EFFECTS OF CLIMATE CHANGE ON CENTRAL AMAZONIAN FORESTS: A TWO DECADES SYNTHESIS OF MONITORING TROPICAL BIODIVERSITY

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Abstract: Central Amazon has been subjected to a higher frequency of extreme climatic events, such as very dry or very wet years, in the last decades. Here, we report a 20-year monitoring of 6 biological groups over 100 km^2 of typical terra-firme forest at Ducke Forest Reserve, Manaus. Most assemblages had a decrease in abundance (9 – 35 %) and richness (8 – 25 %) along time, with some taxonomic and functional reorganization. Taxonomic and functional composition changes along time were more extensive in the valleys for trees and ants, and in first-order streams for fish; while bird and small trees had different patterns of composition change in valleys and plateaus. Although the signal of change was not congruent across all assemblages, patterns indicate that the forest and streams are becoming more dynamic as the hydrological cycle intensifies due to climate changes, and these new environments are already filtering species, at least in some well monitored taxonomic groups. Our data, in combination with other studies, suggest that riparian areas in the valleys are hydrological refuges during droughts, although also susceptible to disturbances induced by excessive precipitation and windstorms. In face of the importance of valleys as refuge, its sensibility and the unknown effects of potential migrations from higher topographic areas due to climate change, the

conservation of large and extensive riparian areas seems to be of surmount importance to the future of Amazonian biodiversity.

Key-words: community ecology; functional ecology; LTER; long-term ecological sites.

INTRODUCTION

Atmospheric concentrations of CO_2 have been rising steadily since the end of the 19th century with a concomitant increase in temperatures around the world (IPCC 2014). This trend has accelerated since the 1970's, and is associated with changes in the distribution patterns of precipitation (Gloor *et al.* 2015, Chaudhari *et al.* 2019). In the Amazon, there is an intensification of the hydrological cycle since the 1980's, with wet seasons becoming wetter and dry seasons drier, and an increase in the frequency of extreme floods and droughts (Gloor *et al.* 2013, 2015). These climatic changes have had dramatic impacts on Amazonian human populations, as in the drought of 2005 (Marengo *et al.* 2008, Marengo & Espinoza 2016) and floods of 2012 and 2014 (Espinoza *et al.* 2014, Marengo & Espinoza 2016), but yet the short and long-term effects on Amazonian biodiversity are not fully documented nor understood.

In response to climate change, organisms can adjust (through phenotypic plasticity) or adapt (through genetic change) to the new environments, or also shift their geographic distributions to where the climate is more suitable (Bellard *et al.* 2012). Several studies (review in Parmesan 2006) have documented changes in phenology due to either plastic or genetic changes (Root *et al.* 2003) and migrations of species towards higher latitudes or altitudes, which are compatible with responses expected under increased temperatures. In the lowland tropics, temperature changes are smaller than in higher latitudes and are not expected to be the main drivers of changes in species behavior and distribution. Instead, changes in precipitation patterns are being much more intense and have been already documented to cause large tree mortality in some regions (Phillips *et al.* 2009, Feldpausch *et al.* 2016) and should be expected to be the main drivers of change in the medium-term.

If not all species and populations can adjust or adapt, we can expect a differential performance of species to the new conditions and extreme climatic events, and thus changes in diversity and composition of biological assemblages. As a general expectation, sensitive species should decrease in abundance whereas tolerant species should increase or remain stable. Therefore, diversity changes will depend on the balance between the loss of sensitive species and the colonization or abundance increase of tolerant species. Changes in phenology, performance and species loss can also change interaction networks, increasing the impact on ecosystem functioning (e.g. Galetti *et al.* 2013, Sakai & Kitajima 2019).

Although land-use change is still the largest source of detrimental impacts to tropical forests, studies suggest that climate change could surpass habitat destruction as the most significant global threat to biodiversity over the next few decades (Leadley *et al.* 2010). Models of vegetation response to climate change have suggested a high probability of Amazon forest dieback in the future (Malhi *et al.* 2009), while physiological studies suggest that trees have the capacity to adjust their functioning to changing environments (Lloyd & Farquhar 2008, Sterck *et al.* 2016). Apart from these large-scale catastrophic predictions, the effects of climate change on tropical forests as an ecosystem and on most biological communities are still in debate and evidence for them are inconclusive. Moreover, there are still more studies of the responses of plant communities to climate change (e.g. Feeley *et al.* 2009, Butt *et al.* 2014, Muelbert *et al.* 2019) than of animal communities, and a predominance of modelling studies, mostly using SDM projections (e.g. Vasconcelos *et al.* 2018, Lima *et al.* 2019, but see Miles *et al.* 2004) over direct monitoring. Detection of direct changes requires repeated observation of fixed localities over time, which is precisely the core of the Long Term Ecological Research Sites (LTER). The LTER program started in the US in 1980, and since then has spread all over the world, with presently over 800 sites on almost all of the Earth biomes (> 30 in Brazil). The main goal of LTER sites is to monitor the many aspects of ecosystem function, to support science-based decision making in order to prevent and help solve environmental and socio-ecological problems.

The effects of changes in precipitation patterns on terrestrial organisms are expected to be modulated by local soil and topographic conditions. The vertical distance to the water table, which can be estimated by the Height Above the Nearest Drainage (HAND, Rennó *et al.* 2008) and soil texture determine soil moisture to plants, and may have a direct impact on organisms living in the soil or on its surface (Baccaro *et al.* 2013, Moulatlet *et al.* 2014, Schietti *et al.* 2014), and indirect impacts on other organisms, through changes in plants. Thus, drought effects on plants are expected to be larger or confined to the upper drier parts of the local topography, while valleys, where the water table is continuously superficial, may be buffered. However, periods of higher precipitation are expected to increase waterlogging and affect more strongly the valleys, where rooting depth is shallow due to soil instability, and the probability of tree death might thus increase with heavy rainfall (Toledo *et al.* 2012). Increased precipitation may also affect the structure of aquatic communities, by modifying substrate availability and changing the dynamics of temporary ponds in the valleys (Pazin *et al.* 2006, Espírito-Santo *et al.* 2009). Thus, the increased waterlogging, higher connectivity of the aquatic system and larger intensities of gap formation should induce stronger changes in plant and animal species composition on valleys, during periods of intense precipitation.

In this paper, we assembled a large dataset of 10-18 years of monitoring of terrestrial (trees, palms, lianas, birds and ants) and aquatic (fish) assemblages in a Long Term Ecological Research (LTER) site in central Amazonia (Brazil). Assemblages were sampled with the same methods across time to determine patterns of change in the abundance, species richness and species taxonomic and functional composition. More specifically, we addressed the following questions: 1) What are the climate trends at the Ducke Reserve along the last 53 years and specifically during the last 18 years, which cover the period of biodiversity monitoring? 2) Are the metrics of assemblage structure changing directionally over time, as climate changes? 3) What are the main functional changes? 4) Do the local environmental conditions modulate assemblage composition changes? We expected that increased frequencies of droughts and periods of intense precipitation observed along the last two decades would lead to directional changes in the abundance, richness and composition of the terrestrial and aquatic assemblages.

MATERIAL AND METHODS

Study area

The study area is located 26 km north of Manaus, Brazil (2º 55 47.80 S; 59º 58 30.34 W) in the Ducke Forest Reserve (hereafter Ducke Reserve), a long-term ecological research site (LTER, or PELD in the portuguese acronym) since 1999. The Ducke Reserve covers 10.000 ha (10 × 10 km) of *terra-firme* tropical rainforest. Although surrounded by the urban sprawl from Manaus city, this area does not suffer any obvious environmental impact within its borders. Mean annual temperature is around 26 ºC, and mean annual rainfall ca. 2570 mm, with a two to three months dry season (< 100 mm rainfall) between July and October (RD meteorological series 1966-2018, see Figure 1). Altitude varies from 30 to 120 m, and soils are derived from tertiary marine sediments from the Alter-do-Chão formation (Chauvel *et al.* 1987). There is a continuum of soil change from the upper flat terraces (locally known as plateaus) to the valleys around watercourses. The ridges and flat terraces have clayey soils, which become sandier as the altitude decreases, with the mineral fraction becoming almost pure sand in the valleys (Chauvel *et al.* 1987). Vegetation is dense *terra-firme* forest, with a closed canopy 30 - 37 m high and emergent trees up to 40 - 45 m (Guillaumet 1987).

Biological monitoring

Monitoring of terrestrial organisms (trees, palms, lianas, ants, birds) was conducted in plots positioned along altitudinal isolines to minimize altitude and soil variation within each plot, and of aquatic organisms (fish) in plots covering all stream sizes present within the reserve (RAPELD method: Magnusson *et al.* 2005, Costa & Magnusson 2010). At Ducke Reserve, there are 72 permanent terrestrial plots distributed regularly at 1 km intervals, over a 64 km² grid formed by 8 km long trails, and 38 aquatic plots installed where the trails crossed streams. All terrestrial groups were sampled in the same plots, although not all plots were sampled for some groups (Table 1).
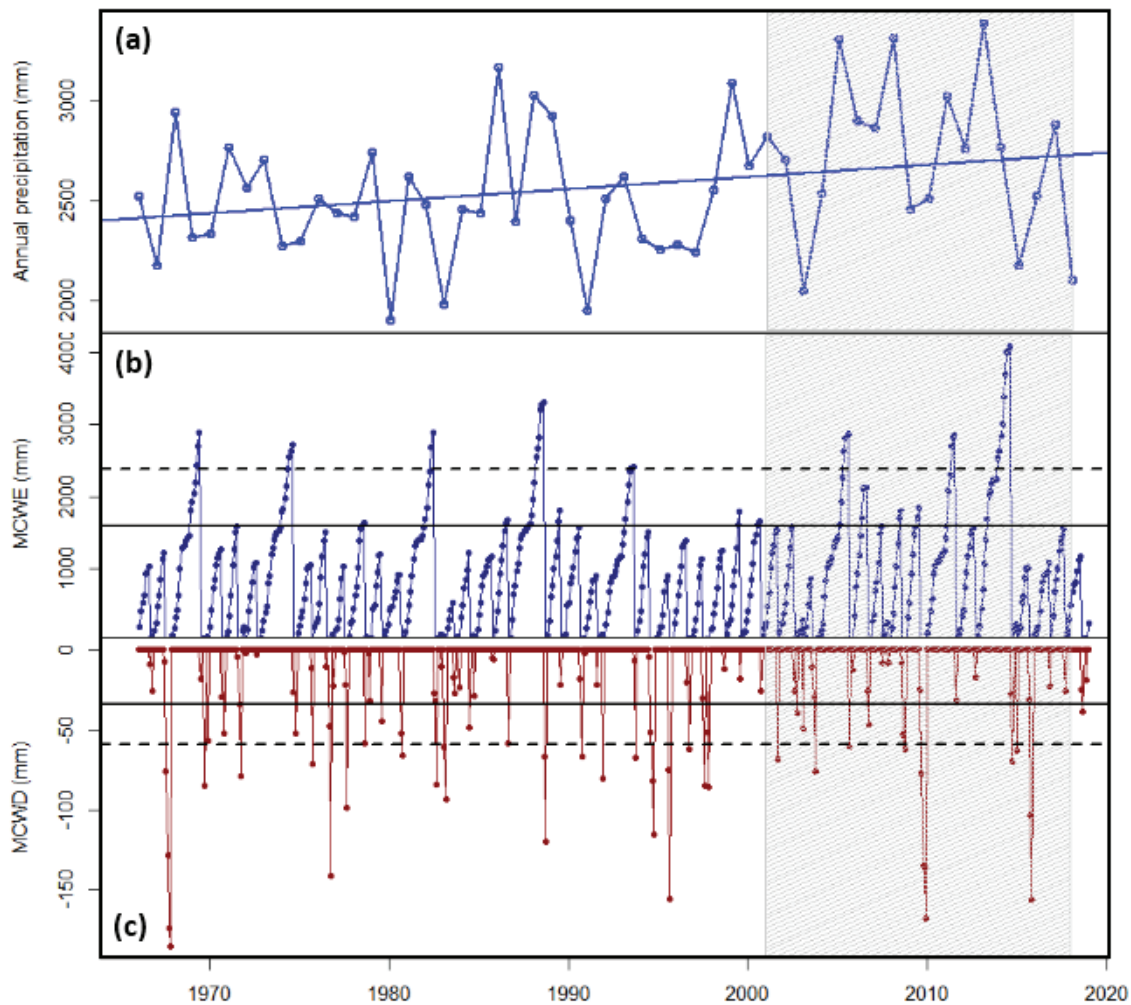
Figure 1. Climatic trends along the last 53 years at Reserva Ducke, highlighting (in grey shadow) the study period (2001-2018). (a) Variation in total annual precipitation, and its increasing trend (regression line). (b) Monthly cumulative values of water excess, CWE, and (c) of water deficit, CWD. Continuous and dashed horizontal black lines indicate values one and two standard deviations higher than the historical mean, respectively.

Trees, palms and lianas: Plots were 250 m long for all terrestrial groups, and width was adjusted as follows for plants: 4 m for trees and palms with 1-10 cm DBH, 20 m for trees and palms with 10 - 30 cm DBH, 40 m for trees and palms over 30 cm DBH, 10 m for lianas with 1 - 5 cm and 40 m for lianas over 5 cm of the diameter at 1.3 m above their rooting point (*D*). The diameter of lianas (*D*) was measured following the protocol given by Gerwing *et al.* (2006). Trees and palms were measured according to the directions of Condit (1998) adapted to RAPELD plots as described on this online protocol (https://ppbio.inpa.gov.br/sites/default/files/ Protocolo_estrutura_vegetacao_2014_0.pdf). Plants were tagged in each census, and thus dynamics are based on known individuals. Only the

family Bignoniaceae was identified at the species level for lianas, therefore analyses involving liana species diversity are restricted to this family.

Birds: Birds were captured in 30 permanent plots, using 16 mist-nets (each 9 m long, 32 mm mesh size) set in pairs at 10 m intervals along the 250 m length of each plot. Mist-nets were opened between 06:00 and 12:00 and inspected every 40 min. Birds were identified and banded with metal bands (Permits SISBIO 34850 and CEMAVE 3576). Each plot was visited once during each sampling period.

Ants: Ants were sampled in 30 permanent plots, using 10 pitfall traps along the 250 m of each plot. The pitfalls had ~ 9.5 cm in diameter and were partially filled with 70 % alcohol with a drop of neutral detergent and left open for 48 h. All

Table 1. Information on the sampling effort across space and time.

Assemblage	Sampling dates	Effort (# plots)
Trees	2001/03; 2003/05; 2007/09; 2014	21
Lianas	2004; 2014	30
Palms	2001/03; 2003/05; 2007/09	72
Ants	2006; 2012; 2014	30
Birds	2002/04; 2009; 2012; 2013; 2014	30
Fish	2001; 2005; 2011; 2018	26

sampling campaigns were undertaken during the dry season.

Fishes: Fish monitoring was conducted in 26 permanent aquatic plots distributed across first- to second- order streams (according to the Stralher classification) based on a 50 m long stream section registered according the *Igarapes* project (Mendonça *et al.* 2005).

Details on the sampling protocols are available in metadata provided for each focal taxon group at http://ppbio.inpa.gov.br/Eng/inventarios/ducke/ and http://www.igarapes.bio.br/). Details on the sampling effort across time and space for each monitored community is given in Table 1. Functional traits measurements are described in Poorter *et al.* (2018) for trees and Borba (2019) for fish. The species membership to functional guilds are described in Groc *et al.* (2014) for ants and Braga (2019) for birds. The list of traits and guilds is given in the supplementary table S1.

Topography and climatic indices

Environmental data was obtained from the PPBio (Programa de Pesquisa em Biodiversidade) database, available at http://ppbio.inpa.gov.br/Eng/inventarios/ducke/. Topography is represented by the height above the nearest drainage (HAND), which was demonstrated to be a good proxy for the water table depth in central Amazonia (Rennó *et al.* 2008). High values of HAND mean high vertical drainage potential and areas associated with ridges and plateaus, while low values of HAND mean lower vertical drainage potential and are associated with riparian (valley) areas. HAND values of zero represent the drainage network and terrains were the water table is at the surface. HAND was calculated using a digital elevation model derived from radar images of the Shuttle Radar Topography Mission

(SRTM) with a spatial resolution of 90 m, and the drainage network that originates HAND was locally validated in the Ducke Reserve (Schietti *et al.* 2014).

Climatic indices were based on monthly cumulative water deficit (CWD) and water excess (CWE) values over a historical period of 53 years (1966-2018). CWD measures drought intensity, and was calculated for each month following (Aragão *et al.* 2007) from precipitation records, as:

$$CWD_n = CWD_{n-1} + PP_n - ET_n$$

where PP_n is the monthly precipitation (observed at the Ducke Reserve station) and ET_n is the monthly evapotranspiration, assumed to be 100 mm per month, hence the deficits are negative numbers. Whenever calculated CWD_n exceeds zero in a given month, the excess water is assumed to runoff, and the CWD_n for that month is reset to zero, thus $CWD_n \leq 0$ for all months.

Following the inverse logic of CWD, we calculated monthly CWE, to express the intensity of waterlogging. For each month that CWD was reset to zero (no water deficit), the value of CWE was set as the volume of PP of that month minus the monthly ET (100 mm). The CWE for next month was calculated in the same way but adding the CWE of previous months.

Statistical analyses

We used non-metric multidimensional scaling (NMDS) to reduce the dimensionality of the taxonomic species composition of each community. NMDS was run over dissimilarities calculated with the Bray-Curtis index on species relative abundances, with the basic settings of metaMDS function of the vegan R package (Oksanen *et al.* 2019), and with extended

dissimilarities for tree and palm communities. The functional composition was reduced by Principal Component Analysis (PCA) when all attributes were continuous measurements (trees and fish) or by Principal Coordinate Analysis (PCoA) based on Bray-Curtis distance matrices, when attributes were categories (ants and birds). The first two axes of ordinations were retained for visualization and posterior tests.

Abundance (or number of occurrences for colonial organisms such as ants), number of species, species composition and functional composition of the initial and last sampling event were compared using paired t-tests. The first two ordination axes of species composition, either taxonomic or functional, were used as input to the analyses of changes in composition. For all analysis, the plot (aquatic or terrestrial) was the sampling unit.

To determine if the rates of change differ among topographic environments, we calculated the difference in assemblage states from first to last sampling period, and fitted linear models to test their associations with HAND variation. The composition change was measured as the Euclidean distance between the initial and final sampling period of each plot in the bivariate ordination space. All analyses were conducted in the R environment (R Core Team, 2019).

RESULTS

Climatic trends

A conta aqui dá 52 anos

Along the last 53 years (1966 - 2018) we observed at Ducke Reserve a significant linear trend of increasing total annual precipitation (+ 6.02 mm.yr^{-1}, $p = 0.055$) and CWE (+ 4.65 mm.yr^{-1}, $p = 0.024$), but not in CWD (+ 0.03 mm.yr^{-1}, $p = 0.53$). Compared to the patterns along previous decades (1966 - 2000), our study period (2001 - 2018) was characterized by a higher relative frequency of anomalies of water excess (17.5 vs 11.6 % for anomalies 1 standard deviation (SD) higher than the mean, and 7.3 vs. 3.8 % for anomalies 2 SD higher than the mean). Anomalies of water deficit had a slightly decreased relative frequency (7.8 % vs 8.8 % for anomalies 1 SD and 5.5 vs. 5.9 % for anomalies 2 SD higher than the mean) (Figure 1).

Is assemblage composition changing along time and in which direction?

The changes in abundance and richness along 10 to 18 years of monitoring were not fully congruent among the six assemblages evaluated, although most of them had a significant decrease in abundance (birds – 30 %, ants – 29 %, lianas – 9 %, fish – 35 %, Figure 2) and richness (birds – 17 %, ants – 25 %, lianas – 21 %) along time, and only trees had an increase in richness (4 %, Figure 3). There was a congruent directional taxonomic composition change across plots along time for fish, ant and palm assemblages (Figure 4, Table 2). Palm species composition changes along time were mostly driven by abundant species. *Astrocaryum gynacanthum*, responsible for 18 % of all palm individuals in the first census, increased 15 % in abundance, while *Iriartella setigera*, responsible for 15 % of individuals in the first census, decreased 6 % in abundance along time.

Functional composition was evaluated only for trees, birds, ants and fish, and there was a significant change along time for all of them (Figure 5, Table 2). Large trees (> 10 cm DBH) had an increase of individuals with higher wood density, leaf density, leaf dry matter content and chlorophyll, and a decrease of individuals with lower specific leaf area, leaf size, leaf area to xylem area allocation, and leaf area ratio, i.e. changed towards a more conservative strategy (Figure 5a). The functional composition of small trees changed over time in the valleys in the same direction described above, but in the plateaus, the change was towards a more acquisitive strategy (lower wood density, higher pith proportion and larger leaf size, Figure 5b). The ant assemblage changed towards a modest higher relative abundance of Cryptobiotic fungus-growers and Ground-dwelling generalist predators, while Leaf-cutter, Raid hunting predators, and Generalist omnivore ants had a large decrease (Figure 5c). The bird assemblages in the valleys changed towards increased relative abundances of small insectivores, small carnivores and small nectarivores, while medium-sized insectivores and large carnivores decreased (Figure 5d). The fish assemblage changed towards larger relative abundances of fish able to explore lateral ponds, fusiform body shape, and able to feed on small food items, and a decrease of those restricted to the main stream channel.
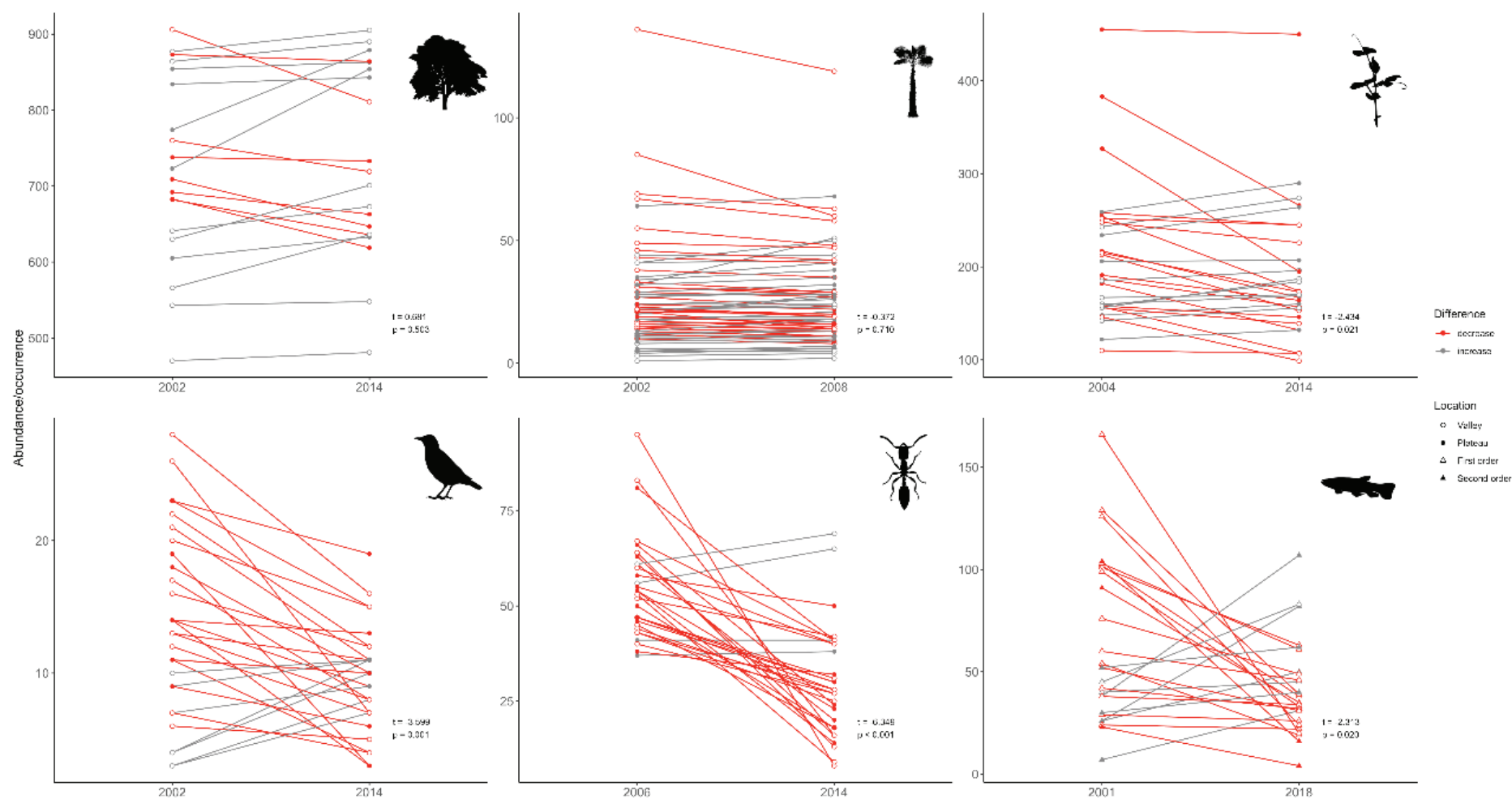
Figure 2. Changes in the abundance of each assemblage (frequency of occurrence for ants) between first and last censuses, in this order from left to right: Trees, Palms, Lianas, Birds, Ants and Fish
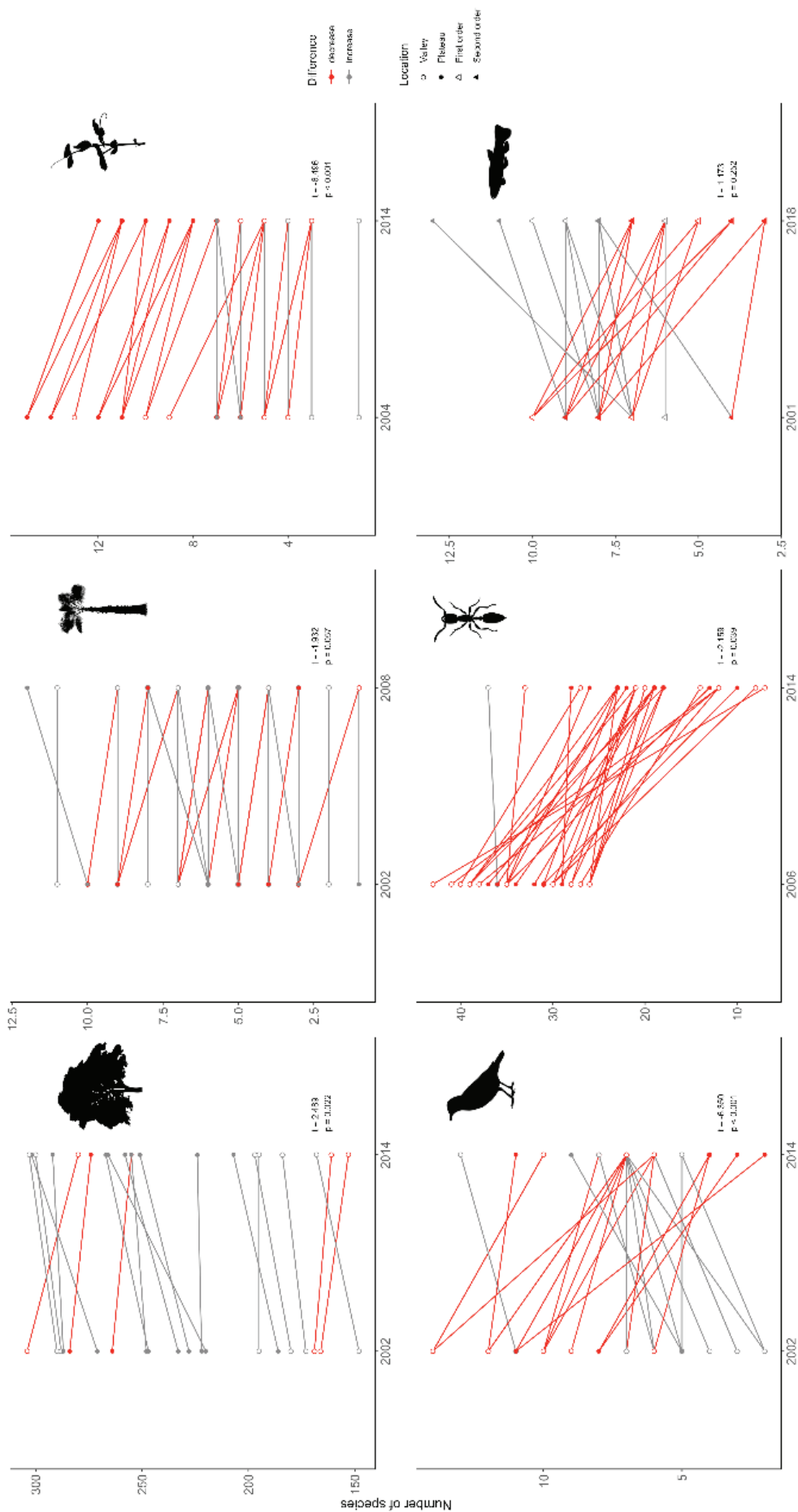
Figure 3. Changes in the richness of each assemblage between first and last censuses, in this order from left to right: Trees, Palms, Lianas, Birds, Ants and Fish.
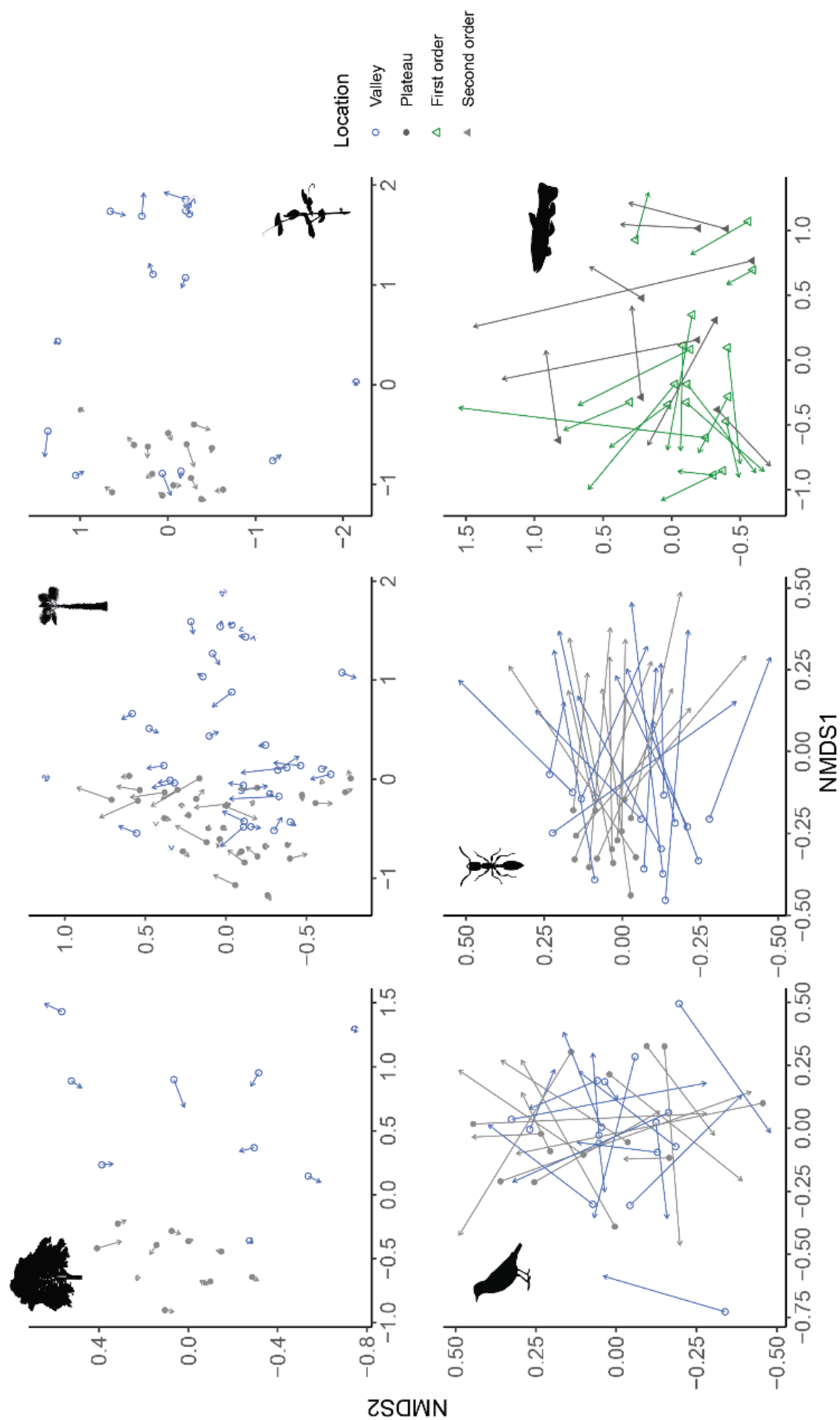
Figure 4. Changes in the taxonomic composition (reduced by NMDS ordination in two axes) of each assemblage between first and last censuses, in this order from left to right: Trees, Palms, Lianas, Birds, Ants and Fish.
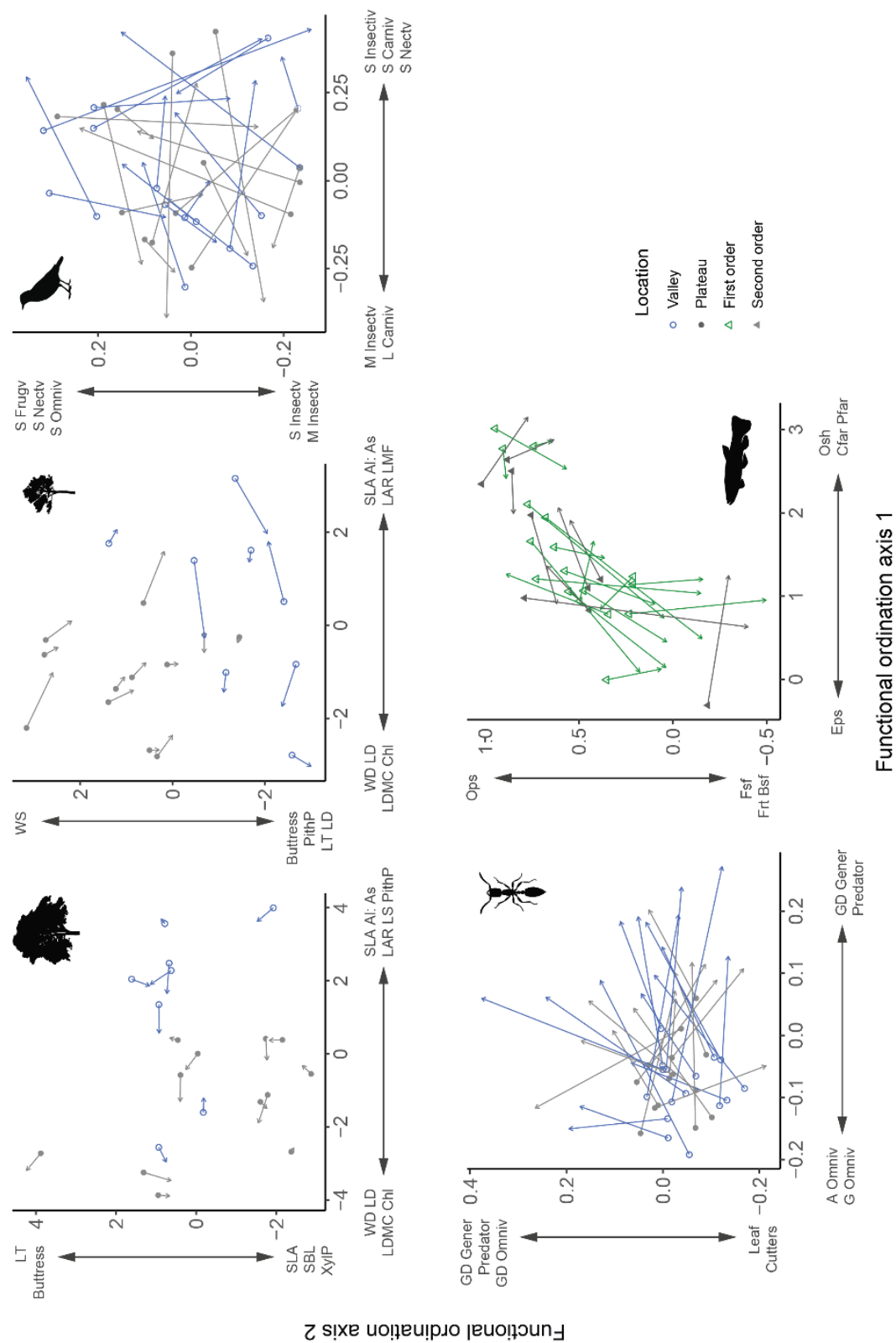
Figure 5. Changes in the functional composition (reduced by PCA or PCoA ordination in two axes) of each assemblage between first and last censuses, in this order from left to right: Large Trees, Small Trees, Birds, Ants and Fish. See Table S1 for the trait and guild's list

Table 2. Results of the paired t-tests comparing taxonomic composition (reduced to 2 axes by NMDS ordination) or functional composition (reduced to 2 axes by PCA or PCoA) between the first and last census of each assemblage.

Composition	Assemblage	Axis1		Axis2		%Variation captured
		t	p	t	p	by ordination
Taxonomic	Trees	1.681	0.109	-1.08	0.29	62
	Palms	0.942	0.350	-3.358	0.001	86
	Lianas	1.023	0.315	-0.883	0.385	73
	Ants	-18.751	<0.001	0.095	0.924	72
	Birds	0.150	0.882	-0.577	0.568	44
	Fish	2.889	0.007	-3.118	0.004	78
Functional	Large trees	2.713	0.013	0.782	0.443	38
	Small trees	0.035	0.973	3.544	0.002	45
	Ants	-8.657	<0.001	-2.808	0.008	77
	Birds	-1.115 (valley -.993)	0.274 (0.001)	0.831	0.413	42
	Fish	0.847	0.405	3.641	0.001	45

Do the local environmental conditions modulate changes in assemblage composition?

The changes in abundance and richness along time were not related to the topography (HAND gradient) for most groups, but lianas had a higher loss of species and individuals at higher HAND values (plateaus). A large decrease in fish abundance occurred in first-order streams, while a modest increase occurred in second-order streams (Figure 2). Taxonomic (Table 3) and functional (Table 4) composition changes along time were more extensive in the valleys for birds and ants, and in first-order streams for fish. The directional taxonomic and functional composition changes also differed among valleys and plateaus for birds and small trees, as described above.

DISCUSSION

The changes detected in plant and animal assemblages along 10 to 18 years of monitoring at Ducke Reserve are compatible with the climatic changes documented across this period. We observed decreases in abundance and richness of several taxa and a taxonomic and functional reorganization of the assemblages. The signal is not congruent across all assemblages and all metrics of change, but still, the patterns suggest increased dynamics, species filtering and a decrease of rare species. Several patterns of change in the assemblages over time were related to the hydro-topographic environments, highlighting that local hydrological conditions can modulate the effects of climate change on plant and animal assemblages over time.

Table 3. Results of the linear models assessing the effect of HAND on the changes in abundance or richness between the first and last census of each assemblage.

Assemblage	Abundance		Richness	
	p	R²	p	R²
Trees	0.73	< 0.01	0.58	0.016
Palms	**0.068**	**0.03**	0.804	< 0.01
Lianas	**0.040**	**0.13**	**0.001**	**0.31**
Ants	0.819	< 0.01	0.868	< 0.01
Birds	0.504	< 0.01	0.579	< 0.01
Fish	**0.051**	**0.01**	0.261	0.11

Table 4. Results of the linear models assessing the effect of HAND on the extension of taxonomic and functional changes between the first and last census of each assemblage.

Assemblage	Taxonomic Composition		Functional Composition	
	p	R^2	p	R^2
Trees	**0.04**	**0.20**	0.321	0.05
Palms	0.598	<0.01	-	-
Lianas	0.963	<0.01	-	-
Ants	0.319	<0.01	**0.002**	**0.25**
Birds	**0.006**	**0.24**	0.228	0.05
Fish	0.243	0.02	0.554	0.03

How patterns of assemblage change link to climate change?

The Manaus region is facing a long-term increase in annual precipitation and frequency of storms, especially in the last decades, and the drought frequency has increased since the 70's across the basin. These climatic trends are not restricted to our LTER site, but have been described for the entire Amazon basin (Gloor *et al.* 2015, Chaudhari *et al.* 2019). This intensification of the hydrological cycle is leading to an increased dynamics of the forest, through higher mortality and recruitment rates of trees in the Manaus LTER site (Esteban 2019) and across several places in the Amazon (Brienen *et al.* 2015, Feldpausch *et al.* 2016, McDowell *et al.* 2018).

These trends in forest dynamics are related to topographic variation at Reserva Ducke, with tree mortality rates increasing mostly in the valleys in periods with high precipitation and storms, and in plateaus during droughts (Esteban 2019). Valleys are naturally more dynamic than plateaus, given the low anchoring stability provided by the waterlogged sandy soils, which increases the probabilities of tree fall during windstorms (Gale & Barfod 1999, Toledo *et al.* 2012), and the larger frequency of storms and prolonged waterlogging are intensifying this dynamics. Most of the trends that we observed in the studied assemblages along time are either restricted to the valleys, differ between valleys and plateaus or are stronger in valleys, what is compatible with both direct effects of climatic changes on trees and fish and potentially indirect effects on ants and birds through the intensified forest dynamics. Lianas had a larger loss of individuals and species along time in the plateaus, where liana recruitment was much lower than mortality, in comparison to the valleys.

This pattern seems to be associated with the less accelerated tree dynamics and lower availability of light in the plateaus, which could restrict the recruitment of lianas (Gerolamo *et al.* 2018).

The increasing mean annual precipitation trend, with little water deficit during the dry season of most years, may have allowed the recruitment of acquisitive small trees in the relatively dry plateaus as a response to increased gap opening by windstorms. Increasing precipitation and consequently higher frequency of floods and soil waterlogging in valleys may have increased the selection of hardwoods, given that softwoods tend to be more vulnerable to prolonged flooding (Lawson *et al.* 2015, Moser *et al.* 2019). The high frequency of storms and increased rain amounts also parallel a change in the stream substrates, which are becoming simpler, i.e. with lower proportional amounts of litter and higher proportional amounts of bare sand (Borba 2019). This simplification of the substrate, and a potentially higher connection between marginal ponds and the mainstream channel seem to be favoring fish able to explore these increased habitats, in detriment of those more specialized in the main channel and litter banks.

It is not clear how ants and birds may have been affected by the climatic trends. For ants, an increase in rainfall and frequency of floods would affect more strongly assemblages on valleys than plateaus, which is consistent with our data. However, how the ant assemblages are changing over time is not fully congruent with predictions based on species distribution data. Generalist ants, especially those that live in polydomous nests, are normally favored, while specialist ant species are negatively affected by predictable seasonal floods of large rivers (Mertl *et al.* 2009) or unpredictable floods of small

streams (Baccaro *et al.* 2013). Our data suggest that a frequency increase of unpredictable floods may also negatively affect generalist species over time, indicating that space-for-time predictions should be done with caution. Some of the changes in ant assemblages may also be linked to the changes in bird assemblages, given that Raid hunting predators, represented mostly by army-ants, are the source of prey for most of the medium and large insectivorous birds, thus their decline could cause some negative impact on predators over time. Although our evidence is only correlative, it turns on an alert signal that climate change may be affecting even trophic relationships, and we should now focus on more integrated observations of these taxa along time. Other insect groups should be included in the long-term monitoring program, since there is evidence of global declines (Dirzo *et al.* 2014, Sánchez-Bayo & Wyckhuys 2019).

Droughts are widely studied and have been considered the strongest drivers of negative responses of tropical forests to climate change (Allen *et al.* 2010, Greenwood *et al.* 2017, McDowell *et al.* 2018). However, as documented here and elsewhere, concomitant to the increase in drought frequencies in the Amazon, there is an increase in precipitation, and their relative impacts on various biological taxa are so far unknown. The patterns documented here suggest that across most taxa, precipitation excess is having a higher impact than droughts. The evidence comes especially from the larger changes and/or specific changes associated to the valleys, where droughts have little effect on the soil moisture, due to the constantly high water-table (Hodnett *et al.* 1997b, 1997a) and increased mortality of trees during droughts was not observed (Esteban 2019).

Are changes in species and functional composition related to climate or other disturbances?

We have evaluated assemblage composition changes within a large (10 x 10 km) undisturbed forest, with the reserve borders still covered with continuous forest, unless for a border at the southwestern corner. Our preliminary analyses did not show community differences across the border and interior plots analyzed in this study. Border effects in central Amazon have been estimated to run around 300 m inside the forest (Laurance *et*

al. 2011) and the permanent plots are at least 1 km of all borders, thus the monitoring plots represent interior communities that do not show signs of having been affected by changes mediated by borders. All monitored streams are borne in the middle of the reserve and are not contaminated by city sewage or other direct sources of pollutants. Thus, given the high integrity of the reserve and lack of any documented sources of impact beyond those in some of the borders, we conclude that any changes documented along time must be due to either stochastic variation or climate change. Stochastic variation would be a very unlikely driver of the congruent pattern of change across most of the plots observed for each community. We are thus confident that most observed patterns of community change are more likely driven by the climatic changes observed in our LTER site. Notwithstanding that, more intensive and integrated observations across biological groups may be necessary to ascertain the causes of changes.

Implications of species composition and functional changes over time

Even with a two-decade period of monitoring, we are still limited in our understanding of the long-term biological changes of long-lived organisms, and some causal links between community patterns and climate change still need to be established by a continued sampling over shorter time intervals. Moreover, there is a limitation of the non-synchronized sampling periods across taxa, which encompass different climatic events, and as such, are not fully comparable. Future efforts will be in coordinating sampling efforts on the same periods and increasing the temporal sampling intensity (ideally at least every two years) will allow direct analyses of climatic variation on community metrics. However, even with such limitations our data points point to congruent species composition changes over time and space that demands attention.

The climate of the central Amazon region at the equatorial latitude has been historically more stable than in its limits (Martin *et al.* 1997, Dynesius & Jansson 2000). Thus, the detection of congruent changes across several taxa is surprising and indicates the non-trivial impacts of this century climatic changes on intact tropical

systems. The decrease in species numbers so far is more linked to rare species, and we cannot say if this may have long-term negative impacts on the regional biodiversity. However, it signals the need for continued monitoring to ascertain the causes and consequences. We found congruent patterns across several taxa, but also some idiosyncratic patterns, which point out to the need for long-term monitoring of several biodiversity groups and their functional traits to understand potential impacts of climate change.

We have shown here that even aquatic systems within old-growth forests may be suffering the impacts of climate change, before we know most of the biodiversity they contain. At the same time, the local riparian and forest cover are important to shape the structural complexity of streams (Leal *et al.* 2016). Thus, there is a clear need to increase the protection of these freshwater systems, including them in systematic conservation planning as suggested by Azevedo-Santos *et al.* (2018) and Frederico *et al.* (2018).

Our results, here and in previous studies (Cordoba 2018, Esteban 2019, Oliveira *et al.* 2019), suggest that riparian areas in the valleys are hydrological refuges for plants during droughts, although these areas are also susceptible to disturbances induced by excessive precipitation and windstorms. As refuges for drought sensitive species, valleys are the ecological equivalents of mountain-tops as refuges for species sensitive to high temperatures (e.g. Antonelli *et al.* 2010, Alcantara *et al.* 2018). As mountain tops, valleys are at the end of the potential distribution shifts for species escaping from climatic change, thus species already associated to valleys have no place to escape. It is difficult to predict what might be the consequences of potential migrations of species associated to the higher topographic positions towards valleys, combined to the increased dynamics imposed by climate change to this habitat. In face of the importance of riparian areas in valleys as biodiversity refuges, their sensitivity to climate change and the unknown effects of potential migrations, the conservation of large and extensive riparian areas are paramount to the future of biodiversity of the Amazon.

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Supplementary Material: Table S1. List of the ant and bird species registered at Reserva Ducke and their associated ecological guilds. Ants were captured with pitfall traps and birds with mist-nets.