Thermally buffered microhabitats recovery in tropical secondary forests following land abandonment

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ABSTRACT

Given the dramatic loss of tropical forests and accelerating climate change, secondary forest regeneration is increasingly recognised as being an important method for reversing losses in biodiversity and carbon stocks. The recolonisation of biodiversity within secondary forests depends in part upon the recovery of forest structure, including the range of microhabitats used by diverse local communities. Here, we investigate the return of critical microhabitats along a successional gradient of secondary forest in the Tropical Andes of Colombia. We measured the abundance of live (bromeliads, tree ferns and moss) and dead (deadwood and leaf litter) microhabitats across three landscapes, each encompassing primary, and young (4–18 yr old) and old secondary forests (19–35 yr old). Considering the increasing rate of climate warming in the region, we also explored whether these microhabitats provide thermally buffered microclimates. We found that secondary forests have different composition and lower complexity of microhabitats than primary forests, but microhabitats appear to be recovering towards primary forest levels. Furthermore, in all forest types, microhabitats had lower maximum temperatures and higher minimum temperatures, thereby serving as thermal buffers that reduced exposure to extreme temperatures. These benefits exist despite ambient temperatures in secondary forests surpassing those of primary forests by 1–2 °C on average. The protection of secondary forest and promotion of further forest regrowth in the Tropical Andes should represent an urgent investment for conservation, and the value of these forests for offering critical microhabitats and buffered microclimates under climate change should not be overlooked.

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1. Introduction

Land-use change is a primary driver of global biodiversity loss (MEA, 2005) and carbon emissions (Grace et al., 2014). During the 1980s and 1990s, >80 million hectares (ha) of tropical forests were converted into cropland and pasture (Gibbs et al., 2010), with the rate of conversion continuing to increase in many tropical regions (Hansen et al., 2013). The conversion of tropical forest to agriculture severely fragments the landscape, dramatically reducing species richness (Foster et al., 2011; Gibson et al., 2011), and causing edge and isolation effects that further increases extinction risk (Ferraz et al., 2003; Schnell et al., 2013).

Despite these trends, there has been a concurrent phase of land abandonment in areas of marginal suitability for agriculture during the past decades in some regions of the tropics (Guariguata and Ostertag, 2001; Sanchez-Cuervo and Aide, 2013). Seventy percent of land abandonment has occurred in hilly or montane areas of Central America, the Andes, Vietnam, and the Philippines (Asner et al., 2009), but with some also occurring in flat regions such as the Amazon and Madagascar (Asner et al., 2009; Rodríguez et al., 2012).

Following land abandonment, natural forests begin to regenerate in many of these areas, with residual seed banks and dispersed seeds underpinning this process (Lindsell et al., 2015). Over time, carbon stocks in secondary forests gradually recover towards levels found in primary forests (Martin et al., 2013; Gilroy et al., 2014). Secondary forests are also rapidly (re-)colonized by animal biotas (Martin et al., 2013; Gilroy et al., 2014; Queiroz et al., 2014), including some species

threatened with extinction (Gilroy et al., 2014) and animal groups that are more prone to extreme temperatures, such as amphibians (Basham et al., 2016).

The precise nature of biodiversity recovery depends on changes in forest structure, including foliage density and tree height, as well as the diversity of small-scale habitat features called microhabitats (MacArthur et al., 1962). Microhabitats are important to a wide range of taxa, for example, logs and tree cavities provide microhabitats for amphibians, birds, small mammals, and invertebrates (Stapp, 1997; Cadavid et al., 2005; Grüebler et al., 2014); epiphytic plants such as bromeliads and bird's nest ferns (*Asplenium*) offer shelter and breeding habitat for amphibian and invertebrate communities (Ellwood and Foster, 2004; Urbina and Galeano, 2009; Silva et al., 2011; Jocque and Field, 2014; McCracken and Forstner, 2014; Scheffers et al., 2014b); and leaf-litter and soil are commonly used by amphibians and invertebrates (Stapp, 1997; McGlynn and Kirksey, 2000; Cadavid et al., 2005; Urbina and Galeano, 2009; Wanger et al., 2010). Microhabitats, along with providing space for breeding and foraging, also provide buffered shelter during extreme weather events, although the latter has only been recorded in primary old-growth forest (Scheffers et al., 2014a), not secondary forests. Thus, the extent of microhabitat recovery in secondary forests is an unknown, but particularly important process to biodiversity recovery in these areas.

In addition to land-use change, biodiversity is also threatened by climate change. Over the last 50 years, the rate of warming has increased significantly while extreme weather events (e.g., droughts and heatwaves) have become more frequent and intense (IPCC, 2014), severely threatening biodiversity globally (Sekercioglu et al., 2008; Chen et al., 2009; Chen et al., 2011; Hannah, 2011; Maclean and Wilson, 2011; Freeman and Class Freeman, 2014). Carbon enhancements under carbon-based payments for ecosystem service schemes (e.g., United Nations Reducing Emissions from Deforestation and Forest Degradation, REDD+) have been implemented to reduce carbon emissions by financially incentivising forest recovery and restoration. Although these programmes offer some biodiversity co-benefits (CBD, 2011; Gilroy et al., 2014), the extent to which carbon accumulation correlates positively with the recovery of microhabitats and microclimates is uncertain. Addressing this question is therefore important for understanding if and how species that depend on such environments will benefit from carbon payments.

Species have limited options in responding to climate change: become extinct; cope or adapt in situ; or shift their ranges to track optimal climates (Lawler et al., 2013), which has already occurred with a large number of species (Parmesan and Yohe, 2003; Hickling et al., 2006). Importantly, for the numerous species that are unable to track their optimal climate niches (Chen et al., 2009), the presence of microhabitats could provide a microclimatic shelter during extreme weather events. Thus, the ability of microhabitats to buffer increased ambient temperatures in secondary forests will likely determine the survival of these species.

Here, we aim to answer: (1) How similar is microhabitat composition in secondary forests to that found in primary forests? (2) How much time since land abandonment is required for the recovery of critical microhabitats? (3) Is there a positive relationship between carbon stock recovery and microhabitat recovery? And (4) how well do microhabitats in secondary forests buffer climate compared to primary forests? Here we answer these key questions by focusing on a successional gradient of secondary forest in the Tropical Andes, which is a global hotspot of extinction risk and species endemism.

2. Methods

2.1. Study area

We chose three study landscapes located within the departments of Antioquia, Risaralda and Chocó, along the Western cordillera of the Colombian Andes (long: −75.8895 to −76.0825, lat: 5.2396 to 5.8251)

(Fig. A.1; following Gilroy et al., 2014). Each site encompasses primary forests, naturally regenerating secondary forests and an agricultural matrix dominated by cattle pasture, with other crops present under very limited cover (<10 ha in total, including maize and plantations of tamarillo *Solanum betaceum* (Gilroy et al., 2014)). The study area covered an altitudinal range of 1290–2680 m above sea level. This region supports one of the highest global diversities of threatened and endemic taxa (Myers et al., 2000; Orme et al., 2005), and is characterised by a long history of cattle farming (Gilroy et al., 2014).

Across these three landscapes (Fig. A.1B, from north to south: Reserva Tangaras, Chocó; Reserva Mesenia-Paramillo, Antioquia; and Cerro Montezuma, Risaralda), we created 29 sampling squares of 400 m × 400 m and spaced by >400 m apart, with squares representing one land-use type (naturally-regenerating young secondary forest from 4 to 18 yr old, old secondary forest from 19 to 35 yr old, and primary old-growth forest). In each square, data were sampled from three sampling points, each spaced by 200 m, giving 87 sampling points in total (following Gilroy et al., 2014).

2.2. Microhabitats

We placed a 25 m × 6 m plot at each of our 87 sampling points, within which we sampled microhabitat abundance, biomass and volume. These three microhabitat metrics will be hereafter referred to as abundance. Elevation was measured in the plot centre. We measured three live (bromeliad, fern, moss) and two dead (deadwood, leaf litter) microhabitats across each plot. Logistic field limitations allowed us to have only 74 plots for dead microhabitats and carbon.

2.2.1. Live vegetation

2.2.1.1. Bromeliads. Epiphytes are particularly vulnerable to forest degradation (Turner et al., 1996), but are important microhabitats for amphibians and invertebrates (Jocque and Field, 2014; Scheffers et al., 2014b). Bromeliads are one of the most abundant epiphytes in the Tropical Andes (Benzing, 2000). We recorded the total number of bromeliads in our plot. Total number of plots (N_{total}) = 87 plots.

2.2.1.2. Tree ferns. Understorey tree ferns (Order Polypodiales) have a single erect trunk and very large fronds, making them important microhabitats for amphibians, mites, spiders and several arthropods including beetles (Shuter and Westoby, 1992; Richards, 2007; Li et al., 2011; Fountain-Jones et al., 2012). We measured height and diameter at breast height (dbh) of all ferns >5 cm dbh (following Gilroy et al., 2014). We estimated tree fern biomass using the allometric equation of (Tiepolo et al., 2002). N_{total}= 87 plots.

2.2.1.3. Moss. Moss is an important microhabitat for insects and amphibians (Tarkowska-Kukuryk and Mieczan, 2014; Lee-Yaw et al., 2015). In each plot, we delimited fifteen 1 m² quadrats (following Urbina and Galeano, 2009). Moss height and density defines how easy species move through it (Lee-Yaw et al., 2015). Therefore, moss was assessed in such a way as to retain moss original structure during measurement. To do this, we derived a metric of moss volume by multiplying depth (an average of four measurements per quadrat) and the percentage of moss coverage (Maanavilja et al., 2014). N_{total}= 15 quadrats per plot ∗ 87 plots = 1305 quadrats.

2.2.2. Dead vegetation

2.2.2.1. Deadwood. Deadwood is a crucial requirement for many arthropod species since it provides a place to hide and forage (Lassauce et al., 2011; Bluhm et al., 2015), while the volume of deadwood can indicate a higher abundance of birds and beetles (Winter et al., 2005). At each sampling point we established a smaller 15 m × 5 m plot, within which we estimated the biomass of all standing or fallen dead trees

(snags) >5 cm dbh (Gilroy et al., 2014). For snags >10 m high we used allometric equations to estimate biomass, applying a deadwood density of 0.31 g cm^{-3} taken from the literature (Gibbon et al., 2010). For snags <10 m high, we assumed the tree was a cylinder and estimated biomass by multiplying volume with wood density. The diameter and length of all pieces of fallen deadwood (coarse woody debris) of ≥5 cm diameter was also recorded, converted into volume and used to estimate biomass (assuming a cylindrical shape). N$_{total}$= 74 plots.

2.2.2.2. Leaf litter. Leaf litter is an essential microhabitat for amphibians and invertebrates, providing physical shelter and foraging space (Urbina and Galeano, 2009; dos Santos Bastos and Harada, 2011; Queiroz et al., 2013). We measured litter dry biomass since the amount (weight) of leaf litter is one of the most important characteristics to determine species abundance and richness (e.g. ants (dos Santos Bastos and Harada, 2011; Queiroz et al., 2013)). Within each smaller 15 m × 5 m plot, we collected all leaf litter, grass and small plants (<0.5 m in height) from 4 × 0.25 m^2 quadrats (Gilroy et al., 2014), following Queiroz et al. (2013). We weighed these samples to the nearest 0.1 g, then used the fresh:dry weight ratio of an oven-dried subsample (10–20%) to estimate the dry biomass of litter (Nascimento and Laurance, 2002). N$_{total}$ = 74 m^2.

2.3. Live non-soil carbon stocks

To calculate live non-soil carbon stocks, within each smaller 15 m × 5 m plot we also measured the diameter at breast height (dbh) of all live trees >5 cm dbh, and measured wood specific gravity using tree cores extracted with an increment borer (two threads, 5.15 mm diameter; Haglöf, Sweden) (Gilroy et al., 2014). We used these values in four allometric biomass estimation equations taken from harvested tree studies (Chave et al., 2005; Alvarez et al., 2012; Feldpausch et al., 2012). We took the mean of the four estimates as the final aboveground estimate for each tree. Palm growth form differs from that of other trees, and so to calculate palm biomass we measured diameter and estimated height, and then used the allometric equation of Sierra et al. (2007). Root biomass was estimated using a published upland forest root:shoot ratio of 0.26 (Cairns et al., 1997). All vines with a dbh of ≥2 cm that were ≤1 m from the long edges of the plot were also measured and vine biomass was estimated using an equation developed in Colombian montane forest (Sierra et al., 2007). We summed the biomass pools for each plot before multiplying by 0.5 to give an estimate of the total live non-soil carbon stock (Gibbon et al., 2010). N$_{total}$ = 74 plots.

2.4. Temperature data

We used 179 iButton data loggers (model: DS1921G-F5; accuracy: 0.5 °C) to record understorey ambient, canopy and microhabitat temperature, and we also set nine iButton hygrochron loggers (model: DS1923; accuracy: 0.1 °C) as a backup to record understorey ambient temperature across all forest types. We placed the iButtons in 17 plots from Cerro Montezuma and 16 plots from Reserva Mesenia-Paramillo, with placement spanning young and old secondary, and primary forests (Table A.1). All loggers recorded data every 2 h from February 2013 to February 2014.

Each iButton was placed inside a re-sealable zipper storage bag (50 mm × 50 mm) to shelter them from precipitation and enclosed within a metal mesh to guard them from rodents. One iButton logger per plot was hung approximately 1 m above the ground to measure understorey ambient temperature (Scheffers et al., 2013a). To identify the (near-)maximum potential ambient air temperature for our study plots, we hung a second iButton in the upper canopy cover of trees between 10 and 13 m above the ground (Scheffers et al., 2013b), as close as possible to directly above the understorey ambient logger depending on canopy accessibility. To minimize exposure to direct solar radiation, canopy, understorey and humidity loggers were secured under a plastic funnel, with all funnels suspended facing north (controlling for diurnal variation in sun position).

Microhabitat temperature loggers were deployed thus: (1) approximately 5 cm under leaf litter (n$_{total}$ = 33); (2) between the leaves of bromeliads (n$_{total}$ = 26); (3) inside holes at the base of trees (tree circumference > 8 cm dbh) (n$_{total}$ = 33); (4) within the roots of ferns (fern circumference > 8 cm dbh) (n$_{total}$ = 33); and (5) at approximately 20 cm depth in soil (n$_{total}$ = 9). All loggers were placed within 8 m of the understorey ambient logger (most within 1 and 4 m). Only one iButton was placed within a particular microhabitat for each plot.

2.5. Statistical analyses

2.5.1. Microhabitat composition

To compare microhabitat composition among secondary and primary forests we used nonmetric multidimensional scaling ordination (NMDS, function "metaMDS" from the vegan package). This technique uses microhabitat abundance data and makes no prior assumptions about habitat-level structuring in the data. To evaluate whether composition differed significantly across the forest types, we transformed our data into a similarity matrix (Bray-Curtis index) and performed an analysis of similarity (ANOSIM). ANOSIM uses ranks of dissimilarities and this test is free from any normality assumptions. A post-hoc permutation test (999 replications) was run to detect which pairs of groups significantly differed. The community analysis was performed using PRIMER 7 (Version 7.0.7; Clarke and Gorley, 2015). We also extract NMDS axis 1 and 2 to create a microhabitat composition metric.

2.5.2. Microhabitat complexity recovery

To compare microhabitat data to a notionally common scale we normalized the data for each microhabitat by rescaling the range from 0 to 1. To create a microhabitat complexity metric we added the normalized data for each microhabitat by forest type. This complexity metric represents a truthful microhabitat abundance value because it sums each microhabitat value, in comparison with the composition metric (derived from NMDS axes) which represents the relationship or similitude of microhabitat data among forest types in a graphical manner. To compare microhabitat complexity of secondary and primary forests, we obtained the ratio of young and old secondary forest complexity compared to primary forest complexity (considering the latter our benchmark of 100%). We then performed a one-way analysis of variance (ANOVA; function "aov") with forest type as our grouping variable.

To determine whether there were differences in the abundance of each microhabitat across forest types, we performed linear mixed effect models (function "lmer"), with sampling square, elevation, and landscape as random factors. All data were log transformed before each analysis, and residuals were assessed for each model considering model assumptions.

2.5.3. Carbon-microhabitat co-benefits

Due to the ecological meaningfulness of carbon and the high correlation between carbon sequestration and forest age, we assessed the relationship between carbon and microhabitat recovery using total live non-soil carbon as our predictive variable. We did so for each of our microhabitats using the normalized microhabitat data, microhabitat complexity metric, and microhabitat composition metric (using NMDS axes 1 and 2). We used quantile regression (function "rq"), from the quantreg package, because our data showed a larger number of outliers than normal, and quantile regressions give more robust estimates against outliers in the response measurements. For the same reason, we analysed the 10th, 50th, and 90th percentile to discover more useful predictive relationships between our variables. All microhabitat data were log transformed prior to analyses.

2.5.4. Microclimates

Our data showed no seasonality patterns, and therefore was not subdivided. Temperature maxima and minima have been successfully
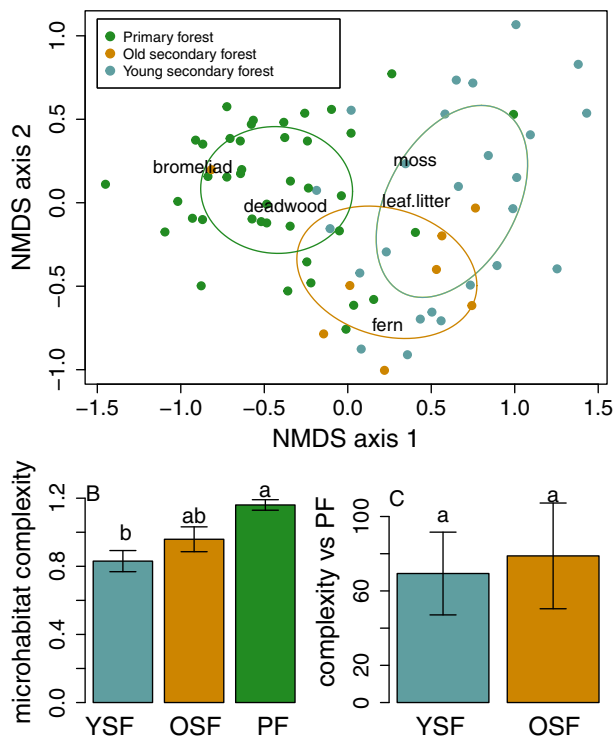
Fig. 1. (A) Nonmetric multidimensional scaling (NMDS) of microhabitat composition among forest types using microhabitat abundance, biomass and volume. Young secondary forests are <19 years old, old secondary forests are >19 years old, and primary forest is undisturbed old-growth. Ellipses represent a grouping function depending on the standard deviation of points with a 95% confidence interval. (B) Recovery of microhabitat complexity among forest types. (C) Secondary forest ratio of microhabitat complexity compared to primary forest (considered as 100%). YSF: young secondary forest; OSF: old secondary forest; PF: primary forest. Values represent normalized data from mean abundance of microhabitats. Error bars represent standard error. Different superscripts represent significant differences ($p < 0.05$).

used to measure microhabitat thermal buffering effect (Shi et al., 2014). Therefore, weekly maximum, minimum and mean temperatures were taken from each iButton per microhabitat per forest type. We used linear mixed effect models ("lme") to determine temperature differences among forest types, including forest type and date as fixed effects, and as random effect we placed iButton identity nested within transect and elevation (the two landscapes in which we placed iButtons do not overlap in elevation, hence we do not need to include landscape as a random factor). p-Values for each model were determined comparing the model versus the null model ("anova"). Significant differences between forest types were assessed via post-hoc Tukey comparisons.

To obtain the rate of increase in microhabitat temperature for every 1 °C increase in understorey ambient temperature we used the temperature data collected every 2 h. Linear models ("lm") were employed to generate a relationship between each microhabitat metric (i.e. bromeliad max, bromeliad min, bromeliad mean, etc.) depending on understorey ambient temperature (ambient max, ambient min, or ambient mean). Residual plots were checked to confirm model assumptions were met. Unless stated otherwise, all statistical analyses were performed in R (Version 3.1.2).

3. Results

3.1. Microhabitat composition

Ordination plots showed that microhabitat composition in secondary forests differed significantly from primary forests (Fig. 1A; ANOSIM, $R = 0.53$, $p = 0.001$). There was some degree of overlap in the microhabitat composition between forest types (Fig. 1A), and pairwise

comparisons revealed no significant differences between young secondary and old secondary forest ($R = 0.05$, $p = 0.25$). In contrast, there was significant dissimilarity between old secondary and primary forest ($R = 0.36$, $p = 0.001$). In the ordination plot, young secondary forests were the furthest away from primary forests, making them the least similar in microhabitat composition ($R = 0.66$, $p = 0.001$). Recovery of secondary forest thus regenerates increasingly similar microhabitat composition to primary forest over time.

3.2. Microhabitat complexity recovery

Considering bromeliads, tree ferns, moss, deadwood and leaf litter, primary forests held a significantly higher microhabitat complexity than young secondary forests ($F_{2,367} = 3.57$, $p < 0.05$). Old secondary forest was intermediate between these forest types, and did not differ significantly from either primary forest or young secondary forest (Fig. 1B). There was, however, no significant difference between young and old secondary forest in their ratio of complexity compared to primary forest (Fig. 1C; $F_{1,8} = 0.07$, $p = 0.79$).

3.2.1. Live vegetation

There was a significant difference between forest types in number of bromeliads ($F = 36.5$, $p < 0.0001$; Table 3): old secondary had three times more bromeliads than young secondary forest, and primary forest had three times more bromeliads than old secondary (Fig. A.2A). Therefore, secondary forests need >35 years of regeneration to fully recover this key microhabitat. Conversely, there was no significant difference between forest types in tree fern biomass ($F = 1.96$, $p = 0.15$; Fig. A.2B; Table 3) or moss volume (Fig. A.2C; $F = 1.32$, $p = 0.27$; Table 3). Thus, even after a short period of time (4 to 18 yr) of forest regeneration, tree ferns and moss volume were recovered.

3.2.2. Dead vegetation

There was significant variation between forest types in deadwood biomass ($F = 8.57$, $p < 0.001$; Table 3): young secondary forests (which did not differ significantly from old secondary forests) had over four-fold less deadwood biomass than primary forest (Fig. A.2D).

Table 1
Carbon-microhabitat co-benefits. Summary from quantile regressions at the 90%, 50%, and 10% quantiles from abundances of five microhabitats (Fig. 2A–H), microhabitat complexity as the sum of all normalized microhabitat data, and microhabitat composition derived from NMDS axes scores (see Fig. 1), along a gradient of young secondary forest, old secondary forest, and primary forest in the Colombian Andes. Bold p values represent significant relationships ($p < 0.05$). See text for detailed methods.

Microhabitat	Quantile	t value	p value
Bromeliad	90%	2.54	**0.01**
	50%	3.78	**<0.001**
	10%	4.79	**<0.001**
Tree fern	90%	0.34	0.73
	50%	1.18	0.24
	10%	0.77	0.44
Moss	90%	−0.60	0.54
	50%	−0.46	0.64
	10%	1.02	0.30
Deadwood	90%	4.00	**<0.001**
	50%	2.08	**0.04**
	10%	2.97	**0.003**
Leaf litter	90%	−0.49	0.62
	50%	0.06	0.94
	10%	−1.29	0.19
Complexity	90%	0.80	0.42
	50%	2.82	**0.005**
	10%	1.27	0.20
Composition NMDS axis 1	90%	−4.23	**<0.001**
	50%	−4.36	**<0.001**
	10%	−2.82	**0.006**
Composition NMDS axis 2	90%	−0.94	0.34
	50%	−0.45	0.65
	10%	1.31	0.19
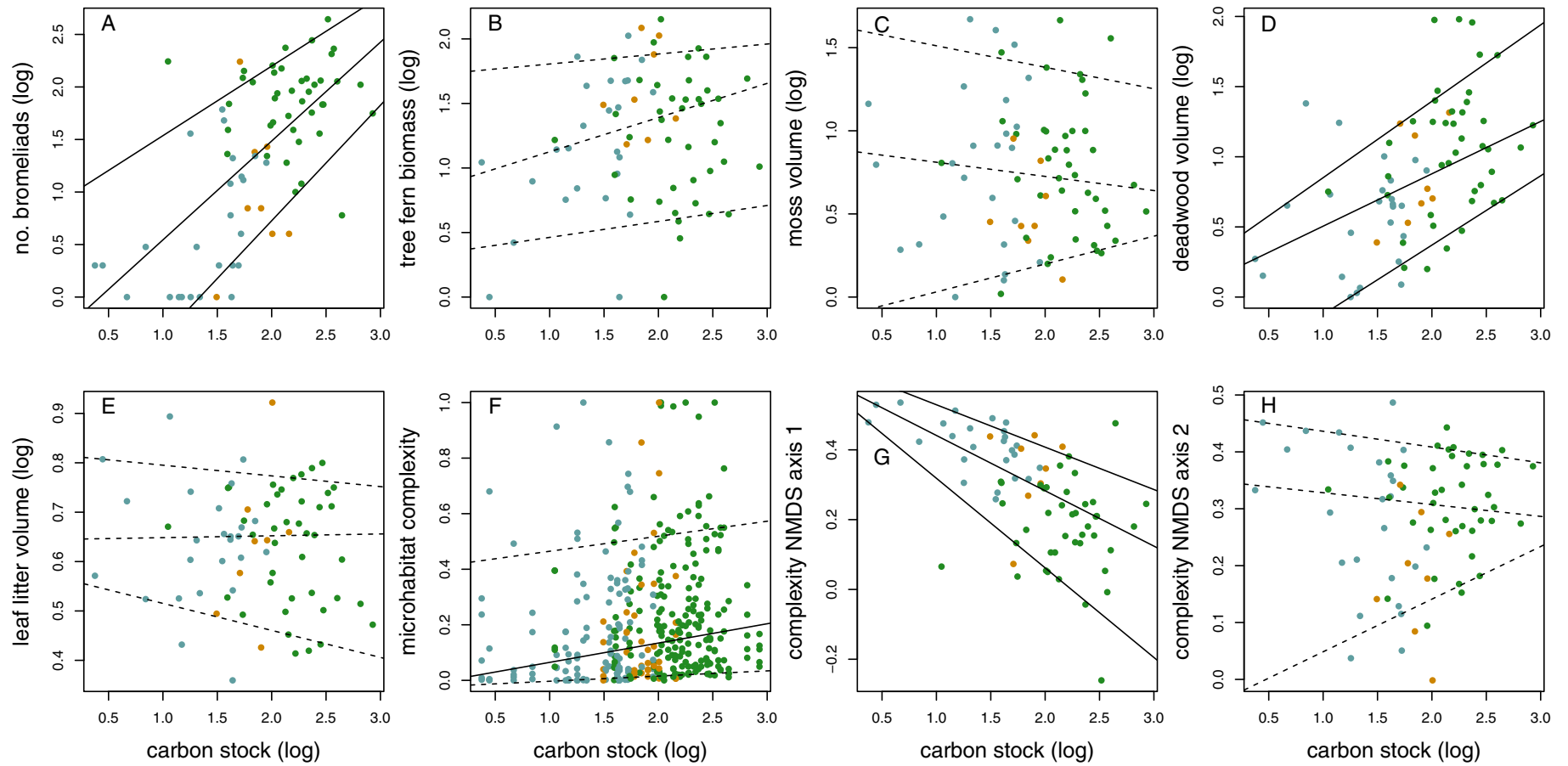
Fig. 2. Carbon and microhabitat co-benefits for bromeliads (A), tree ferns (B), moss (C), deadwood (D), leaf litter (E), microhabitat complexity (F), and NMDS axis 1 (G), and axis 2 (H). Quantile regressions of microhabitat abundance data between young (<19 yr old) secondary forest (blue points), old (19–35 yr old) secondary forest (orange points), and primary forest (dark green points). Lines represent 10th (bottom line), 50th (middle line), and 90th (top line) quantiles. Solid lines represent significant relationships (*p* < 0.05). Dash lines represent non-significant relationships.

Table 2

Mean comparisons of daily maximum, daily mean, and daily minimum environmental temperature, and the rate of temperature increase for every 1 °C increase in understorey ambient temperature per forest type. Values shown are mean ± SE. Superscripts reveal pairwise differences at $p < 0.05$. Key to abbreviations: PF, primary forest; OSF, old secondary forest (19–35 yr); YSF, young secondary forest (4–18 yr).

	Forest type	PF	OSF	YSF	L. ratio	p	df
Canopy	Max	20.19 ± 0.09	21.06 ± 0.01	21.71 ± 0.12	21.72	**<0.001**	458
	Mean	16.46 ± 0.04	16.82 ± 0.04	16.86 ± 0.05	51.39	**<0.001**	458
	Min	14.21 ± 0.03	14.31 ± 0.03	14.22 ± 0.04	16.39	**<0.001**	458
	Rate	1.368	1.362	1.140			
Understorey ambient	Max	18.78 ± 0.06[B]	19.79 ± 0.07[AB]	20.18 ± 0.09[A]	57.85	**<0.001**	2054
	Mean	16.60 ± 0.04	17.29 ± 0.04	16.87 ± 0.05	110.60	**<0.001**	2054
	Min	14.95 ± 0.04	15.43 ± 0.04	15.58 ± 0.05	61.58	**<0.001**	2054
	Rate	–	–	–			
Bromeliad	Max	18.00 ± 0.06	19.41 ± 0.07	18.39 ± 0.08	30.64	**<0.001**	1009
	Mean	16.02 ± 0.04	17.07 ± 0.04	15.85 ± 0.05	36.61	**<0.001**	1009
	Min	14.45 ± 0.04	15.25 ± 0.04	13.94 ± 0.05	6.18	0.102	1009
	Rate	0.927	0.901	0.754			
Tree fern	Max	16.51 ± 0.04	18.04 ± 0.03	18.23 ± 0.06	33.36	**<0.001**	1350
	Mean	15.72 ± 0.04	17.06 ± 0.03	16.70 ± 0.05	120.16	**<0.001**	1350
	Min	15.02 ± 0.04	16.10 ± 0.03	15.45 ± 0.06	25.95	**<0.001**	1350
	Rate	0.463	0.473	0.546			
Tree hole	Max	16.54 ± 0.03	17.64 ± 0.03	17.87 ± 0.03	12.07	**0.03**	1413
	Mean	15.87 ± 0.04	17.05 ± 0.03	16.92 ± 0.03	175.43	**<0.001**	1413
	Min	15.18 ± 0.04	16.40 ± 0.03	16.12 ± 0.04	46.44	**<0.001**	1413
	Rate	0.448	0.356	0.303			
Leaf litter	Max	16.85 ± 0.04	18.24 ± 0.05	18.51 ± 0.05	15.09	0.01	1384
	Mean	15.91 ± 0.04	17.12 ± 0.04	16.89 ± 0.04	87.48	**<0.001**	1384
	Min	15.05 ± 0.04	16.07 ± 0.04	15.67 ± 0.04	20.86	**<0.001**	1384
	Rate	0.547	0.560	0.503			
Soil	Max	14.83 ± 0.02	14.79 ± 0.01	15.71 ± 0.02	10.42	0.06	373
	Mean	14.45 ± 0.02[B]	14.70 ± 0.01[B]	15.45 ± 0.02[A]	9.25	**0.009**	1384
	Min	14.13 ± 0.02[B]	14.60 ± 0.01[B]	15.20 ± 0.02[A]	11.25	**0.04**	1384
	Rate	0.124	0.043	0.124			

Nevertheless, old secondary forest had accumulated almost half (44%) of the total deadwood volume found in primary forests just 35 years post-land abandonment (Fig. A.2D). Leaf litter biomass did not differ significantly between forest types (F = 5.54, $p < 0.05$; Fig. A.2E; Table 3), thus this critical microhabitat recovered even in the early stages of forest regrowth.

3.3. Carbon-microhabitat co-benefits

3.3.1. Live vegetation

Bromeliad abundance showed a positive relationship with carbon stock increase. They increased significantly with carbon stock at the 10th ($t = 4.79$, $p < 0.001$), 50th ($t = 3.78$, $p < 0.001$), and 90th ($t = 2.54$, $p = 0.01$) quantiles (Table 1; Fig. 2A). Tree fern biomass and moss volume showed no significant relationship with carbon stock at any of the quantiles (Table 1; Fig. 2C).

3.3.2. Dead vegetation

Deadwood volume showed a positive relationship with carbon stock increase. Deadwood volume increased significantly with carbon at the 10th ($t = 2.97$, $p = 0.003$), 50th ($t = 2.08$, $p = 0.04$), and 90th ($t = 4.4$, $p < 0.001$) quantiles (Fig. 2D). Conversely, there was no relationship between leaf litter biomass and carbon stock at any of the quantiles ($p > 0.19$; Table 1; Fig. 2E).

3.3.3. Microhabitat complexity and composition

Microhabitat complexity showed a positive increase with carbon at the 50th quantile ($t = 2.82$, $p = 0.005$), whereas the 10th and 90th quantiles showed no relationship ($t > 0.80$, $p > 0.20$; Table 1; Fig. 2F). Microhabitat composition derived from NMDS axis 1 showed a negative

relation with carbon at the 10th ($t = -4.23$, $p < 0.001$), 50th ($t = -4.36$, $p < 0.001$), and 90th ($t = -2.82$, $p = 0.006$) quantiles (Table 1; Fig. 2G). Forest types, therefore, can be distinguished by their carbon stock accumulation. Conversely, there was no relationship between NMDS axis 2 and carbon stock ($p > 0.19$; Table 1; Fig. 2H).

3.4. Microclimates

The maximum ambient temperature in the understorey was lower than in the canopy in all forest types (Table 2; Fig. 3A, B). The daily maximum ambient temperature in the primary forest understorey was cooler than that in young secondary forests (z value = 2.98, $p = 0.007$; Fig. 3B2, B4). However, the maximum ambient temperature in the understorey in old secondary forests was not significantly different from primary or young secondary forests ($p > 0.29$; Table 2).

Daily maximum temperatures within microhabitats were on average cooler than understorey ambient and canopy, whereas the daily minimum temperature within microhabitat was on average warmer than understorey and canopy ambient (except for bromeliads; Fig. 3C). Thus, these microhabitats are reducing exposure and serving as thermal buffers by keeping cooler temperatures when it is warm and warmer temperatures when it is cold. During the day, microhabitats thermally buffered the understorey ambient temperature maxima by 0.78 °C to 2.27 °C in primary forest, by 0.38 °C to 2.15 °C in old secondary forest, and by 1.67 °C to 2.31 °C in young secondary forest. At night, microhabitats buffered the understorey ambient temperature minima by 0.07 °C to 0.23 °C in primary forest and by 0.64 °C to 0.97 °C in old secondary forest. In young secondary forest, only leaf litter and tree holes were warmer than understorey ambient night-time temperature by 0.09 °C and 0.54 °C, respectively (Table 2; Fig. 3). In contrast, soil

Fig. 3. Annual temperature variation recorded every 2 h (A1–G1), mean maximum temperature (A2–G2), mean average temperature (A3–G3), and mean minimum temperature (A4–G4) from Feb. 2014 to Feb. 2015 for canopy (A), understorey ambient (B), bromeliad (C), tree fern (D), tree hole (E), leaf litter (F) and soil (G) in naturally regenerating young secondary forest (YSF, <19 yr; blue), old secondary forest (OSF, 19–35 yr; orange), and primary forest (PF; dark green) in the Colombian Andes. The bottom and top of the boxplots represent the first and third quartiles, respectively, the bold line represents the median, and the points represent outliers from all the studied time series. Similar superscripts represent no significant differences ($p < 0.05$).
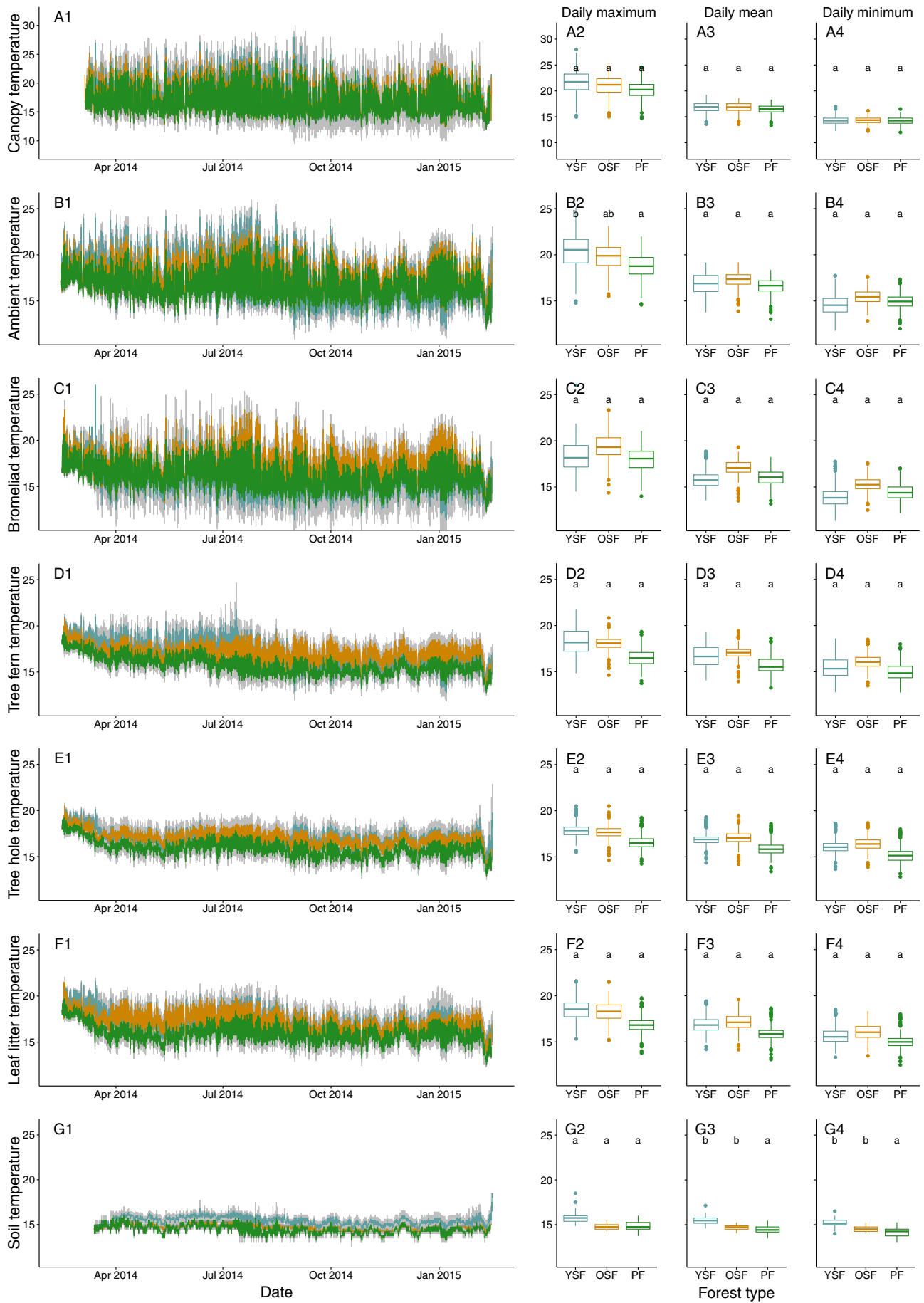
Table 3
Microhabitat abundance, biomass and volume across forest type. Values shown are mean ± SE. Key to abbreviations: PF, primary forest; OSF, old secondary forest (19–35 yr); YSF, young secondary forest (4–18 yr).

Microhabitat	PF	OSF	YSF
Bromeliad abundance	100.87 ± 13.24	30 ± 20.71	10.16 ± 3.18
Tree fern biomass	29.13 ± 4.68	52.04 ± 14.94	25.36 ± 5.35
Moss volume	8.11 ± 1.54	2.9 ± 0.91	9.9 ± 2.48
Deadwood biomass	18.54 ± 3.76	8.18 ± 2.49	4.38 ± 1.07
Leaf litter biomass	3.41 ± 0.17	3.54 ± 0.61	3.5 ± 0.24

minimum and mean temperature was significantly lower in primary and old secondary forests compared to young secondary forests ($p < 0.04$; Table 2; Fig. 3G). All microhabitats warmed at a slower rate (<1 °C microhabitat: 1 °C ambient) than understorey ambient (Table 2; Fig. 3).

4. Discussion

The regrowth of secondary forest on abandoned farmlands is prevalent across the tropics, and these forests are important for biodiversity and carbon stock recovery (Gilroy et al., 2014). Our study suggests that as abandoned lands regenerate as forests, their functional value also increases through the accumulation and diversification of critical microhabitats. Specifically, we document a chronological recovery of microhabitat complexity and a general trend towards niche diversification in older secondary forests. While we found that forest types have different microhabitat composition, secondary forest approached primary forest levels of microhabitat complexity over time. In turn, recovered microhabitats buffered against extreme low and high temperatures in a similar manner to those in primary forest. Moreover, the high correlation between carbon stocks and forest age suggests positive carbon-microhabitat co-benefits as forests regrow. Thus, investment to protect or enhance carbon stocks in secondary forests under carbon-based payments for ecosystem services (PES, e.g., REDD+) will also support an abundance of thermally buffered microhabitats.

4.1. Microhabitat composition

The extent to which secondary forests support biodiversity is strongly linked to the presence and abundance of critical microhabitats (Michel and Winter, 2009). Our study indicates that microhabitat composition in primary forests differs from secondary forests, and that these differences tend to be most pronounced between young secondary and primary forests. This underlines the need to protect primary forests, in order to avoid loss of specialist species that are strongly dependent on certain microhabitats. Moreover, young and old secondary forests did display some similarities in microhabitat composition, suggesting that even from early stages of forest development some microhabitats are already available for biodiversity (Cadavid et al., 2005; Urbina-Cardona et al., 2006).

4.2. Microhabitat complexity recovery across habitat types

We found a highly variable, yet predictable, recovery of microhabitats across forest types (Bittner and Breckle, 1995; Oldekop et al., 2012; Woziwoda et al., 2014). Nevertheless, microhabitat complexity in our study recovered chronologically from young to old secondary forests and this increase in ecological complexity has documented benefits for vertebrates and invertebrate diversity and abundance even in young secondary forests (Lassauce et al., 2011; Jocque and Field, 2014; Scheffers et al., 2014b; Bluhm et al., 2015). As such, our study provides strong support for allocating secondary growth forests as an important conservation tool for recovering biodiversity and reversing extinction risk (Chazdon, 2014; Queiroz et al., 2014).

There is a clear transition from young secondary forests rich in moss and leaf litter to primary forests that also contain more than ten times the number of bromeliads and more than four times the deadwood biomass than young secondary forests. Importantly, bromeliad abundance and deadwood biomass levels in secondary forest reach almost half of those found in primary forest within 35 years following land abandonment (Fig. A.2A, A.2D). The high elevation of our study sites likely supports a faster recovery rate of bromeliads than lower altitude forests. For example, we found similar recovery rates to those documented in the Venezuelan Andes (Barthlott et al., 2001), whereas Australian tropical rainforests (<900 m a.s.l.) showed a slower rate of recovery of epiphyte richness (Shoo et al., 2016), lowland rainforests in Panama (140 m a.s.l.) have not shown any epiphytic recovery after 35 years of forest growth (Woods and DeWalt, 2013), and a pan-tropical meta-analysis showed very slow recovery of epiphytic richness, especially of species that are found in undisturbed forest (Martin et al., 2013). Such a dichotomy probably reflects bromeliad requirements for cooler, wetter climates like the Andes in comparison with more seasonal and hotter lowlands (Ruiz et al., 2012). As amplifiers of biodiversity, bromeliad recovery in secondary forests may offer additional niche space. Bromeliad abundance and deadwood volume are strongly linked to forest age (Barthlott et al., 2001; Woods and DeWalt, 2013; McGarvey et al., 2015), and translocation of bromeliads into medium-aged secondary forests may be a useful tool in applied forest management (Donnelly, 1989).

4.3. Linking forest carbon and microhabitat recovery

Climate change scenarios predict increasing temperatures and variable rainfall in the Tropical Andes, which may hinder forest and microhabitat recovery (IPCC, 2014). Carbon-based payments for ecosystem services (PES) initiatives seek to maximize carbon storage and sequestration as part of a global scheme for climate change mediation, but may also offer important co-benefits for localized biodiversity conservation (Strassburg et al., 2010; Phelps et al., 2012; Gilroy et al., 2014). Our study showed a strong positive relationship between carbon stock and microhabitat complexity, which underpins ecological resilience and increases the benefits to biodiversity (CBD, 2011). Recovery potential appears to be high in secondary forests across the Neotropics (from Mexico to Chile), with considerable capacity for carbon sequestration and storage (Poorter et al., 2016). Although, secondary forests have lower carbon stocks and biodiversity than primary forests (Poorter et al., 2016), recovery of these stocks may now be linked to microhabitat complexity recovery. This also underscores that the Tropical Andes, which is a global hotspot of endemism and extinction risk, are of great interest for promoting carbon enhancements via natural forest regeneration – particularly given that it would be cheap to do so in this region (see Gilroy et al., 2014), and that such projects would offer strong carbon, microhabitat, and biodiversity benefits.

4.4. Are secondary forests climate change ready?

Microhabitats in secondary forest showed temperature-buffering abilities similar in magnitude to those found in primary forests, suggesting that all forest types provide species with climate microrefugia. This is particularly important in young secondary forests since their daily maximum temperatures are higher than in primary forests. The low rate of temperature increase in microhabitats also shows that species are thermally protected for longer periods of time under extreme temperature increases than would otherwise be the case in understorey ambient temperatures (see also Scheffers et al., 2014a for primary forests). Our findings suggest that microhabitats will become an increasingly important resource to help ectotherm communities mitigate the negative impacts of climate change (Huey and Tewksbury, 2009), especially in the Tropical Andes where extreme weather events have

become more intense and frequent and overall temperatures have increased (Ruiz et al., 2012).

Of concern, much tropical montane vegetation depends on specific environmental characteristics to thrive and is highly sensitive to climate change (Morueta-Holme et al., 2015). Climate change could therefore negatively affect the abundance of critical living microhabitats, and perhaps more so in recovering secondary forests. For instance, mosses and bromeliads need constant moisture to grow (Nadkarni, 2000; Merrifield and Royce, 2002), such that a drastic decline in moisture could reduce their abundance. This could in turn, threaten many bird, amphibian and invertebrate species (Merrifield and Royce, 2002; Panizzo, 2011; Scheffers et al., 2014b; Silva and Piratelli, 2014).

4.5. Survey limitations

Our study sites are restricted to naturally regenerating secondary forests in an agricultural matrix dominated by pasture. It is therefore difficult to extrapolate our results to other agricultural systems, as different taxa may respond differently to particular crops (Edwards et al., 2014; Jordani et al., 2015). Our results are also restricted to secondary forests near primary forest, whether small isolated fragments of secondary forests that can have lower buffering potential would show the same results is unknown (Ewers and Banks-Leite, 2013). Moreover, whether similar recovery rates would occur in isolated secondary forests and whether microhabitat recovery would be so rapid in other ecosystems outside the Tropical Andes, especially in hotter and drier lowlands, are both critical unanswered questions.

5. Conclusions

Old secondary forests have high carbon storage potential, and our results suggest that the abundance of critical microhabitats in secondary forests is recovering, sometimes to levels found in a primary forest. A higher abundance of microhabitats increases landscape resilience by returning structure to forests and as such enhances ecological integrity (Ruiz-Jaen and Aide, 2004). This provides habitat for a range of local species, including many at risk of extinction. While protecting primary forests remains a critical conservation goal (Gibson et al., 2011), we live in an era of increasingly human-dominated landscapes (Lewis et al., 2015). While we acknowledge the importance of primary forests, the protection or promotion of secondary forest regrowth is often a more economically feasible strategy of protecting microhabitat rich and climate change resilient forests (Fisher et al., 2011). The critical role of secondary forests should not be overlooked as we seek solutions to the biodiversity crisis, both now and under future climate change.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.07.038.

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