.05$). There was no statistical difference in the density of trees observed in the LMH, UHF and ULF forest types ($p > 0.05$). However, the density of trees in the latter two forest types was significantly lower ($p < 0.05$) than observed in the SFM, LHF, and

Table 3 The density of the seventeen plants species associated with each vegetation type

Vegetation type	Area sampled (ha) and number of trees	Mean density (trees/ha)
Seasonally flooded mixed high and low forest (SFM)	115.4/3910	33.9[a,b]
Lowland high forest (LHF)	88.4/3329	37.7[a,b]
Lowland mixed high and low forest (LMH)	41.1/794	19.3
Upland high forest (UHF)	50.7/997	19.7[b]
Upland low forest (ULF)[c]	15.7/166	10.59
Mountain mixed high and low forest (MMF)	35.4/1232	34.8[a,b]

Classes with the same letter codes (a, b, and c) indicate that the mean densities of trees were significantly different at the 0.05 probability level

Table 4 The density of the seventeen plants species associated with each land tenure class

Tenure class	Area sampled (ha) and number of trees	Mean density (trees/ha)
Amerindian lands	213.6/5993	28.1
Protected area (logging permitted)	16/480	30
Protected area (no logging)	33.9/1334	39.4
State-owned lands	104.5/2954	28.3

MMF forest types. The lowest density of trees was observed in the ULF forest type (Table 3). It should be noted though, that the highest number of trees were sampled in the SFM forest type, with the larger area covered here resulting in a lower density of trees than the LHF forest type.

Land tenure class

In contrast to forest types, where statistical differences in the mean density of the aggregated sample were observed, land tenure classes showed no statistical difference (p = 0.2492). Protected Area (no logging) had the highest density of trees (Table 4), followed by Protected Area (logging permitted). While the highest number of plants was sampled from Amerindian Lands, the mean density of plants was lowest in this land tenure class. The density of trees and, by extension the ES with which they are associated, was highest on the Protected Areas (both logging permitted and no logging) than Amerindian lands and State-Owned Lands where larger samples were obtained.

Density of select species by forest types and land tenure classes

While the density of the aggregated sample of seventeen multiple-use plants showed differences across forest types and no differences across land tenure classes, the situation was different for the five most abundant species (Fig. 2). Mean density for *C. commune* (Table 5) was significantly different between LHF and LMH, while UHF had a significantly lower mean density than LHF, LMH, and MMF forest types, respectively. For *M. bidentata* significant differences in mean density were observed between the SFM and ULF forest types, as was the case for *P. campestris*. Our analysis showed that significant

differences in mean densities existed for *L. alba* in the LHF and ULF forest types. The analysis of mean density across land tenure classes (Table 6) suggested that no significant differences existed (p > 0.05) for all five species.

Beyond the statistical comparison of densities across the two frames of reference, when the ranked densities of the five selected species were examined across forest types and land tenure classes, a number of differences were observed. For vegetation types, three of the five species (*L. alba, P. campestris* and *M. bidentata*) had the highest density in the SFM forests. Two species (*C. commune* and *C. guianensis*) had the highest density in the MMF forests. Four species—*C. commune, L. alba*, *P. campestris* and *M. bidentata*—had the second highest density in the LHF forest type while *C. guianensis* second highest density was observed in the SFM forest type. With the exception of the two species that had the highest density in the MMF forest type, when considering the first and second highest ranked densities, the highest densities were found in the SFM and LHF forest types.

Unlike forest types, when the highest density of the five species were considered relative to land tenure classes, a wider range was observed. Two species (*L. alba* and *M. bidentata*), had the highest density in Protected Area (Logging Permitted), while another two species (*C. commune* and *C. guianensis*) had the highest density in State-Owned Lands. The other species (*P. campestris*) had the highest density on Amerindian Lands. When the second highest density of species was considered, two species (*P. campestris* and *M. bidentata*) were on Amerindian Lands, two in Protected Areas (No Logging; *C. commune* and *L. alba*) and one (*P. campestris*) on State-Owned Lands. None of the five species had the highest density in Protected Area (No Logging).
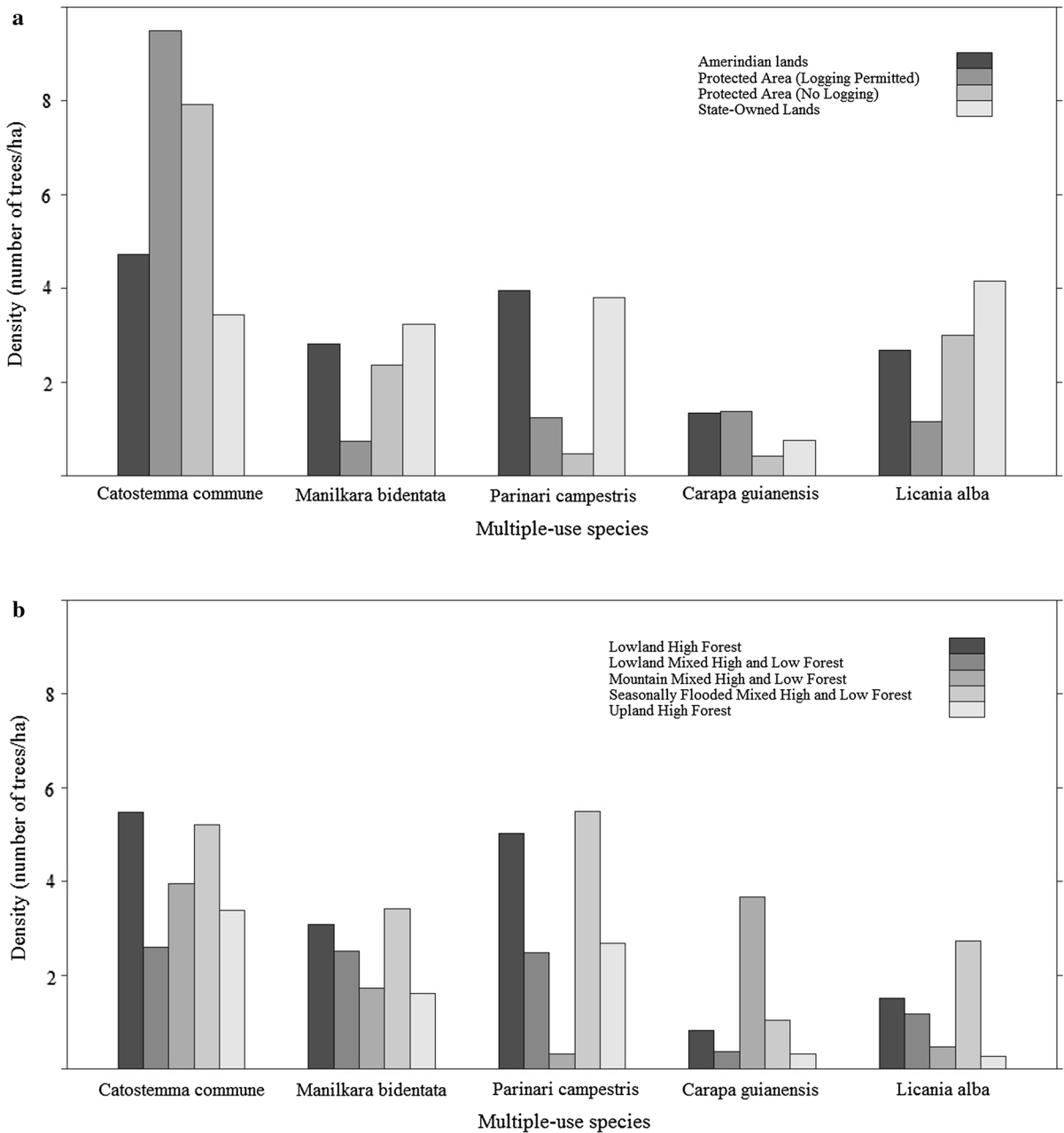
Fig. 2 **a** Distribution of the five select multiple-use species by forest types Mean densities that are significantly different are shown in Table 5. **b** Distribution of the five select multiple-use species by land tenure classes

Discussion and conclusions

At the inception, this paper set out to illustrate how two frames of reference, land tenure class, and forest type, influence the distribution of plant species from which indigenous peoples derive ES. In the overall scheme of landscape ecology, this paper is in direct response to Wu (2013a) call for landscape ecologists to study the implications of "changing landscapes" on the sustainability of ES, and Turner et al. (2013) note that heterogeneous landscapes can impact ES sustainability, by providing insights from a tropical setting. This paper does not consider change within each land tenure classes, per se, but rather makes the point that

Table 5 Mean density (standard error in parenthesis) of the five most abundant multiple-use species across vegetation types

Vegetation type	Plant species				
	Catostemma commune Sandwith	*Licania alba* (Bernouli) Cuatrec. and *L. majuscula* Harvey ex Gomont	*Parinari campestris* Aubl.	*Carapa guianensis* Aubl., *C. procera* DC	*Manilkara bidentata* (A.DC.) Chev.
Seasonally flooded mixed high and low forest (SFM)	5.21 (0.99)	2.74 (0.42)	5.49 (0.91)	1.05 (0.37)	3.42[d] (0.71)
Lowland high forest (LHF)	5.48[a,b] (0.71)	1.51[c] (0.54)	5.02 (1.28)	0.82 (0.41)	3.09 (0.63)
Lowland mixed high and low forest (LMH)	2.6[a,b] (0.79)	1.18 (0.49)	2.49 (0.78)	0.38 (0.38)	2.51 (0.97)
Upland high forest (UHF)	3.38[b] (1.08)	0.27 (0.56)	2.69 (1.3)	0.32 (0.17)	1.62 (0.44)
Upland low forest (ULF)	0	0.05[c] (0.12)	0	0	0.01[d] (0.02)
Mountain mixed high and low forest (MMF)	5.96[b] (1.12)	0.47 (0.50)	0.32 (0.12)	3.67 (1.29)	1.73 (0.63)

Classes with the same letter codes (a, b, c and d) indicate that the mean densities of trees were significantly different at the 0.05 probability level

Table 6 Mean density (standard error in parenthesis) of the five most abundant multiple-use species across land tenure classes

Land tenure class	Plant species				
	Catostemma commune Sandwith	*Licania alba* (Bernouli) Cuatrec. and *L. majuscula* Harvey ex Gomont	*Parinari campestris* Aubl.	*Carapa guianensis* Aubl., *C. procera* DC	*Manilkara bidentata* (A.DC.) Chev.
Amerindian lands	4.72 (0.65)	2.68 (0.84)	3.95 (0.85)	1.35 (0.43)	2.81 (0.51)
Protected area (logging permitted)	9.49 (3.08)	0.88 (0.36)	0.93 (0.87)	1.37 (0.48)	0.56 (0.5)
Protected area (no logging)	7.92 (2.26)	3.0 (1.12)	0.48 (1.63)	0.42 (0.27)	2.36 (0.91)
State-owned lands	3.44 (0.82)	4.15 (1.12)	3.81 (2.16)	0.75 (0.38)	3.23 (0.80)

Note that mean densities are not significantly different across tenure classes at the 0.05 probability level

land ownership will influence how plants are treated and should become a part of considerations for studies on landscape heterogeneity influence on ES distribution. Upon completion of the analysis, a few points have emerged that may be useful to the landscape ecology community and managing ES in the tropics in particular.

First, our analysis seemed to have suggested that the distribution of plant species relative to land tenure classes is an important consideration in heterogeneous landscapes. While it is difficult to anticipate how future land-use may change in the various land tenure classes considered in this paper, the fact that different

land ownership arrangements exist, and that each can have a different outcome as to whether a species is exploited or protected, requires attention. Even though the densities of the plant species varied more widely by forest types than land tenure classes (see Tables 3, 4, 5, 6; Fig. 3) for both the aggregated sample and individual species, it seemed more plausible that a species can be exploited or protected based on who's land it is found. Certainly, forest type provided insights into where a species is likely to be found, but is less likely to show where disturbance and land-use change that can compromise the ES will likely occur. While the LHF, SFM, and MMF forest types
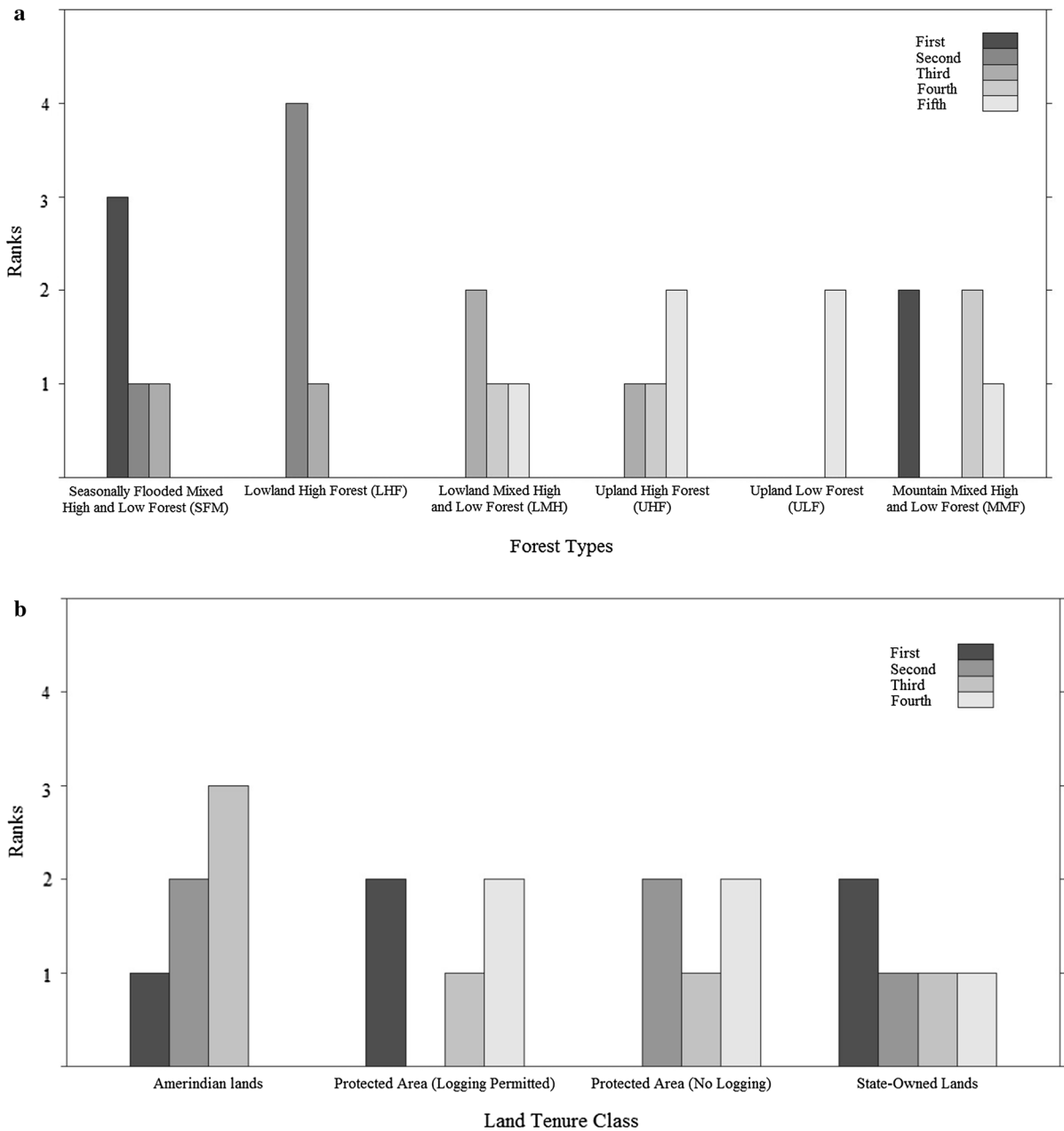
Fig. 3 **a** The rank of the five select multiple-use species across forest types. **b** The rank of the five select multiple-se species across land tenure classes

had the highest density of plants (see Table 3) in the aggregated sample, wider distributions for the single species (see Table and Fig. 3) were observed. In this sense, the distribution by forest types was predictable. But since forest types transcended land tenure boundaries, exposure to exploitation will similarly vary

across space. If an Amerindian community decides to protect a species, for example, but there is no agreement with managers on state-owned property, the ES associated with that species can be compromised on the latter land tenure class. In the real world study area setting, there are no guidelines suggesting

how logging permits may be allowed within the vicinity of indigenous lands, so a species that is important to indigenous peoples and their wildlife can potentially be treated differently across these land tenure boundaries. On the ground, land tenure types determine the type of pressures that may be exerted on a plant species, driven by economic rather than ecological forces, suggesting that land tenure needs closer attention when analyzing the well-being of plant species associated with important ES. Generally, ecologists avoid political, economic, and social issues in arriving at their conclusions (see Peters 1996; Sheil and van Heist 2000), but ecological processes, especially those relating to sustainable forest management (see Vandermeer and Perfecto 1995), do not occur in isolation of political, social and economic issues. It is therefore important that managers in the tropics consider their landscape realities, including how land ownership will impact species exploitation.

Secondly, forest types are important to study species distribution to understand how indigenous peoples' activities influence the presence of ES within a landscape. The land tenure boundaries considered in this paper were imposed upon the indigenous peoples-influenced landscape, areas of land that historically had no boundaries. Therefore, while direct impacts on ES were not considered on this paper, the fact that a map containing different tenure boundaries is present in the Rupununi represents a changing landscape in the context of Wu (2013b). Prior to the imposition of boundaries, forest type alone would be sufficient to consider in studying species distribution. In this regard, it was not surprising that the highest species densities were associated with forest types within which indigenous peoples practice swidden agriculture, hunt, and gather, similar to what is observed elsewhere in the Neotropics (e.g., Huber and Zent 1995). However, like other Neotropical landscapes, the configuration is changing, and forest types may be less important in predicting where impacts may occur.

Thirdly, plant distribution patterns within land tenure classes need to be examined in greater detail. While this paper used density as the measure to study how an aggregate sample and individual species were distributed, it is perhaps distribution patterns within these frames of reference that will determine the sustainability of a species and the ES with which it is associated. Loggers, for example, will more than likely

request state-owned lands if they had a sense of where in space a species of interest is found and whether this will make an investment in its exploitation worthwhile. Therefore, in addition to where species are found, their spatial distribution and what this may mean for exploitation needs to be considered. Additional work is therefore required to determine distribution patterns for both the aggregate sample and individual species to understand the livelihood of exploitation and hence depletion of ES. It is possible that different land tenure types may present a different spatial distribution pattern for a species or the aggregate sample, making it necessary to consider where there may be hotspots for exploitation. In fact, Turner et al. (2013) pointed out that managing spatially explicit relationships among different ES can sustain landscape resilience and help to protect ES. Future work will consider spatial distribution patterns by land tenure classes (and forest types) and the likelihood of land-use change being influenced by these.

Fourthly, the sample size and composition used to understand how the plants are distributed by the two frames of reference is important. This paper was perhaps one of the first to consider more than one species and more than one land tenure class in studying their implications for ES distribution. At the level of individual plant species (Table 4), different outcomes were observed compared to the aggregated sample. The density of the five species (Table 6) across forest types showed that three (L. alba, P. campestris and M. bidentata) had the highest density in SFM forests. This was in stark contrast to the aggregated sample which had the highest density in LHF forest types. Therefore, depending on the purpose of the analysis, different outcomes can be reached based on the sample. It appears that if our interest is in indigenous peoples' livelihoods and landscape sustainability, and considering the wide range of ES they derive from their forests (Table 1), that using a larger sample of plants and their accompanying ecosystem services will be more appropriate. If there is concern over the well-being of a particular ES and species, then focusing on that species may be appropriate. Either way, our results do seem to suggest that working across land tenure boundary lines is important for managing ES within tropical landscapes.

Finally, at the core of this paper was the question, "what is the most appropriate frame of reference for assessing ES sustainability in the tropics, forest type or

land tenure?" Based on our results, it appears as though both frames of references are relevant within certain contexts. At the landscape scale, with many land tenure classes, assessing ecological parameters, such as plant density, may provide more meaningful insights if land tenure classes are the frame of reference. In cases where only one land tenure class is considered, however, forest type may provide more meaningful insights into where to protect a species. Our concern is this paper was with spatially heterogeneous landscapes, defined by the number of land tenure classes and forest types, and the potential these may have for changing landscapes and impacting ES distribution (see ; Turner et al. 2013; Wu 2013a). Change in disturbance regimes and LUCC are likely to emanate from within land tenure classes in the tropics and therefore understanding how the motivations for resource use and protection within these need to be better understood by the landscape ecology community. Including land tenure boundaries as a part of the landscape ecologist's toolkit within the tropics is important to modeling how ES distribution can be sustained for indigenous peoples and wildlife alike.

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