

Stability in a changing world – palm community dynamics in the hyperdiverse western Amazon over 17 years

INGRID OLIVARES^{1*}, JENS-CHRISTIAN SVENNING¹, PETER M. VAN BODEGOM², RENATO VALENCIA³ and HENRIK BALSLEV¹

¹Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark, ²Institute of Environmental Sciences CML, Leiden University, Einsteinweg 2, 2333 CC Leiden, The Netherlands, ³Laboratorio de Ecología de Plantas, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Av. 12 de Octubre 1076 y Roca, Quito, Ecuador

Abstract

Are the hyperdiverse local forests of the western Amazon undergoing changes linked to global and local drivers such as climate change, or successional dynamics? We analyzed local climatic records to assess potential climatic changes in Yasuní National Park, Ecuador, and compared two censuses (1995, 2012) of a palm community to assess changes in community structure and composition. Over 17 years, the structure and composition of this palm community remained remarkably stable. Soil humidity was significantly lower and canopy conditions were significantly more open in 2012 compared to 1995, but local climatic records showed that no significant changes in precipitation, temperature or river level have occurred during the last decade. Thus, we found no evidence of recent directional shifts in climate or the palm community in Yasuní. The absence of changes in local climate and plant community dynamics in Yasuní contrasts with recent findings from eastern Amazon, where environmental change is driving significant changes in ecosystem dynamics. Our findings suggest that until now, local forests in the northwest Amazon may have escaped pressure from climate change. The stability of this rich palm community embedded in the hyperdiverse Yasuní National Park underlines its uniqueness as a sanctuary for the protection of Amazonian diversity from global change impacts.

Keywords: Areaceae, biodiversity, climate change, climatic records, community ecology, directional changes, forest dynamics, forest monitoring, global change, Yasuní National Park

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Introduction

Warming and seasonality have increased in central and eastern Amazon (Malhi & Wright, 2004; Gloor *et al.*, 2015) and evidence for climate-driven changes exists even for the largest forested areas in the tropics (Trumbore *et al.*, 2015). Many tropical forests, including the Amazon basin, exhibit accelerated turnover and increased aboveground biomass of trees (Phillips *et al.*, 1998, 2008, 2009). Long-term records of forest dynamics demonstrated a replacement of moisture-adapted species by drought-tolerant species in Central American forests (Condit *et al.*, 1996; Enquist & Enquist, 2011). In Amazonian plant communities, climate-generalists and drought-tolerant species increased in abundance (Butt *et al.*, 2014) and the combined effect of climatic changes

and other factors such as CO₂ enrichment and fragmentation in central and eastern areas are expected to cause an overall decline of the ecosystem's ability to store carbon (Brienen *et al.*, 2015). Other directional changes are currently taking place. For instance, productivity, mortality, and recruitment have increased in forest fragments and interiors in the central Amazon as a result of a synergistic effect between climate change and CO₂ enrichment (Laurance *et al.*, 2014).

In contrast, climate change in the western Amazon has been of low intensity during the last decades, and in contrast to eastern areas, it is expected to cause less changes in the distribution, diversity, and function of forests (Olivares *et al.*, 2015). The northwest Amazon is the only tropical rain forest area without a warming trend between 1960 and 1998, and there is no evidence for decreased precipitation during the same period (Malhi & Wright, 2004; Gloor *et al.*, 2015). Concomitantly, the northwest Amazon harbor sites without negative trends in tree survivorship or forest productivity and biomass (Brienen *et al.*, 2015). However, there are

*Present address: Institute of Systematic Botany, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland

Correspondence: Henrik Balslev, tel. +45 8715 6568, e-mail: henrik.balslev@bios.au.dk

surprisingly few studies on long-term forest dynamics for western Amazon forests (Bass *et al.*, 2010), limiting our ability to assess whether such persistence is a general phenomenon for this region. Such studies are urgently needed because this area is crucial for the survival of thousands of plant and animal species (Bass *et al.*, 2010).

Within the hyperdiverse Amazon region, palm species are iconic elements and are abundant in most forest types (Gentry, 1988; Henderson *et al.*, 1995; Kahn & de Granville, 1992). The understory is occupied by small *Geonoma* and *Chamaedorea* species, while tall palms like *Iriartea deltoidea* and *Oenocarpus bataua* dominate the canopy. Notably, the most abundant tree species across the Amazon basin is a palm, *Euterpe precatoria* (ter Steege *et al.*, 2013). Another palm, *I. deltoidea*, is the most common tree in the western Amazon basin (Pitman, 2000; Macía & Svenning, 2005). It thus follows that studying palm communities is important to understand the dynamics of Amazonian forests.

The distribution and diversity of palms can change rapidly in response to increasing drought (Condit *et al.*, 1996; Walther *et al.*, 2007), because many are sensitive to water availability, as also seen in their strong links to precipitation patterns at continental scales (Bjorholm *et al.*, 2005) and topographic–hydrological gradients at local scales (Kahn & de Castro, 1985; Svenning, 1999; Kahn & de Granville, 1992). Even the absence of climatic change in northwest Amazon does not guarantee that forest dynamics is not affected. Palms are highly dependent on frugivorous birds and mammals for their dispersal (Zona & Henderson, 1989), and several studies have documented strong effects of defaunation on palm abundance and recruitment (Galetti *et al.*, 2006, 2013; Fadini *et al.*, 2009; Sica *et al.*, 2014). Hence, deforestation caused by oil concessions and the construction of new roads (Finer *et al.*, 2014), widespread defaunation (Espinosa *et al.*, 2014; Ghanem & Voigt, 2014) and changes in indigenous population densities and land use (Pitman, 2000) might be affecting palm community dynamics in the western Amazon. Moreover, atmospheric CO₂ levels continue to increase (Keeling & Whorf, 2005), with potential effects on plant communities. It is thus important to better understand the response of the region's palm communities to these ongoing global changes.

Developing an understanding of tropical rain forest ecosystem dynamics in an era of global change requires both experimental and observational approaches. Observational approaches lack the control of environmental factors that experimentation provides, but natural forest areas include rich and intricate networks of interactions that may shape biological responses and are difficult to capture in experiments. Thus, long-term

forest monitoring is important for assessing the processes that determine ecosystem responses. Using this approach, we analyzed the climatic record at Yasuní Scientific Station, Ecuador, and combined data from a 1995 census and a 2012 recensus of the palm community near the station to address two main questions: (i) Were there changes in precipitation, temperature or river level over the period 1995–2012? (ii) Were there differences in palm species richness and number of individuals recorded at each census?

We use null models of community structure and composition to determine whether observed current and previous patterns of community assembly reflect directional changes. We define stable community dynamics as the absence of significant changes in species composition and abundance (McGill *et al.*, 2015). This is, to our knowledge, the first long-term monitoring study of palm community dynamics in the Amazon basin.

Materials and methods

Study site

Data were collected in the western Amazon basin in the Yasuní National Park (0°40'29"S, 76°23'51"W) in eastern Ecuador. Low Piedmont hills at 100–300 m above sea level and small floodplains shape the landscape. The area has been disturbed by oil exploration, and a road that crosses the park since 1994 has facilitated the establishment of indigenous settlements in formerly unoccupied parts and has increased the possibilities for bushmeat hunting. Nevertheless, specific locations where sampling was done are all old-growth forest. *Terra firme* forest is the main habitat in Yasuní, while periodically inundated bottomlands and permanent swamps also occur (Pitman, 2000). Rainfall and temperature data spanning the last decade have been gathered at Yasuní Scientific Station. Although there have been years without data (including the period between 2011 and 2015 for rainfall and temperature, and 2012 and 2015 for river level), these gaps do not affect the overall record (Fig. 1). The level of the Tiputini River at the Yasuní Scientific Station was measured as the distance between the water surface and a fixed arbitrary point in the riverbank. The climate in Yasuní is perhumid and hot; mean annual precipitation is c. 3000 mm with a peak of rainfall during May–June. The mean annual temperature is 26–28 °C (Svenning, 1999).

Sampling design

In 2012, we recensused 18 transects of 5 × 500 m (0.25 ha) originally established in 1995 in areas within 0.5–8 km of the Yasuní Scientific Station (Appendix S1). Transects were located and measured following a standardized protocol (Balslev *et al.*, 2010), and the minimal distance between transects was 100 m, while the maximum distance was 12.5 km.

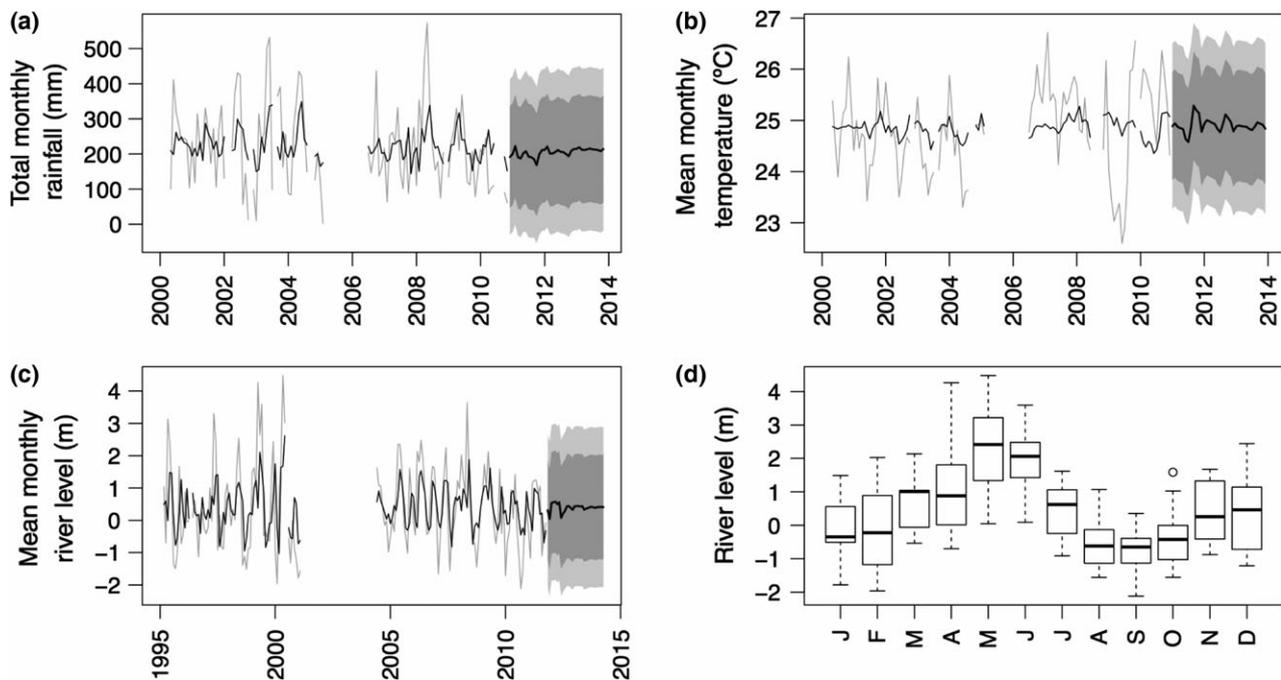


Fig. 1 Climatic time series for the last decade at Yasuní Scientific Station. Time series plots show the observed (gray lines) and ARIMA fitted (black lines) values for rainfall (a); temperature (b); and river level (c); boxplots show the monthly variation in river level height (d). Fitted models indicate that all climatic variables remained constant during the previous decade, and no directional trends were expected during the following 3 years after last measurements (80% and 95% confidence intervals shaded in dark and light gray, respectively).

Transects are dispersed in an area of more than 50 km² that covers the main topographic types of this Amazonian landscape: bottomlands ($N = 6$), slopes ($N = 7$), and ridges ($N = 5$). Ridges and bottomland transects are areas with homogeneous physiography, without overlap of habitats. Ridge transects follow the highest points (200–300 m above sea level) in well-drained upland *terra firme* forests. Bottomland transects are located in flat areas, periodically flooded by rivers or streams, some of them are well-drained areas, while others maintain high soil moisture throughout the year (Balslev *et al.*, 2010; Kristiansen *et al.*, 2011, 2012). Slope transects are perpendicular to elevation curves and they combine environmental features from the *terra firme* and the bottomlands and therefore have heterogeneous relief and moisture conditions.

Hydrology and canopy structure

In 1995, we recorded soil moisture and the presence of canopy gaps along each transect following a standardized protocol (Balslev *et al.*, 2010). Soil moisture is an estimation of the persistence of water within the soil, and was recorded in three categories where 0 = dry soil, 1 = muddy soil and 2 = standing water. Gaps were defined as vertical openings extending from ≤ 2 m above the ground to the sky (Brokaw, 1982). In 2012, we recensused soil moisture and the presence of canopy gaps using the same method, to assess whether these environmental factors had changed between 1995 and 2012.

Palm species inventory

Within each transect and during both censuses (1995 and 2012), all palm individuals were counted and identified to species. Palm individuals were not tagged, but the transect areas were. In 1995, all transects were carefully tagged every five meters with 1 m vertical plastic tubes. In 2012, we found all tubes and delimited each transect total area with a rope before counting all palm individuals. Each individual was assigned to one of the three categories; seedlings were individuals with undivided leaves, juveniles were individuals without evidence of reproduction, and adults were individuals with evidence of reproduction. One of the authors of this study (HB) participated in both censuses and was responsible for the identification of species. For clonal and multistemmed species, each ramet was counted as a separate individual. Voucher specimens were collected and deposited in herbaria in Aarhus (AAU) and Quito (QCA). Identification initially followed Henderson *et al.* (1995) but was subsequently updated to follow the latest taxonomic monographs and revisions (Henderson, 2011a,b).

Data analyses

Environmental changes. To investigate whether there have been temporal changes in climatic conditions at Yasuní Scientific Station, we used autoregressive integrated moving average (ARIMA) models for time series spanning the years 2000–2010 (rainfall and temperature) and 1995–2011 (river level). We used the results from ARIMA models to forecast

climatic trends within the next 3 years after the last year recorded. We tested the differences in soil moisture content and the number of canopy gaps from 1995 to 2012 using paired *t*-tests.

Palm abundance data. We performed all analyses using relative abundance values, that is, the number of palm individuals – per species or per transect – found relative to the total number of palms in each census. We included all palm species found, but we used only the total number of juvenile and adult individuals (hereafter also referred as abundance), excluding seedlings because they may exhibit ephemeral and divergent patterns in abundance relative to adults or juveniles (Metz, 2012).

Changes in the number of palm individuals per transect from 1995 to 2012. First, we used a paired *t*-test to assess the changes in total number of palm individuals per transect. As a confirmatory test, we used an analysis of variance with repeated measures (RM-ANOVA). Three factors and their interactions were assessed (i) census: time of census between 1995 and 2012, (ii) habitat: bottomland, slope, ridge, and (iii) life stage: juveniles and adults.

Changes in the relative number of palm individuals per species from 1995 to 2012. Using the net change or delta (Δ) for the relative number of individuals, we performed an analysis of variance for the 41 species recorded. To evaluate whether the change in number of individuals differed among life stages (juvenile or adult), growth forms (small or large palms) or habits (solitary or clonal), we assessed these factors and the interactions among life stage and the last two.

All data analysis were performed using the software R 3.2.2, (2015) (<http://www.r-project.org/>).

Results

Environmental changes

There has not been any changes in total monthly rainfall, mean temperature, and mean river level per month during the last decade in Yasuní. Residuals of the ARIMA models for each variable were randomly distributed, and there were no significant lags at 95% confidence interval (results not shown); thus, the models obtained (Fig. 1) provide the best fit to the data. Model-based forecasts for the following 3 years reflected that there are no directional climatic trends (Fig. 1). Still, in 2012, soils were significantly drier ($t = 4.2162$, $df = 17$, P -value = 0.0006), and there were more canopy gaps ($t = -6.3785$, $df = 17$, P -value = 6.9e-06) than in 1995.

Changes in total number of species and individuals

In 1995, we recorded 42 species and 24 496 palm individuals. In 2012, we found 37 species and 17 934 palm

individuals (Table S1). In our analyses, we included only juvenile and adult individuals, which translated into 9854 individuals from 41 species recorded in 1995 and 10 199 individuals from 37 species recorded in 2012. One species, *Mauritia flexuosa*, was excluded from the analyses for 1995 because only two seedlings were recorded.

Between 1995 and 2012, the palm community did not experience significant changes in the number of individuals (paired *t*-test = -0.7562 , $df = 17$, P -value = 0.4599; Fig. 2). This was confirmed by the RM-ANOVA, which showed differences among life stages and habitat, but not among censuses (Table 1). In both years, juveniles were more abundant than adults and bottomlands had the highest abundance of palms (Tables S1 and S2).

Changes in the number of palm individuals per species from 1995 to 2012

The absence of change in the number of individuals held for each of the 37 palm species found in both censuses independently of life stage, growth form, and habit (Table S3). Juveniles and adults of four species were not recorded in 2012 namely, *Bactris schultesii* (11 individuals in 1995), *Desmoncus orthacanthos* (six

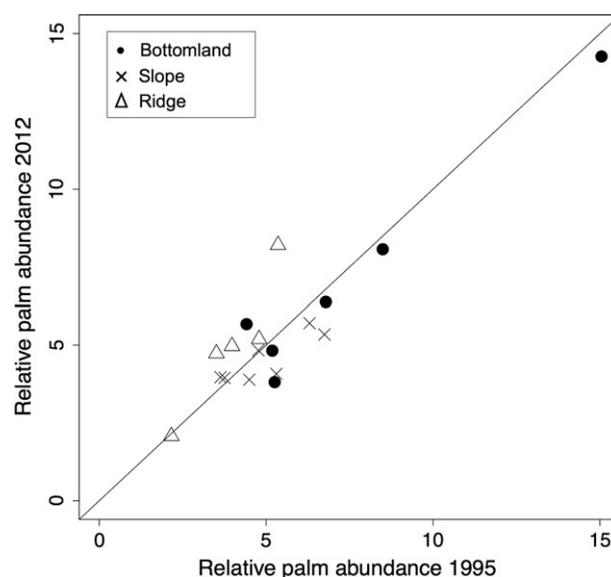


Fig. 2 Relative palm abundance change. Comparison of the relative palm abundance (percentage number of individuals with respect to the total) in 1995 vs. 2012 for 18 transects in the rain forests of Yasuní National Park. Each mark corresponds to one transect. Marks falling on the 1 : 1 line indicate no change in palm abundance for that transect. Marks falling either above or below the line indicate transects with increasing or decreasing palm abundance, respectively, but none differed from random expectations.

Table 1 RM-ANOVA for the determinants of palm abundance in 18 transects in the rain forest of Yasuní National Park in 1995 and 2012

| | Df | Sum Sq | Mean Sq | F-value | P-value |
|-----------------------------|----|-----------|---------|---------|--------------|
| Habitat | 2 | 292 931 | 146 466 | 7.5074 | 0.001231** |
| Life stage | 1 | 867 464 | 867 464 | 44.4636 | 9.186e-09*** |
| Census | 1 | 1653 | 1653 | 0.0847 | 0.771985 |
| Habitat: life stage | 2 | 6783 | 3391 | 0.1738 | 0.840859 |
| Census: habitat | 2 | 19 174 | 9587 | 0.4914 | 0.614213 |
| Census: life stage | 1 | 3570 | 3570 | 0.1830 | 0.670344 |
| Census: habitat: life stage | 2 | 10 378 | 5189 | 0.2660 | 0.767367 |
| Residuals | 60 | 1 170 571 | 19 510 | | |

Three effects and their interactions were assessed to test for abundance changes: (i) census: time of census (1995 and 2012); (ii) habitat: bottomland, slope, ridge; (iii) life stage: juveniles and adults. Significance: ** $P < 0.01$, *** $P < 0.001$.

individuals), *Geonoma interrupta* (five individuals), *Geonoma triglochis* (three individuals). The abundance of these species represented less than 0.001% of the total number of individuals found in 1995, and therefore, their absence did not emerge as any major change. Overall, no significant 1995–2012 census changes occurred in any of the species in this palm community of Yasuní (Fig. 3).

Discussion

Over 17 years since the mid-1990s, a palm community in Yasuní National Park has not undergone any significant change at the landscape scale. We did not find changes between 1995 and 2012 in the total number of individuals or for any single palm species. Even the abundance of a dominant species such as *I. deltoidea*, which is highly sensitive to drought (Pallqui *et al.*, 2014), remained constant. This stability (*sensu* McGill *et al.*, 2015) coincided with constant patterns in temperature, rainfall, and river level over this multidecadal period. The higher frequency of canopy gaps and decrease in soil moisture likely reflect interannual fluctuations rather than directional climatic changes. The high density of individuals observed in both life stages (juveniles and adults) and across all habitat types (Table S2) indicates ongoing recruitment and consistent adult performance.

Our results underscore that the studied landscape in Yasuní has remained stable in terms of environmental conditions and palm community dynamics over the last two decades. Palms are good indicators of Amazonian forests dynamics because they are common throughout the entire region, and their floristic patterns are similar to other common groups such as melastomes and pteridophytes (Vormisto *et al.*, 2000). The family is particularly abundant in the western Amazon (Montufar & Pintaud, 2006), representing 10% of all trees greater than 10 cm DBH in several 1 ha

(Pitman, 2000) and 25 ha inventories (Valencia *et al.*, 2004) of forest in Yasuní. Amazonian palm genera are widespread, but species are usually constrained by soil and hydrological gradients. Thus, at local scales, different species characterize each topographic unit (Svenning, 1999), and at the regional scale, all Amazonian forest types contain specific palm representatives (Balslev *et al.*, 2011). Further, palms are morphologically diverse, and most Amazonian forest harbor small and large palm species that occupy most forest strata (Henderson, 1995). A variety of Amazonian life forms exists, including clonal or solitary palms with subterranean, aerial, or climbing stems, and with simple or divided leaves of various lengths from a few centimeters to several meters (Henderson, 1995). This study captured all the variation of this representative plant group in the hyperdiverse forests of Yasuní. Our findings should therefore be considered as a robust example of the current stability in the forest communities of the northwestern Amazon.

Interestingly, our results contrast with those from central, east, and southern Amazon, where climate change (Malhi & Wright, 2004; Gloor *et al.*, 2015) and deforestation (Soares-Filho *et al.*, 2006) are stronger. For instance, Laurance *et al.* (2014) monitored 69 1-ha permanent plots in forest edges and preserved forest interiors in the central Amazon from 1980 to 2012. They showed that mortality and recruitment of trees and lianas in edge and forest interiors have accelerated over time. Here, however, we show that palm abundance has not changed at the landscape scale in the western Amazon. While our study did not explicitly determine dynamic rates (e.g., mortality, productivity), the stability in abundance for palms overall and per species was highly consistent for all transects, and hence serves as robust indicator of community stability in this tropical forest landscape. This lack of change coincides with results from an analysis of the 25-ha permanent plot at Yasuní, where there is no evidence that trees ≥ 1 cm

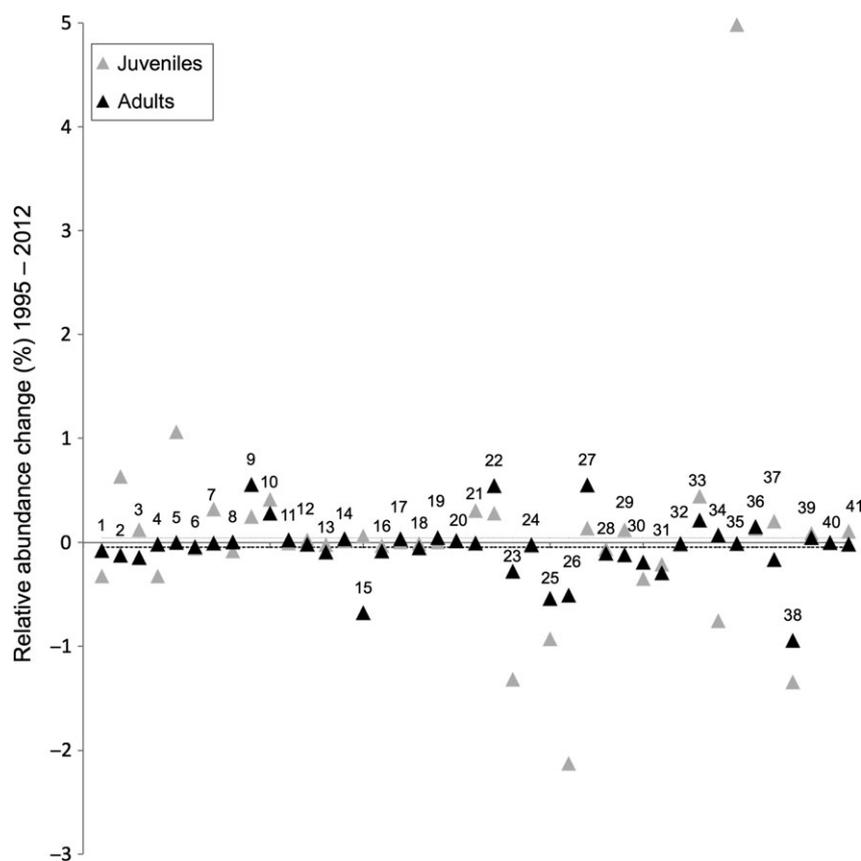


Fig. 3 Changes in the relative number of individuals from 1995 to 2012 for 41 palm species in Yasuní National Park. The abundance change in juveniles and adults is shown for each species, values correspond to the relative change with respect to the total palms found in each census. No significant changes occurred for any species (see Table S3 for ANOVA results). Dotted lines show the average percentage of abundance change for all adults (in black) and all juveniles (in gray) from 1995 to 2012. 1 = *Aiphanes ulei*; 2 = *Ammandra decasperma*; 3 = *Aphandra natalia*; 4 = *Astrocaryum chambira*; 5 = *Astrocaryum urostachys*; 6 = *Attalea butyracea*; 7 = *Attalea insignis*; 8 = *Attalea maripa*; 9 = *Bactris concinna* var. *concinna*; 10 = *Bactris corosilla*; 11 = *Bactris maraja* var. *juvuensis*; 12 = *Bactris maraja* var. *maraja*; 13 = *Bactris schultesii*; 14 = *Bactris simplicifrons*; 15 = *Chamaedorea pauciflora*; 16 = *Chamaedorea pinnatifrons*; 17 = *Desmoncus giganteus*; 18 = *Desmoncus mitis* subsp. *mitis*; 19 = *Desmoncus orthacanthos*; 20 = *Desmoncus polyacanthos*; 21 = *Euterpe precatoria*; 22 = *Geonoma aspidiifolia*; 23 = *Geonoma brongniartii* *brongniartii*; 24 = *Geonoma interrupta*; 25 = *Geonoma macrostachys* var. *acaulis*; 26 = *Geonoma macrostachys* var. *macrostachys*; 27 = *Geonoma maxima* subsp. *multiramosa*; 28 = *Geonoma stricta* subsp. *arundinacea*; 29 = *Geonoma stricta* subsp. *stricta*; 30 = *Geonoma stricta* var. *trailli*; 31 = *Geonoma supracostata*; 32 = *Geonoma triglochis*; 33 = *Hyospathe elegans*; 34 = *Iriarteia deltoidea*; 35 = *Oenocarpus bataua*; 36 = *Oenocarpus minor*; 37 = *Phytelephas tenuicaulis*; 38 = *Prestoea schultzeana*; 39 = *Socratea exorrhiza*; 40 = *Syagrus sancona* 41 = *Wettinia maynensis*.

DBH have changed in density or biomass between 1995 and 2003 (Valencia *et al.*, 2009). Given the stability in climate in the western Amazon compared to its southern and eastern counterparts, this pattern is expected to hold under future climate scenarios (Cook & Vizy, 2008).

At the local scale, eastern Amazonian forests are able to maintain their photosynthetic capacity after long periods of soil drought (Rowland *et al.*, 2015), and reestablish low mortality rates after extreme drought events (Laurance *et al.*, 2001). However, a major issue in the eastern Amazon is the combined effect of extreme droughts and high fragmentation, which increases the frequency of fire events (Brando *et al.*,

2014). Fire is a factor that can transform Amazonian forests' structure and composition in short periods of time (Nepstad *et al.*, 1999) and at large scales (Cochrane & Laurance, 2002). Western Amazon forests are instead more humid (Malhi & Wright, 2004) and less fragmented (Bonilla-Bedoya *et al.*, 2014). Therefore, they should be less susceptible to changes in biomass and productivity.

Despite the fact that climate in this part of Yasuní has not changed, the area is under the influence of other factors such as road building, increasing CO₂ levels, and defaunation. All these are factors that threaten forest ecosystem functioning and could have driven palm community changes. In this regard, the palm

community might be even resistant to changes in CO₂ enrichment and defaunation or they might cause lag effects (e.g., Osuri *et al.*, 2016). If such a resistance or lag effects exist, their specific mechanisms should be tackled in further community dynamic studies.

Unfortunately, up to now, local studies monitoring western Amazon forests in the long term have been almost nonexistent. Data from a few permanent plots have been gathered during the last decade, but instead of being analyzed at the local or landscape scale, such as in central and eastern Amazon, their findings have been mostly reported as part of regional analyses (e.g., Brienen *et al.*, 2015), limiting our ability to discern the scale-specific dynamics. Clearly needed studies include a spatial analysis that evaluates the effect of road distance on the abundance of palms, and others that compare the dynamics of palms in less defaunated areas of Yasuní.

The observed stability in community composition and environmental conditions in this Yasuní forest landscape is important as it indicates that western Amazonian forests can still be maintaining their structure and functioning despite the ongoing global changes. Western Amazon forests encompass exceptional biological richness (Bass *et al.*, 2010) and act as corridors between low- and highland areas, strongly needed for the climate-tracking migrations of many species in the region (Feeley, 2012). Furthermore, these forests play a key role in the carbon balance of the whole basin, because they assimilate and fix larger amounts of carbon than those in the east (Malhi *et al.*, 2006; Aragao *et al.*, 2014). Our study adds to evidence that large areas of well-preserved forests in western Amazonia may so far have been less exposed to the ongoing global changes than other areas have suffered from, further highlighting their conservation importance. If northwestern forest communities are preserved, they are expected to withstand the impact of global changes due to their stable climatic conditions (Olivares *et al.*, 2015). Avoiding fragmentation in Yasuní is likely paramount to avoid the negative cascading effects that the central and eastern areas of the Amazon are already facing.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Environmental variables and palms data recorded in 1995 and 2012.

Table S2. Palm species and total number of individuals per life stage and for each census.

Table S3. Analysis of variance of palm abundance change for 21 species and three species attributes.

Appendix S1. Study area at the Yasuní Scientific Station within Yasuní National Park, Ecuador.