Research

Potential trajectories of old-growth Neotropical forest functional composition under climate change

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Quantifying relationships between plant functional traits and abiotic gradients is valuable for evaluating potential responses of forest communities to climate change. However, the trajectories of change expected to occur in tropical forest functional characteristics as a function of future climate variation are largely unknown. We modeled community level trait values of Costa Rican rain forests as a function of current and future climate, and quantified potential changes in functional composition. We calculated per-plot community weighted mean (CWM) trait values for leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen (N) and phosphorus (P) content, and wood basic specific gravity (WSG), for tree and palm species in 127 0.25 ha plots. We modeled the response of CWM traits to current temperature and precipitation gradients using generalized additive modeling. We then predicted and mapped CWM traits values under current and future climate, and quantified potential changes under a global warming scenario (RCP8.5, year 2050). We calculated the area within the multi trait functional space occupied by forest plots under both current and future climate, and determined potential changes in functional space occupied by forest plots. Overall, precipitation predicted CWM traits better than temperature. Models indicated increases in CWM SLA, N and P, and a decrease in CWM LDMC under climate change. Lowland forest communities converged on a single direction of change towards more acquisitive CWM trait values, indicating a change in forest functional composition resulting from a changed climate. Functional space occupied by forest plots was reduced by 50% under the future climate. Functional composition changes may have further effects on forests ecosystem services. Assessing functional trait spatial-gradients can help bridge the gap between species-based biogeography and biogeochemical approaches to strengthen biodiversity and ecosystem services conservation efforts.

Understanding relationships between vegetation patterns and environmental characteristics is a central theme dating to the earliest studies of plant community ecology (Egerton 2013). A shift in approaches to modelling vegetation and community composition along environmental gradients has occurred in recent decades, in which vegetation–environment relationships are studied using plant functional traits rather than species taxonomic identity alone (Keddy 1992, Wright et al. 2005, Shipley et al. 2006, Ordoñez et al. 2009, Swenson and Weiser 2010, Douma et al. 2012, van Bodegom et al. 2012, Siefert et al. 2013). Plant functional traits are defined as any morphological, physiological or phenological feature measurable at the individual level and influencing its performance (Violle et al. 2007). As a result, functional traits limit the range of environments in which plant species can grow and survive, thus constraining their spatial distributions and geographic ranges. Because functional traits are also strongly related to ecosystem functioning (de Bello et al.

2010), conceptual frameworks have been developed where traits are considered key components of ecosystem processes and services (Hooper et al. 2005, Díaz et al. 2007, 2011, Cadotte et al. 2011, Lavorel 2013).

Functional properties of plant communities can be summarized by different metrics related to the diversity or central tendency of functional traits values (Mouchet et al. 2010). In particular, the community weighted mean (CWM) trait value, i.e. the average trait value calculated as the sum of species trait values weighted by their relative abundance in the community (Garnier et al. 2004, Díaz et al. 2007) is a promising approach to characterization of community functional properties in ways that are useful for quantifying ecosystem functioning (Garnier et al. 2004, Ruiz-Jaen and Potvin 2011, Conti and Díaz 2013, Dias et al. 2013, Lavorel 2013, Finegan et al. 2015), plant community relationships to environmental variables (Shipley et al. 2006, Swenson and Weiser 2010, Kleyer et al. 2012, de Bello et al. 2013, Siefert

et al. 2013, Fortunel et al. 2014), forest temporal dynamics (van der Sande et al. 2016) and shifts in plant community composition related to global change drivers (Dubuis et al. 2013, Mokany et al. 2015). Functional traits may therefore be valuable for forecasting the response of plant communities to climate change. However, the question of how tropical forest functional characteristics will change as a result of climate change remains largely unresolved.

Evidence for climate change is unequivocal, with projected impacts on all global ecosystems (IPCC 2013). In the tropics, while trends vary locally, precipitation has generally increased over the last decade, with concomitant increases in the number of heavy precipitation and drought events (IPCC 2013). In Central America and northern South America, evidence shows a general warming trend over the 1961–2003 period, with rainfall events intensifying due to a larger contribution of wet and very wet days to total annual rainfall (Aguilar et al. 2005). However, Central America is expected to become warmer and undergo precipitation changes in future climate scenarios (Neelin et al. 2006) resulting in decreased water availability for vegetation (Imbach et al. 2012). The magnitude of climate change in this region is expected to be larger than in any other tropical region (Giorgi 2006), moving ecosystems out of their historical temperature range relatively sooner than at higher latitudes (Hawkins and Sutton 2012, Mora et al. 2013).

Climate change will cause major changes in ecosystem structure and function (IPCC 2013). In particular, shifts in plant community assemblages, ecological interactions among species and in species geographical ranges are expected to bring predominantly negative consequences for biodiversity and ecosystem goods and services (IPCC 2013). In the Amazon Basin it is suggested that projected climatic change will favor plan-growth strategies associated with the acquisitive end on the leaf economic spectrum (Reu et al. 2011). In Costa Rica it has been shown that tree growth is affected by dry-season conditions and variation in mean annual nighttime temperatures (Clark et al. 2010). Recent changes in relative abundances of tree species of different temperature tolerances along an altitudinal transect also in Costa Rica are consistent with effects of warming, indicating that individuals of many tropical tree species will not be able to tolerate future warming, and that their persistence will depend on successful migration (Feeley et al. 2013). Tropical lowland forests may experience a net loss of plant species richness – biotic attrition – due to climate regimes shifting beyond the tolerance range of many plant species (Colwell et al. 2008). However, rates of biotic attrition may be markedly less than predicted given inaccurate estimates of thermal niches derived from observations or collection records, and a higher number of species than previously predicted may be able to persist in the hot tropics despite temperatures exceeding their known thermal tolerances (Feeley and Silman 2010).

In comparison to species-based and coarse scale models based on a priori functional types (Krinner et al. 2005, Thuiller et al. 2006, Küster et al. 2011), the use of continuous functional trait data allows for a better understanding of plant community response to environmental changes (Violle et al. 2014). Trait data may therefore improve vegetation models widely used to assess biosphere–climate

interactions (Boulangeat et al. 2012, van Bodegom et al. 2012, 2014, Violle et al. 2014). Because tropical tree species richness is high and species exhibit differential sensitivity to changes in climate, it is appropriate to model changes in plant community functional composition to assess how tropical forest will respond to global change. However, to our knowledge a relatively small number of studies have attempted to predict trait values from environmental determinants and map their spatial distribution, Swenson and Weiser (2010), Dubuis et al. (2013), van Bodegom et al. (2014), Göldel et al. (2015), Mokany et al. (2015). Of these studies only van Bodegom et al. (2014) and Göldel et al. (2015), respectively conducted at global and regional scale, address tropical areas; and only Dubuis et al. (2013) and Mokany et al. (2015) relate their work to climate change. Here, we conduct exploratory analyses of the relationship between old-growth rain forest CWM trait values and climatic gradients under current and future conditions, to examine potential changes in community functional composition. We calculate per-plot CWM trait values using abundance data together with values of six functional traits for 257 tree and palm species in 127 forest plots distributed across a 6166 km^2 landscape in northern Costa Rica. Our specific objectives are to 1) model the response of CWM traits to current climate predictors, 2) use the modeled relationships to predict and map current and future values of CWM traits under a set of 17 climate general circulation models within a future climate change scenario, and 3) determine potential changes in both individual CWM trait values and multi-trait functional space occupied by forest plots. Modelled future climates for our study area maintain high rainfall and have increased temperatures. We assume that future temperatures remain within the thermo-tolerance range of the current tree species of the area, and test the consequent hypothesis that CWM trait values become more acquisitive – CWM N and SLA increase, and CWM LDMC and WSG decrease.

Methods

Study area

The study area covers 6166 km^2 and extends from the highlands of the Central mountain range of Costa Rica to the lowlands of the San Juan River, which forms the Nicaraguan border (Fig. 1). Elevation ranges from near sea level to 2881 m a.s.l. The study area includes the San Juan-La Selva Biological Corridor, an important ecological conservation initiative that provides habitat connectivity for many forest species along the Mesoamerican biological Corridor (Morse et al. 2009, DeClerck et al. 2010). Gridded data sets for the study area (Hijmans et al. 2005) indicate a mean annual temperature range from 10.8°C to 26.2°C, and a mean annual precipitation range from 2134 mm to 4932 mm. Temperature and precipitation vary with elevation and distance from the Caribbean coast (Fig. 1). While part of the landscape is farmland, more than 40% of its area corresponds to mature and secondary forests (Fagan et al. 2013). Old-growth forests are well differentiated by species composition and climatic and edaphic characteristics into three main vegetation types: two
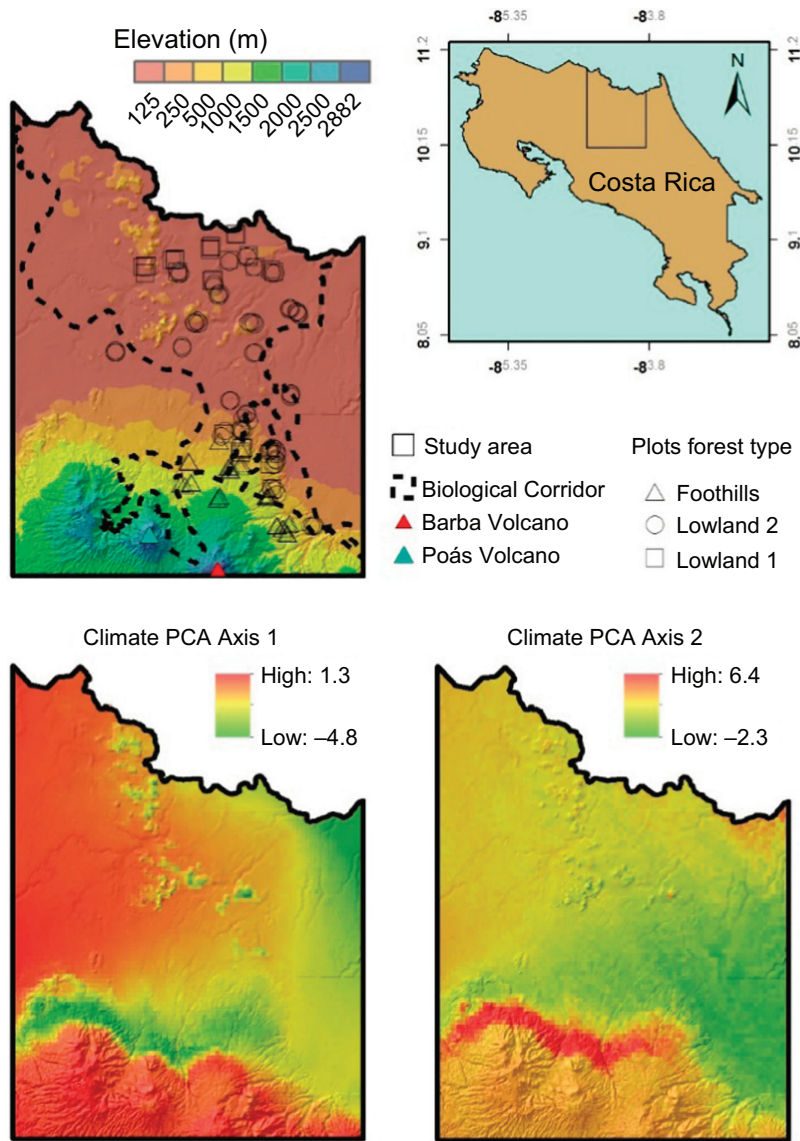
Figure 1. Study area location in northern Costa Rica, Central America. Vegetation plots are distributed following the altitudinal gradient within or close to the limits of the San Juan La Selva Biological Corridor. Plots are classified into one foothills forest type and two lowland forest types following Sesnie et al. (2009). Eight temperature and precipitation variables were summarized in two principal component analysis (PCA) axes of variation (Fig. 2). PCA axis 1 represents a precipitation gradient (with higher values related to higher precipitation seasonality and lower values to higher total annual precipitation). Axis 2 represents both a temperature and precipitation gradient (with higher values associated with higher seasonal precipitation and higher precipitation during the wettest month, and lower values related to higher temperatures across the year and higher temperature seasonality).

lowland forest types and one foothill forest type at higher elevations (Sesnie et al. 2009).

Species and functional trait data

Abundance data of canopy tree ($\geq$ 30 cm diameter at breast height, dbh) and palm ($\geq$ 10 cm dbh) species were retrieved from a data set of 127 0.25 ha old-growth forest plots established by Sesnie et al. (2009) across the study area (40–1200 m a.s.l.; Fig. 1). Detailed information on plot establishment, measurement of individuals and species identification can be found in Sesnie et al. (2009). All tree and palm species registered in vegetation plots and identified to the level of species or genus (n = 253) were selected for trait

measurement. Trait measurements carried out in this study complemented an existing tree and palm species trait database collected as part of the Diversus Collaborative Research Network (IAI CRN) project and partially published in Kattge et al. (2011). We measured six functional traits summarizing species leaf and wood plant economic spectra, and known to covary with climate at the individual plant or leaf level (Reich and Oleksyn 2004, Wright et al. 2004, 2005, Chave et al. 2009, Ordoñez et al. 2009), including leaf area (LA, mm^2), specific leaf area (SLA, mm^2 mg^{-1}), leaf dry matter content (LDMC, mg g^{-1}), leaf nitrogen (N mg g^{-1}) and phosphorus (P mg g^{-1}) content, and wood basic specific gravity (WSG, g cm^{-3}). We used standardized protocols for trait measurements. Collecting and storing protocols

from Pérez-Harguindeguy et al. (2013), rehydration protocols from Garnier et al. (2001), and measurements protocols from Pérez-Harguindeguy et al. (2013) were followed for leaf traits. For WSG we followed Williamson and Wiemann (2010). Foliar traits and WSG were respectively measured in five and three individuals per species collected within the study area. The average trait value per species was combined with species relative abundance per plot to calculate CWM values of each trait per plot. CWM traits were computed using the 'FD' package (Laliberté et al. 2014) in R (ver. 2.15.2, R Core Team).

We are aware that palms are an a priori functional group given their properties of wood anatomy, growth form and status as monocotyledons. Palms included in the analysis are four arboreal species (*Euterpe precatoria*, *Iriartea deltoidea*, *Welfia regia*, *Socratea exorrhiza*) which are key elements of the canopy of these (Sesnie et al. 2009) and other Costa Rican old-growth forests (Chain-Guadarrama et al. 2012), contributing to species beta diversity across environmental gradients. Given their abundance and probable biomass input to ecosystem cycles, and the fact that palms share the forest canopy with tree species, they are floristically and functionally important in these ecosystems and should be considered together with trees when calculating CWM trait values. Analyses for the tree community without palms are presented in Supplementary material Appendix 2.

Climate data

We used eight bioclimatic predictor variables derived from interpolated weather station data representing mean climate conditions for the 1950–2000 period (Hijmans et al. 2005) and downscaled to ~1 km resolution grids (<www.worldclim.org>). All bioclimatic variables are derived from monthly temperature and rainfall values. We selected annual mean temperature, minimum temperature of the coldest month, maximum temperature of the warmest month and standard deviation of temperature as a measure of temperature seasonality (Table 1). Precipitation variables included mean annual precipitation, precipitation of the driest month, precipitation of the wettest month and coefficient of variation of precipitation (Table 1).

Future climate data (Table 1) for the year 2050 (mean monthly values for the 2041–2060 period) were derived from outputs of 17 general circulation models (GCMs) under a high radiative forcing scenario of 8.5 W m^{-2} (~1370 ppm CO^2 eq) by the year 2100 (RCP 8.5; van Vuuren et al. 2011). These data are from the Coupled Model Intercomparison Project, Phase 5 (CMIP5), and were used on the Fifth Assessment IPCC report (AR5) (IPCC 2013). Coarse GCM outputs were downscaled to 30 arc-seconds (aproximately 1 km^2 in our study area) using the delta method, adding future climate anomalies to a high resolution historical climatology (WorldClim 1.4, Hijmans et al. 2005, <www.worldclim.org>). GCMs under the selected scenario showed a range in mean annual temperature increment of 1.4–2.9°C over the study area. In contrast, precipitation increased or decreased depending on the location and climate model selected. 12 of the 17 models suggest an increase in mean annual precipitation, in the range 3–836 mm. Precipitation of the wettest month is also expected to increase (13 of 17 models showed positive anomalies), while negative precipitation anomalies for the driest month are expected (10 of 17 models show positive anomalies). The RCP8.5 scenario thus indicates higher temperatures and continuing high rainfall, but with more marked differences between the driest and wettest months

Data analysis

Assessing the response of CWM traits to climate
The response of individual CWM traits to climate predictors was assessed through generalized additive mixed models (GAMMs) using the 'gamm' function in the R package 'mgcv' (Wood 2011). A Gaussian distribution and a P-splines smooth term were used. To take into account the lack of independence of residuals due to spatial autocorrelation, GAMMs included a spherical correlation function. The use of GAMMs allowed us to assess nonlinear relationships observed between CWM trait values and environmental variables and consider the lack of spatial independence in the errors through spatial correlation functions. Moreover, by using smoothing functions GAMMs are more flexible and result in a much better fit when non-linear relationships predominate. In particular, penalized splines (p-splines) smoothing functions use fewer knots which is related with

Table 1. Summary statistics of current and future (year 2050) climate in the San Juan La Selva region. Future climate data correspond to average values from 17 general circulation models (GCMs) under a high radiative scenario (RCP 8.5).

Variable (units)	Current		Future	
	Mean ± SE	Range	Mean ± SE	Range
AnnTemp (°C)	24.1 ± 0.04	10.8–26.2	26.2 ± 0.04	12.9–28.3
MaxTempWM (°C)	30.2 ± 0.04	15.7–32.8	32.2 ± 0.04	17.7–34.9
MinTempCM (°C)	18.6 ± 0.04	5.8–20.8	20.7 ± 0.04	7.9–22.9
TempSD (°C)	6.6 ± 0.01	4.9–8.0	6.6 ± 0.01	5.0–7.8
AnnPrec (mm)	3607.8 ± 6.6	2134–4932	3687.3 ± 7.0	2215.2–5007.4
PrecWettM (mm)	460.1 ± 0.69	223–648	561.7 ± 1.1	296.7–817.1
PrecDriesM (mm)	108.6 ± 0.55	8–188	105.9 ± 0.52	7.9–182.5
PrecCV (%)	39.4 ± 0.12	20–80	45.4 ± 0.09	30.9–82.2

AnnTemp: annual mean temperature; MaxTempWM: maximum temperature of the warmest month; MinTempCM: minimum temperature of the coldest month; TempSD: standard deviation of temperature; AnnPrec: mean annual precipitation; PrecWettM: precipitation of the wettest month; PrecDriesM: precipitation of the driest month; PrecCV: coefficient of variation of precipitation.

lower overfitting problems. P-splines are also more reliable at the extremes of the data. i.e. they do not suffer from boundary effects, in which the spreading of a fitted curve outside of the (physical) domain of the data is generally accompanied by bending toward zero.

Before performing GAMMs, we used a kernel principal components analysis (KPCA), a nonlinear form of PCA, to reduce the multidimensional climate variability and to extract orthogonal axes of climatic variation for use in the GAMM modeling, as well as to avoid problems due to collinearity among climatic predictors. The 'kpca' function in R package 'kernlab' (Karatzoglou et al. 2004) was used to run KPCA. Universal Transverse Mercator (UTM) latitude and longitude coordinates were also added to the models as predictors to assess any spatial trends in CWM traits and as covariates of climatic predictor variables.

Modelling of current and future CWM traits

CWM trait values under current climatic constraints corresponded to the fitted values from the GAMMs described above. To obtain future CWM trait values, we first applied the KPCA fitted model for current climatic data on future climate data from 17 GCMs to obtain axes of future climatic variation. We then used the fitted models of the response of CWM traits to current climate to predict trait CWMs under future climate conditions for each sample plot under each of the 17 GCMs. Using continuous climate grids, we followed the same procedure to predict current and future values of each CWM trait across the entire landscape. Continuous forest cover was assumed even though old-growth forest cover is ~34% of the total study area (Shaver et al. 2015). CWM trait values were assumed to change under future climate conditions when the mean future value calculated from all 17 GCMs projections was below (indicating a decrease) or above (increase) the 95% confidence interval around fitted values from GAMMs. Proportional change was calculated both at the plot level and at landscape level, respectively as the percentage of total plots or pixels showing significant increases or decreases in their CWM trait values. Moreover, at the landscape level, the likelihood of change for each pixel was estimated as the percentage of scenarios showing a significant decrease, increase or no change in CWM traits, relative to the 95% confidence intervals around current fitted CWM traits from GAMMs.

Assessing changes in multi-trait community functional composition

Using a PCA, plots were ordinated in the multivariate space of the six CWM trait values predicted from GAMMs under current climatic conditions. The 'prcomp' function in R package 'stats' was used to perform PCA. Using the same fitted PCA, plots were ordinated in the functional space using their future average CWM trait values (from 17 assessed GCMs). The direction and magnitude of temporal changes in plot functional composition were assessed as follows. Through bivariate kernel functions we calculated the probability density of forest plots within the functional space of the two first PCA axes both under current and future climate conditions. The 'kernelUD' function in R package 'adehabitat' (Calenge 2006) was used to perform the two-dimensional kernel density estimations. The functional space no longer occupied by

plots given their future CWM trait values ('lost' functional space), the new functional space occupied by plots given their future CWM trait values ('gained' functional space), and the space shared by current and future functional space ('shared functional space) were calculated. Functions 'kernel.area' and 'kerneloverlap' respectively, in the R 'adehabitat' package were used for these calculations of functional space.

Data deposition

Results

Response of CWM traits to current climatic variables

Kernel PCA axes, explaining 89.6% of total variance, depict the climate variation among plots across two major climatic gradients (Fig. 2). PCA Axis 1 represented a precipitation gradient, being positively correlated with precipitation seasonality and negatively correlated with mean annual precipitation and precipitation of the wettest and driest months (Supplementary material Appendix 1 Table A1). Along PCA Axis 2, vegetation plots were differentiated in relation to temperature and precipitation variables. Temperature variables were all negatively correlated with this axis, while precipitation of the wettest month and coefficient of variation of precipitation were weakly positively associated with it (Supplementary material Appendix 1 Table A1). Due mainly
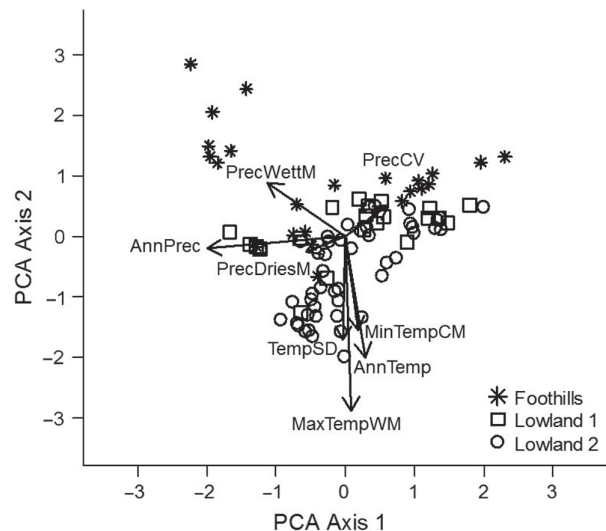

Figure 2. Results from a kernel principal component analysis to ordinate 127 vegetation plots in the multivariate space of eight temperature and precipitation variables. AnnTemp: annual mean temperature; MinTempCM: minimum temperature of the coldest month; MaxTempWM: maximum temperature of the warmest month; TempSD: standard deviation of temperature; AnnPrec: mean annual precipitation; PrecDriesM: precipitation of the driest month; PrecWettM: precipitation of the wettest month; PrecCV: coefficient of variation of precipitation.

to the temperature gradient, foothill forest plots were well separated along PCA Axis 2 from most of the lowland forest plots.

GAMMs assessing the response of individual CWM traits to climate gradients explained variance in the range between 54.4% (CWM LA) to 18.2% (CWM WSG) (Fig. 3; Supplementary material Appendix 1 Table A2 and Fig. A1). CWM LA, SLA, LDMC and N were better predicted ($R^2_{adj} > 30\%$) than CWM P and WSG ($R^2_{adj} < 0.24$); all relationships were with the precipitation gradient of PCA Axis 1 except that for LDMC, which responded to the temperature gradient of Axis 2. Non-linear relationships predominated between PCA axes and CWM traits (Fig. 3). UTM X coordinates were a significant factor for LA, SLA, N and P (Supplementary material Appendix 1 Table A2).

Prediction of community weighted mean traits under current and future climatic constraints

Future climate models indicated that CWM SLA, P and N will increase in most of the 127 plots (Fig. 4; Supplementary material Appendix 1 Table A3). The proportion of plots showing no changes in CWM N values (54%) was higher than for CWM SLA and P (< 15% in both cases). A decrease in CWM LDMC was observed in > 50% of plots under future climate. This decrease was highest in plots in the upper range of current values (Fig. 4). No clear tendency was observed for LA and WSG CWMs, with similar proportions of plots showing increases and decreases, particularly in the case of WSG (Fig. 4).
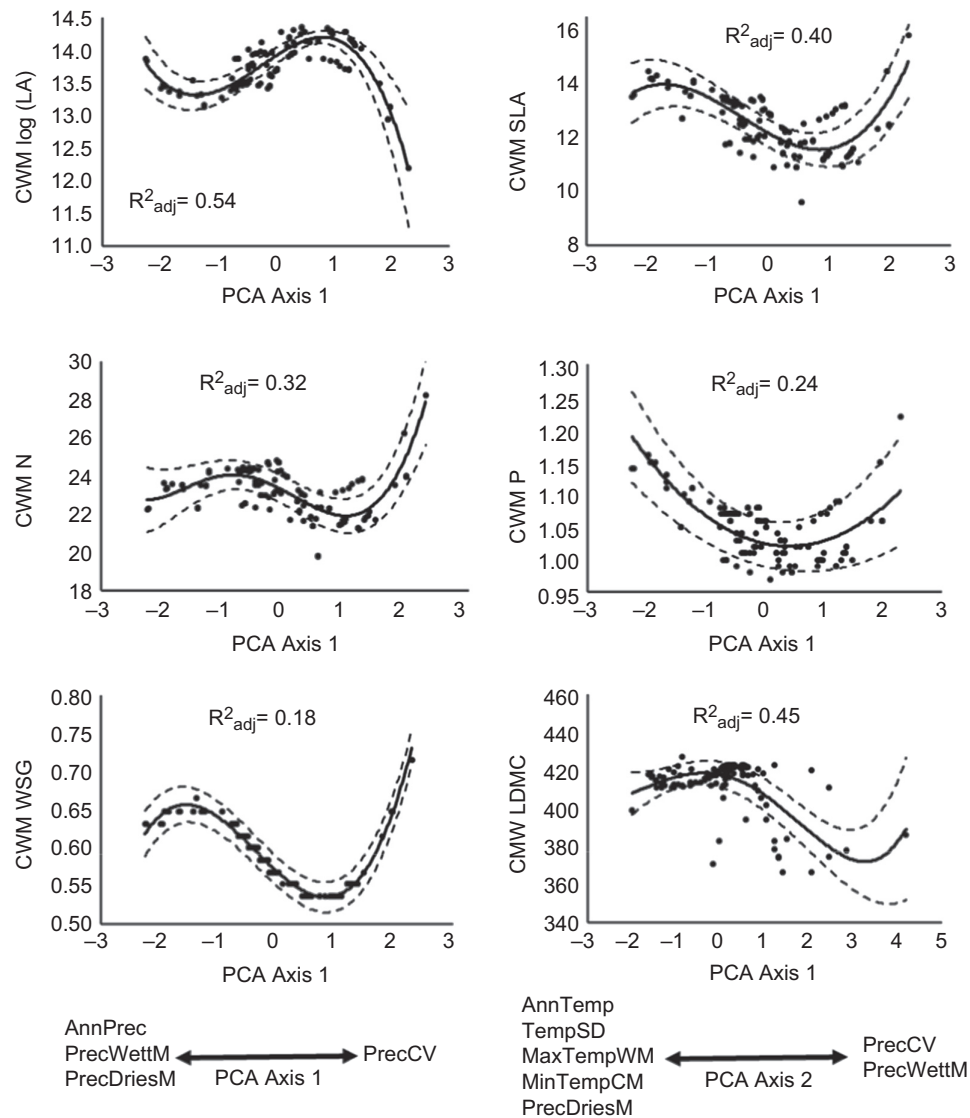

Figure 3. Generalized additive regression models illustrating the relationship between CWM traits and the most significant climate PCA axes of variation. Fitted values are plotted. Dashed lines represent the 95% confidence interval. Explained deviance (R^2_{adj}) represents a significant model (p < 0.001). Negative relationships (to the left of the arrow) and positive relationships (to the right of the arrow) between climate variables and PCA Axes 1 and 2 are shown at the bottom.
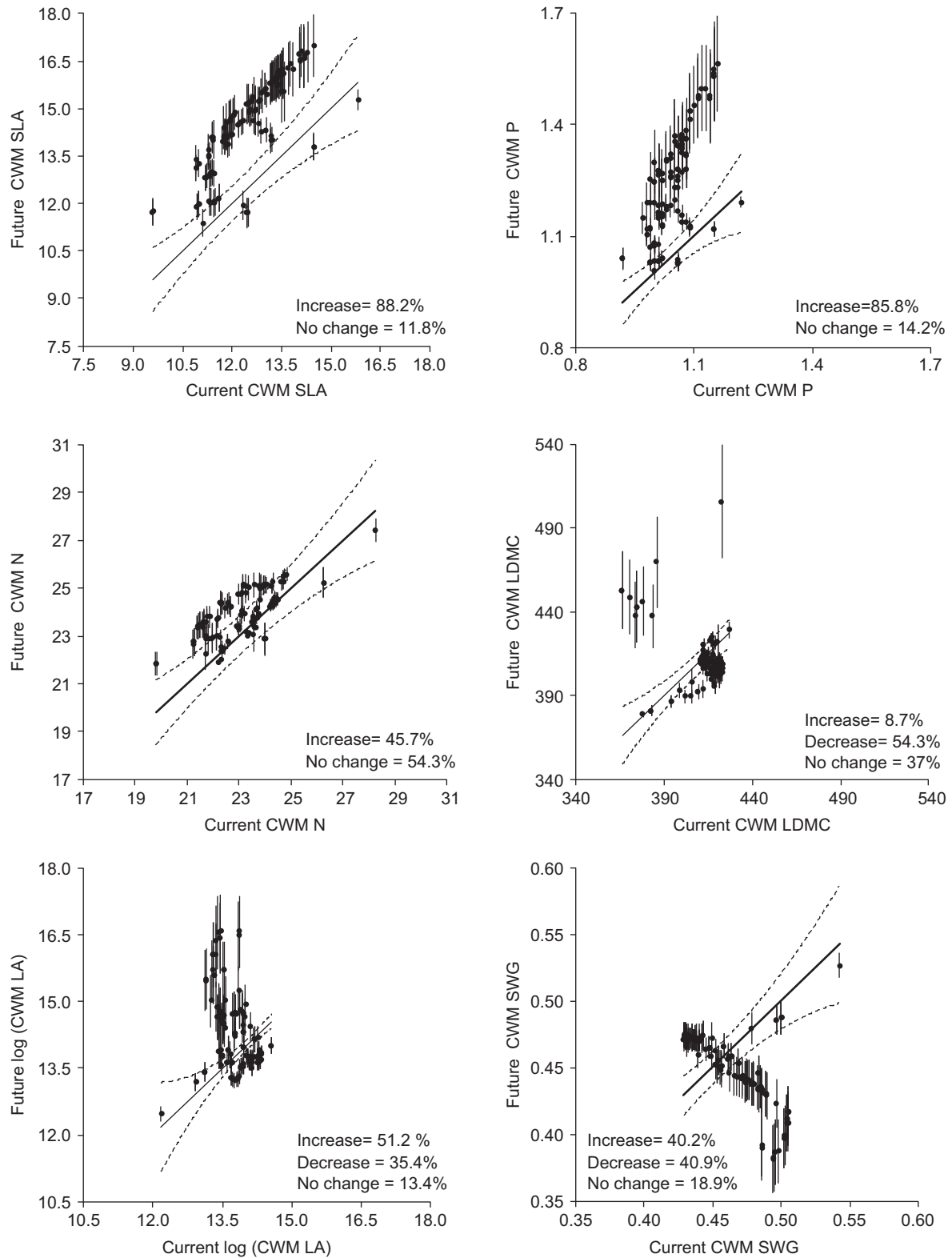
Figure 4. Predicted community weighted mean values of six functional traits for 127 forest plots under current and future climate. The area within dashed lines (95% prediction interval) represents the CWM trait values predicted by generalize additive models under current climate. Points indicate the average predicted CWM trait values under future climate (2050, RCP 8.5) and vertical black lines ± standard error from 17 climate general circulation models. Future average predicted CWM trait values lying within current-climate prediction boundaries indicate lack of predictive capacity on trait changes under future climate. Future average predicted CWM trait values above and below current climate prediction boundaries respectively indicate future increase or decrease in plots CWM traits. The proportion of total number of plots showing increase, decrease or no change under future climate is indicated in the lower right corner of each plot.

Changes in community functional composition

Axis 1 and Axis 2 of the PCA using current plot CWM traits explained 76 and 13% of total variance, respectively (Fig. 5a; Supplementary material Appendix 1 Table A4). CWM SLA, P, N and WSG were positively correlated with PCA Axis 1, and CWM LA and LDMC negatively correlated with this axis (Supplementary material Appendix 1 Table A4). CWM LDMC had the strongest trait correlation – positive – PCA Axis 2 (Supplementary material Appendix 1 Table A4). The modelled increases over time in CWM N, SLA, P values, and the decrease in LDMC values (Fig. 4) resulted in the aggregation of plots and a consequent 50.4% reduction of the functional space (Fig. 5a). Of the total functional space occupied by forest plots under current climate, 67% percent was lost, while the remaining 33% was shared with future functional space.

Notably, 35% of the future functional space was gained, corresponding to combinations of CWM trait values not found in the current landscape. Under the future climate scenario, lowland forest plots moved towards higher values on PCA Axis 1, due to increasing CWM N, SLA, P and WSG (Fig. 5c, d). These lowland forest plots also moved towards negative values on PCA Axis 2, due to a smaller decrease in CWM LDMC. No clear overall trend was observed for those plots within the foothills forest type (Fig. 5b).

Landscape patterns of CWM traits along climatic gradients

Similar areas of increase and decrease in CWM SLA and P values were observed across the landscape. Higher certainty
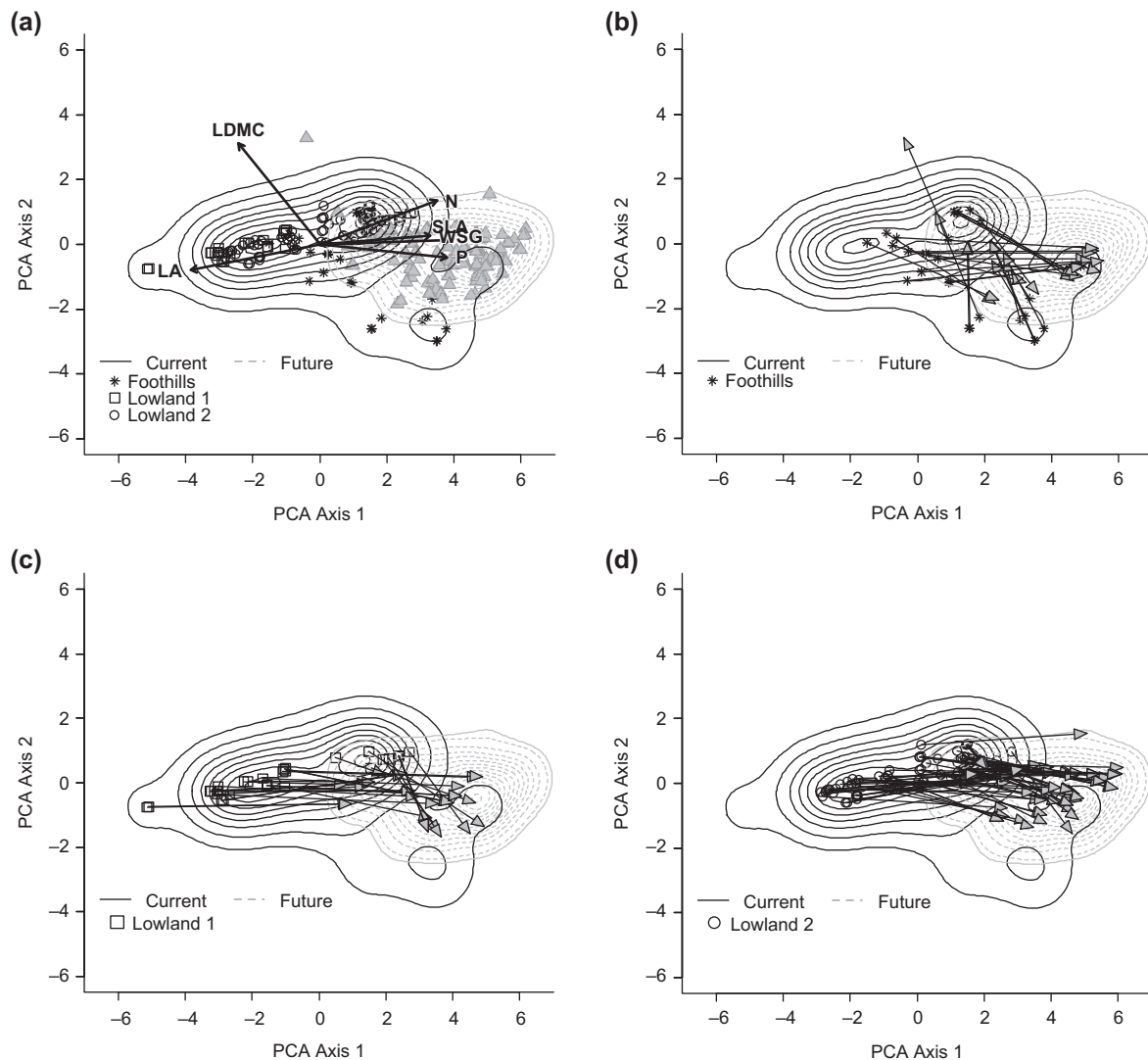

Figure 5. Ordination of 127 forest plots within a two-dimensional functional space given their CWM traits values under current and future climate. No filled symbols in (a, b, c, d) represent forest plots ordinated in the functional space given their CWM traits predicted under current climate conditions. These different symbols denote three different forest types to which plots belong to. Grey filled triangles in (a, b, c, d) represent forest plots ordinated in the functional space given their six CWM traits values predicted under future climate. In (a, b, c, d) black continuous contours are the probability density function of forest plots in the two dimensional functional space under current climate, and dotted grey contours the probability density function of forest plots in the functional space under future climate. In (b, c, d) arrows indicate the direction and magnitude of climate-induced shift for foothills (b) and lowland (c, d) forest plots. Black arrows in (a) indicate the association of six CWM traits with two PCA axes of variation.

for future predicted values was observed for N, P and SLA CWMs with respectively 56, 47 and 46% of total landscape area showing likely probability of change. Using the likelihood scale recommended by IPCC (Mastrandrea et al. 2010) to communicate uncertainty, we considered that a change is likely to occur if it is observed in ≥ 66% of the 17 GCMs assessed for this RCP8.5 scenario. Large areas of decrease in CWM LDMC, indicating a range reduction in values of this CWM trait in the landscape, were observed towards the northwest region of the landscape. CWM LA values respectively increased and decreased in the eastern and center portions of the study region, while patterns in CWM

WSG showed the inverse trends. However, future trends in LA, WSG, and specially LDMC showed less convergence among climate models, showing small proportions of total landscape area with likely probabilities of change (Fig. 6).

Discussion

Understanding the effects of climate change on vegetation remains a major challenge in ecology, particularly for highly diverse tropical forests. In our study we were able to successfully build models of CWM trait response to climatic
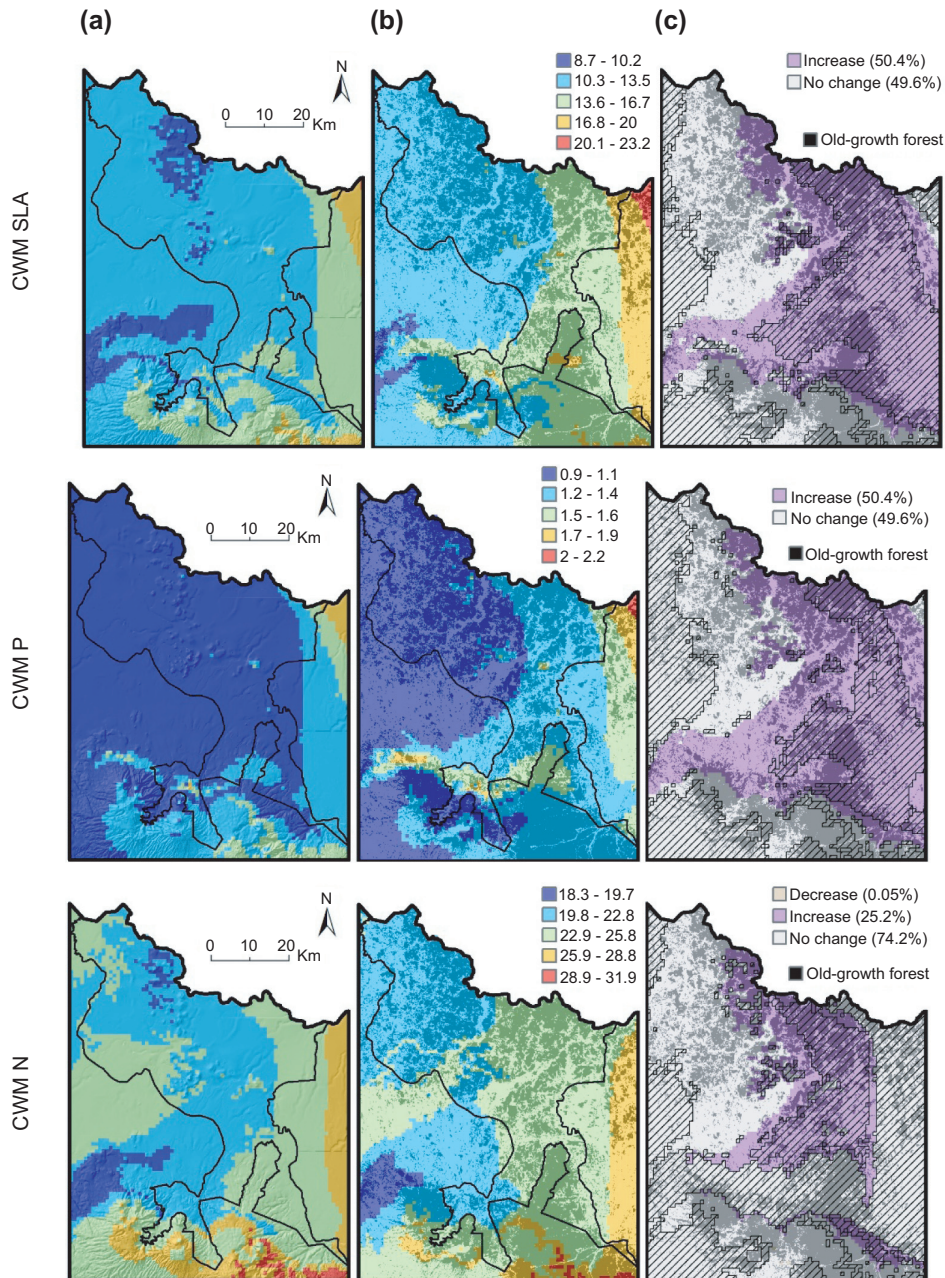

Figure 6. Predicted CWM traits for (a) current and (b) future climatic conditions (year 2050) under the RCP 8.5 for the San Juan La Selva region of northeast Costa Rica. In (b) the mean value from 17 global climatic models is shown. Future areas of increase, decrease or no change in CWM traits (c) indicate that mean future predicted values are above, below or within 95% confidence intervals of current predictions from generalized additive mixed models (GAMMs). Dashed areas indicate that projected changes are likely to occur (a change is found in ≥ 66% of future climate models). In (b) and (c) remnant old-growth forest is shown in black.
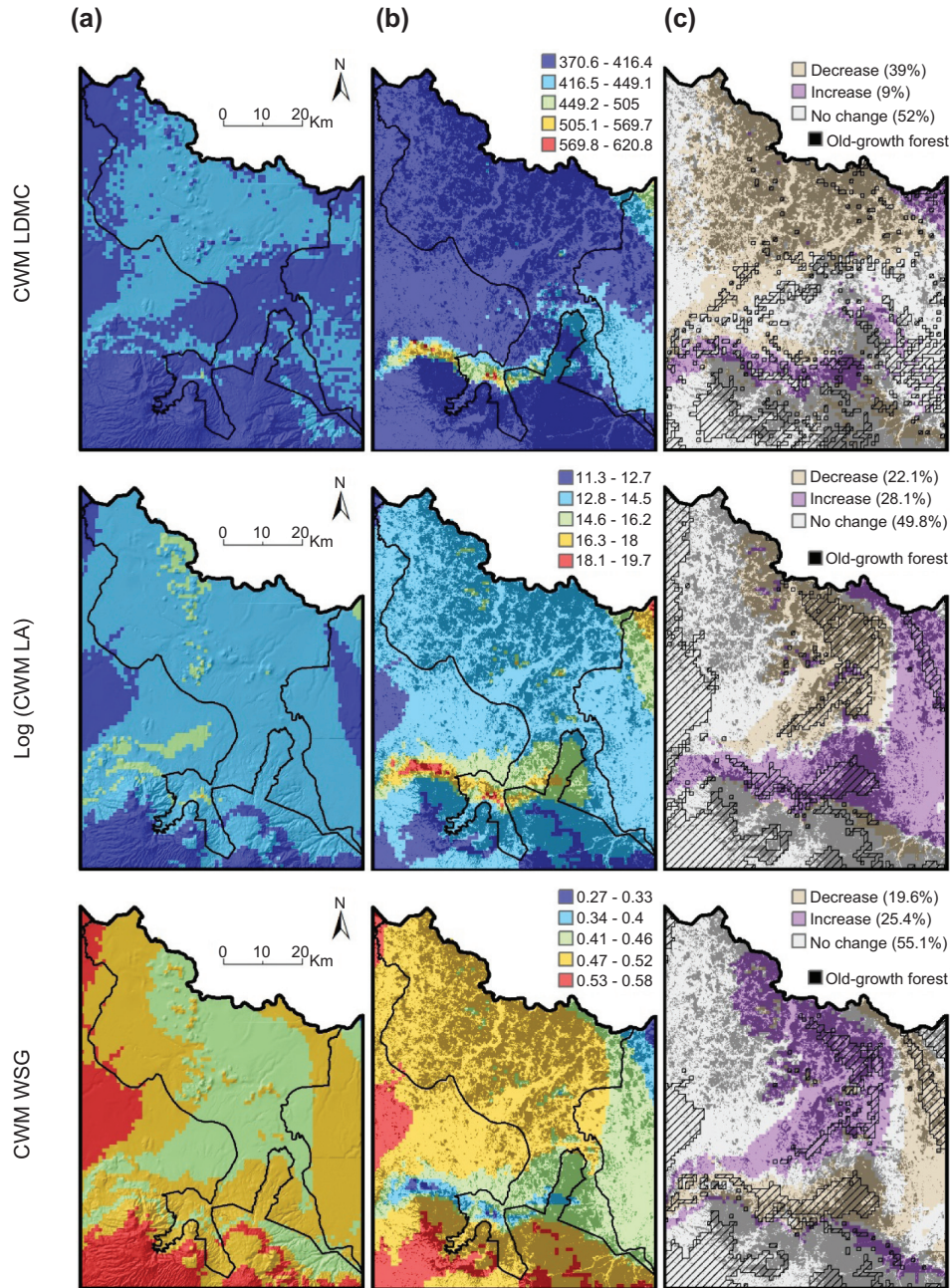
Figure 6. Continued

gradients to predict and spatially project current and future community weighted mean values for six functional traits related to the stem and leaf economic spectrum of plant species. We found that the precipitation gradient in our study area was a more important predictor of CWM traits than the temperature gradient. Our predictions of current and future functional properties of lowland and foothills forests, allowed us to assess the direction and magnitude of the potential climate-induced change. We found clear trends towards higher values of CWM SLA, P and N, and lower values of CWM LDMC, and the reduction of functional trait space occupied by 127 old-growth forest plots. Overall, our results suggest that a high-emissions climate change scenario will lead to forests with more acquisitive weighted

mean trait values, as well as to a homogenization among forest communities in terms of their functional composition or identity.

Climatic gradients underlying variation in community functional composition

CWM trait values responded to the current precipitation gradient, which as modelled in Worldclim is characterized by greater rainfall seasonality to the west and in higher altitude areas within the Central Mountain Range. In accordance with precipitation projections previously described for Central America (IPCC 2013), there was a large variation

in future precipitation trends among the 17 climate GCMs we assessed (RCP 8.5, year 2050). In spite of this, we found a clear tendency in future forest functional composition, with up to 56% of the study area showing likely changes in single CWM traits. Although studies of forest composition along altitudinal gradients have been used to highlight the potential impact of temperature change on biological communities (Colwell et al. 2008, Malhi et al. 2010, Feeley et al. 2013), our results suggest that future precipitation patterns may have greater influence than temperature on the functional composition in lowland and premontane forests.

The 17 updated GCM models (IPCC 2013) used in our study pointed to an average temperature increase of 2.1°C, which results in < 2% of our study area showing a no-analog future climate (i.e. climatic conditions that do not presently exist; Fitzpatrick and Hargrove 2009) when assessing values of climate PCA Axis 1, and < 1 % on climate PCA Axis 2. As potential future temperatures are largely within the current temperature range, we believe biotic attrition (Colwell et al. 2008) is unlikely to occur. If this were to happen, modelling would have to consider the possibility that the current tree species are replaced by radically different plant functional types (Dubuis et al. 2013).

Future changes in functional composition of old-growth forest communities

Our results suggest that lowland forest plant communities will undergo changes in their functional composition towards lower values of CWM LDMC and higher values of CWM N, SLA, and P. These future CWM trait values suggest a shift from forest dominated by more conservative tree species with tougher, nutrient poor leaves and slower growth, to communities with more acquisitive tree species with fast nutrient acquisition and turnover, associated with softer, nitrogen-rich leaves and fast growth (Wright et al. 2004, 2010, Poorter et al. 2009, Lavorel 2013, Adler et al. 2014). Other studies have showed how tropical forest CWM trait values change predictably on a conservative-acquisitive spectrum, in relation to disturbance from forestry operations (Carreño-Rocabado et al. 2012) and possible historical disturbance (van der Sande et al. 2016). Our study suggests that climate-related changes in forest functional composition in our landscape are accompanied by a reduction of functional space, a homogenization of forest functional composition, and new combination of CWM trait values within new functional space. Such changes may have repercussions in ecosystem functioning, since CWM leaf and stem traits and plant functional groups influence ecosystem processes such as above-ground biomass storage (Ruiz-Jaen and Potvin 2011, Conti and Díaz 2013, Finegan et al. 2015), litter decomposition (Cornwell et al. 2008, Brovkin et al. 2012, Freschet et al. 2012), and soil N and P pools and primary productivity (Hooper and Vitousek 1997, Brovkin et al. 2012). Other studies suggest that 'faster' tropical forests dominated by fast-growing acquisitive species associated with high light use efficiency and high productivity are expected under a warmer world (Reu et al. 2011). In our study, the modelled shift to 'faster' forests could result either from an increment in the relative abundance of species with

higher specific leaf area, leaf nitrogen and phosphorous content and lower leaf dry matter content, or due to phenotypic plasticity where – assuming that future temperature regimes are within the thermal tolerance ranges of these tree species – more acquisitive leaf trait values will be assumed. Currently, fast-growing acquisitive species are present in these forests (Finegan et al. 1999) potentially providing the species base for these changes. Soil nitrogen is not a limiting resource in these tropical forests (Sollins 1998). Because predicting future trends of N availability is not straightforward (Chapin et al. 2012, chapter 14) we assume it will not become limiting under the climate change scenario used in our study. If forest functional composition becomes more acquisitive, then CWM P should also, in principle, increase. However, lowland tropical rain forest ecosystem processes are widely believed to be P-limited due to substrate factors (Vitousek et al. 2010, Cleveland et al. 2011) and currently there is no plausible climatic mechanism to explain variation in P availability (Vitousek et al. 2010). Implications of substrate-determined phosphorous limitation and its possible interactions with nitrogen cycles in lowland tropical forests (Cleveland et al. 2011) on potential changes in CWM P under future climates remain to be clarified by further studies.

Our study represents the first attempt to model tropical forest plant functional composition under future climate, and our approach could be applied to analysis of potential response of vegetation to climate change in any biome. Our study assumes that relationships between functional traits and environment at the plant or leaf level scale up to the community (Finegan et al. 2015), and we believe that CWM traits can be used to simulate response of vegetation to climate change. Using a modelling approach, we report potential shifts in community functional composition in old-growth Costa Rican forests, where models based on future changes in precipitation and temperature gradients suggest future lowland communities with softer, more nutrient rich leaves than is currently the case. We not only observed a change from CWM traits values associated with dominance by more conservative species to CWM trait values associated with dominance by more acquisitive species, but also a reduction of the multi trait functional space currently occupied by old-growth forests given their CWM trait values. This potential future functional composition may have further effects on ecosystem functioning and ecosystem services currently delivered by these tropical rainforests. Finally, our work supports current functional biogeography research (Violle et al. 2014) by describing and explaining regional distribution of forests forms and functions. Improved knowledge of the responses of plant traits to environmental change can help bridge the gap between species-based biogeography and biogeochemical research (Violle et al. 2014).

Future perspectives

In line with our objectives of modelling the response of functional properties of tropical forest to climatic variation, our models contained only climatic predictors. We did not explore edaphic variables known to influence functional trait values (ter Steege et al. 2006, Fyllas et al. 2009, Ordoñez et al. 2009, Dubuis et al. 2013, Fujita et al. 2013, Fortunel

et al. 2014, Maire et al. 2015). Based on available research indicating that soil variables covary with climate and elevation (Grieve et al. 1990, Lieberman et al. 1996, Sesnie et al. 2009, Chain-Guadarrama et al. 2012), we speculate that climate will be the main driver of vegetation change in the coming decades, and that soil and vegetation will respond to climate as an integrated system (cf. Chapin et al. 2012, chapter 2). Nevertheless, future work should investigate both climate and soil variables simultaneously.

Old-growth forest covers approximately 34% of our study area (Shaver et al. 2015; Fig. 6), and is embedded within a diverse agricultural matrix (Shaver et al. 2015). Land cover change due to deforestation and agricultural intensification is simplifying and homogenizing the matrix between old-growth forest patches, affecting their connectivity (Shaver et al. 2015). We did not explore historical land use and cover change and current landscape configuration components in our modelling, which may disrupt the natural trait variation found within and across plant communities (Abelleira Martínez et al. 2016). One reason for this is that our sampling protocol was designed to minimize possible changes in forest due to adjacent non-forest areas (Sesnie et al. 2009), and previous studies in the same landscape suggest edge effects are not strong (Schedlbauer et al. 2007, Bouroncle and Finegan 2011). Therefore, we are confident that our results are largely free of effects of landscape modification, though we consider that future modelling could usefully take into account landscape composition and structure.

We did not measure intraspecific trait variation, which can account for a significant proportion of total trait variation in some circumstances (Hulshof and Swenson 2010, Albert et al. 2010, Lepš et al. 2011, Siefert et al. 2015). However, our study area is large (6166 km²) and has high species diversity (253 species sampled for traits) and the importance of intraspecific variation has been shown to decrease with increasing geographic scale (Albert et al. 2011, Siefert et al. 2015) as well as increasing species richness (Siefert et al. 2015) and turnover (Lepš et al. 2011). But again, CWM trait response models like ours are potentially open to improvement and refinement, in this case by the measurement of intraspecific trait variation of dominant tree and palm species.

Finally, given that palms can be considered an a priori functional group, we carried out a modelling exercise after removing palms from the dataset (Supplementary material Appendix 2). Without palms, the relationship of CWM LA and WSG with climate became non-significant, probably because while only four of the 253 species sampled for traits are palms, they are abundant and have extreme values of these traits. Conversely, the relationships of CWM P, SLA and LDMC with climate remained significant and had the same form, although with reduced R2 values. Modelled future patterns remained the same for these CWM traits. Without palms, different modelling results were found for CWM N. CMW N was significantly related to the second axis of the climate PCA, not the first, and modelled future values were lower, not higher, than current values. These changes may be also due to low leaf N content of palms and their high relative abundance. Finally, without palms, modelled future functional space increased rather than decreasing. These results indicate that forest canopy response to climate change may be driven by functional differences between palms and dicot tree species and the relative abundance of these two functional groups. Future work should investigate this possibility.

In summary, our statistical models of the response of CWM functional traits to current and future climate and their spatial projections allows to assess potential climate-induced changes of functional composition of tropical forests and to identify areas prone to change in forest function and therefore ecosystem service provision.

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