

# **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 upon the recovery of forest structure, including the range of microhabitats used by diverse 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 and old secondary forests. 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 that the abundance of bromeliads and deadwood recover towards primary levels. Each microhabitat reduces exposure to extreme temperatures, serving as thermal buffers by reducing maximum and increasing minimum temperatures among all forest types. 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 secondary forests for offering critical microhabitats and buffered microclimates under climate change should not be overlooked.

## **Keywords:**

Carbon enhancement • Choco-Andes • microclimate buffering • global climate change • secondary forest regeneration

## Introduction

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

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

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

The precise nature of biodiversity recovery depends on forest structure – the properties that define a forest's general appearance, including foliage density and height, as well as the range of critical small-scale habitat features or microhabitats (MacArthur, MacArthur et al. 1962). Microhabitats are used by a wide range of taxa: Logs and tree cavities provide habitat for amphibians, birds, small mammals, and invertebrates (Stapp 1997; Cadavid, Roman-Valencia et al. 2005; Gruebler, Widmer 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, Carvalho et al. 2011; Jocque and Field 2014; McCracken and Forstner 2014; Scheffers, Phillips et al. 2014); and leaf-litter and soil are commonly used by amphibians and invertebrates (Stapp 1997; McGlynn and Kirksey 2000; Cadavid, Roman-Valencia et al. 2005; Urbina and Galeano 2009; Wanger, Iskandar 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, Edwards et al. 2014), not secondary forests. Thus, the extent of microhabitat recovery in secondary forests is an unknown but critically 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 heat-waves) have become more frequent and intense (IPCC 2014), severely threatening biodiversity globally (Sekercioglu, Schneider et al. 2008; Chen, Shiu et al. 2009; Chen, Hill 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+), can be implemented to reduce carbon emissions by financially incentivising forest recovery and restoration. Although these programmes offer some positive biodiversity co-benefits (CBD 2011; Gilroy, Woodcock et al. 2014), whether they have a positive impact on microhabitats and microclimates – and thus the species depending on them – is unknown.

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, Ruesch et al. 2013), which has already occurred with a large number of species (Parmesan and Yohe 2003; Hickling, Roy et al. 2006). Nonetheless, for the numerous species that are unable to track their optimal climate niches (Chen, Shiu 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.

## **Methods**

### **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. S1; following (Gilroy, Woodcock 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 hectares in total, including maize and plantations of tamarillo *Solanum betaceum* (Gilroy, Woodcock et al. 2014). The study area covered an altitudinal range of 1,290-2,680 m above sea level. This region supports one of the highest global diversities of threatened and endemic taxa (Myers, Mittermeier et al. 2000; Orme, Davies et al. 2005), and is characterised by a long history of cattle farming (Gilroy, Woodcock et al. 2014).

Across these three landscapes (Fig. S1B, from north to south: Reserva Tangaras, Chocó; Reserva Mesenia-Paramillo, Antioquia; and Cerro Montezuma, Risaralda), we created 29 sampling squares of 400 m x 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, totalling 87 sampling points each spaced by 200 m (following (Gilroy, Woodcock et al. 2014)).

### **Microhabitats**

We placed a 25 m x 6 m plot at each of our 87 sampling points, within which we sampled microhabitat 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.

#### Live vegetation:

*Bromeliads* - Epiphytes are particularly vulnerable to forest degradation (Turner, Chua et al. 1996), but are important microhabitats for amphibians and invertebrates (Jocque and Field 2014; Scheffers, Phillips et al. 2014). 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 ( $N_{\text{total}}$ ) = 87 plots.

*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, Wang et al. 2011; Fountain-Jones, McQuillan et al. 2012). We measured height and diameter at breast height (dbh) of all ferns >5 cm dbh (following (Gilroy, Woodcock et al. 2014)). We estimated tree fern biomass using the allometric equation of (Tiepolo, Calmon et al. 2002).  $N_{\text{total}}$  = 87 plots.

*Moss* – Moss is an important microhabitat for insects and amphibians (Tarkowska-Kukuryk and Mieczan 2014; Lee-Yaw, Sechley et al. 2015). In each plot, we delimited fifteen 1 m<sup>2</sup> quadrats (following (Urbina and Galeano 2009)). Moss height and density defines how easy species move through it (Lee-Yaw, Sechley 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, Aapala et al. 2014).  $N_{\text{total}}$  = 15 quadrats per plot \* 87 plots = 1,305 quadrats.

#### Dead vegetation:

*Deadwood* – Deadwood is a critical requirement for many arthropod species since it provides a place to hide and forage (Lassauce, Paillet et al. 2011; Bluhm, Scheu et al. 2015),

while the volume of deadwood can indicate a higher abundance of birds and beetles (Winter, Flade et al. 2005). At each point we established a smaller 15 m x 5 m plot, within which we estimated the biomass of all standing or fallen dead trees (snags) >5 cm dbh (Gilroy, Woodcock et al. 2014). For snags >10 m high we used allometric equations to estimate biomass, applying a deadwood density of  $0.31 \text{ g cm}^{-3}$  taken from the literature (Gibbon, Silman 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  $\geq 5 \text{ cm dbh}$  was also recorded, converted into volume and used to estimate biomass (assuming a cylindrical shape).  $N_{\text{total}} = 74$  plots.

*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, Ribas 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, Ribas et al. 2013)). Within each smaller 15 m x 5 m plot, we collected all leaf litter, grass and small plants (<0.5m in height) from 4 x 0.25 m<sup>2</sup> quadrats within each plot (Gilroy, Woodcock et al. 2014), following (Queiroz, Ribas 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).  $N_{\text{total}} = 74 \text{ m}^2$  quadrats.

### **Live non-soil carbon stocks**

To calculate live non-soil carbon stocks, within each smaller 15 m x 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, 5.15mm diameter; Haglöf, Sweden) (Gilroy, Woodcock et al. 2014). We used these values in four allometric biomass estimation equations taken from harvested tree studies (Chave, Andalo et al. 2005; Alvarez, Duque et al. 2012; Feldpausch, Lloyd 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, del Valle

et al. 2007). Root biomass was estimated using a published upland forest root:shoot ratio of 0.26 (Cairns, Brown et al. 1997). All vines with a dbh of  $\geq 2$  cm that were  $\leq 1$  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, del Valle 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, Silman et al. 2010).  $N_{\text{total}} = 74$  plots.

### **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 S1). All loggers recorded data every two hours from February 2013 to February 2014.

Each iButton was placed inside a re-sealable zipper storage bag (50 mm X 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, Brunner et al. 2013). 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 ten and thirteen meters above the ground (Scheffers, Phillips et al. 2013), 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 ( $n_{\text{total}}=33$ ); (2) between the leaves of bromeliads ( $n_{\text{total}}=26$ ); (3) inside holes at the base of trees (tree circumference > 8cm DBH) ( $n_{\text{total}}=33$ ); (4) within the roots of ferns (fern circumference > 8cm DBH) ( $n_{\text{total}}=33$ ); and (5) at approximately 20 cm depth in soil ( $n_{\text{total}}=9$ ). All loggers were placed within 8 m of the understorey ambient logger



(most within one and four metres). Only one iButton was placed within a particular microhabitat for each plot.

## **Statistical Analyses**

### *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, KR, Gorley, RN, 2015). We also extract NMDS axis 1 and 2 to create a microhabitat composition metric.

### *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 forest, we obtained the ratio of young and old secondary forest complexity compared to primary forest complexity (considering the latter our benchmark of 100 percent). 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.

#### *Carbon-microhabitat co-benefits*

Forest structure is a main factor of the global carbon cycle (trees and foliage determining carbon storage and sequestration) (Schulze, Beck et al. 2005; Houghton, Hall et al. 2009). 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.

#### *Microclimates*

Our data showed no seasonality patterns, and therefore was not subdivided. Temperature maxima and minima have been successfully used to measure microhabitat thermal buffering effect (Shi, Paull et al. 2014). Therefore, weekly maximum, minimum and mean temperatures were taken from each iButton per microhabitat per forest type. We used weekly (taking weekly max, min and mean temperatures) models instead of daily models because of their lower AIC values. 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 hours. 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).

## Results

### *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 is 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 regarding their microhabitat composition ( $R = 0.66$ ,  $p = 0.001$ ). Recovery of secondary forest thus regenerates increasingly similar microhabitat composition to primary forest over time.

### *Microhabitat complexity recovery*

Considering bromeliads, tree ferns, moss, deadwood and leaf litter, primary forests held a significantly higher microhabitat complexity than young secondary forests ( $F_{2,367} = 3.57$ ,  $p < 0.05$ ), although there was no difference between young and old 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;  $F_{1,8} = 0.07$ ,  $p = 0.79$ ).

Live vegetation - There was a significant difference between forest types in number of bromeliads ( $F = 36.5$ ,  $p < 0.0001$ ): old secondary had more bromeliads than young secondary forest, and in turn, primary forest had more bromeliads than old secondary (Fig

S2A). Therefore, secondary forests need more than 35 years of regeneration to fully recover this critical microhabitat. Conversely, there was no significant difference between forest types in tree fern biomass ( $F = 1.96$ ,  $p = 0.15$ ; Fig S2B) or moss volume (Fig S2C;  $F = 1.32$ ,  $p = 0.27$ ). Thus, even after a short period of time (4 to 18 years) of forest regeneration, tree ferns and moss volume were recovered.

Dead vegetation - There was significant variation between forest types in deadwood ( $F = 8.57$ ,  $p < 0.001$ ): Young secondary forests (which did not differ significantly from old secondary forests) had less deadwood volume than primary forest (Fig S2D). 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 S2D). Leaf litter volume did not differ significantly between forest types ( $F = 5.54$ ,  $p = 0.02$ ; Fig S2E), thus this critical microhabitat recovered even in early stages of forest regrowth.

#### *Carbon-microhabitat co-benefits*

Live vegetation – Bromeliad abundance showed a positive relationship with carbon stock increase. They increased significantly with carbon stock at the 10<sup>th</sup> ( $t = 4.79$ ,  $p < 0.001$ ), 50<sup>th</sup> ( $t = 3.78$ ,  $p < 0.001$ ), and 90<sup>th</sup> ( $t = 2.54$ ,  $p = 0.01$ ) 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).

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

Microhabitat complexity and composition – Microhabitat complexity showed a positive increase with carbon at the 50<sup>th</sup> quantile ( $t = 2.82$ ,  $p = 0.005$ ), whereas the 10<sup>th</sup> and 90<sup>th</sup> 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 10<sup>th</sup> ( $t = -4.23$ ,  $p < 0.001$ ), 50<sup>th</sup> ( $t = -4.36$ ,  $p < 0.001$ ), and 90<sup>th</sup> ( $t = -2.82$ ,  $p = 0.006$ ) 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).

### *Microclimates*

The maximum ambient temperature in the understorey was lower than in the canopy in all forest types (Table2; Fig. 3A and 3B). The daily maximum ambient temperature in the understorey of primary forest was cooler than that in young secondary forests ( $z$  value = 2.98,  $p = 0.007$ ; Fig. 3B2 and 3B4). However, the maximum ambient temperature in the understorey in old secondary forests was not significantly different from primary or young secondary forests ( $p > 0.29$ ; Table2).

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  $0.78^{\circ}\text{C}$  to  $2.27^{\circ}\text{C}$  in primary forest, by  $0.38^{\circ}\text{C}$  to  $2.15^{\circ}\text{C}$  in old secondary forest, and by  $1.67^{\circ}\text{C}$  to  $2.31^{\circ}\text{C}$  in young secondary forest. At night, microhabitats buffered the understorey ambient temperature minima by  $0.07^{\circ}\text{C}$  to  $0.23^{\circ}\text{C}$  in primary forest and by  $0.64^{\circ}\text{C}$  to  $0.97^{\circ}\text{C}$  in old secondary forest. In young secondary forest, only leaf litter and tree holes were warmer than understorey ambient night-time temperature by  $0.09^{\circ}\text{C}$  and  $0.54^{\circ}\text{C}$ , respectively (Table2; Fig. 3). In contrast, soil minimum and mean temperature was significantly lower in primary and old secondary forests compared to young secondary forests ( $p > 0.04$ ; (Table2; Fig. 3G). All microhabitats warmed at a slower rate ( $<1^{\circ}\text{C}$  microhabitat :  $1^{\circ}\text{C}$  ambient) than understorey ambient (Table2; Fig. 3).

### **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, Woodcock 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 toward 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, suggesting 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.

#### *Microhabitat composition*

Our study indicates that microhabitat composition in primary forests varies greatly from secondary forests. The extent to which secondary forests support biodiversity is strongly linked to the presence and abundance of critical microhabitats (Michel and Winter 2009). Young and old secondary forests have similar microhabitat composition, suggesting that even from early stages of forest development some microhabitats are already available for biodiversity (Cadavid, Roman-Valencia et al. 2005; Urbina-Cardona, Olivares-Pérez et al. 2006).

#### *Microhabitat complexity recovery across habitat types*

We found a highly variable yet predictable recovery of microhabitats across forest types (Bittner and Breckle 1995; Oldekop, Bebbington et al. 2012; Woziwoda, Parzych 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, Paillet et al. 2011; Jocque and Field 2014; Scheffers, Phillips et al. 2014; Bluhm, Scheu 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, Beilin et al. 2014).

There is a clear transition from young secondary forests rich in moss and leaf litter to bromeliad and deadwood-rich primary forests. Importantly, bromeliad and deadwood levels in secondary forest reach almost half of those found in primary forest within 35 years following land abandonment (Fig. S2A and S2D). 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 as the Venezuelan Andes (Barthlott, Schmit-Neuerburg et al. 2001), whereas 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). Such a dichotomy probably reflects bromeliad requirements for cooler, wetter climates like the Andes in comparison with seasonal and hotter lowlands (Ruiz, Martinson 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, Schmit-Neuerburg et al. 2001; Woods and DeWalt 2013; McGarvey, Thompson et al. 2015), and translocation of bromeliads into medium-aged secondary forests may be a useful tool in applied forest management.

#### *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 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, Kelly et al. 2010; Phelps, Friess et al. 2012; Gilroy, Woodcock et al. 2014). However, to our knowledge, we have for the first time showed a strong positive relationship between carbon stock and microhabitat complexity, which underpins ecological resilience and increases the benefits to biodiversity (CBD 2011). Forest resilience is strong in secondary forests along the Neotropics (from Mexico to Chile), where they show high carbon sequestering potential and great carbon storage (Poorter, Ongers et al. 2016). Although, secondary forests have lower carbon stocks and biodiversity than primary forests (Poorter, Ongers et al. 2016), their recovery 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, given that it would be cheap to do so in this

region (see (Gilroy, Woodcock et al. 2014)), and that such projects would offer strong carbon, microhabitat, and biodiversity benefits (Gilroy, Woodcock et al. 2014).

### *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. 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, Edwards et al. 2014) 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, Martinson 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, Engemann et al. 2015). Thus climate change could 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, and as a consequence, threaten many bird, amphibian and invertebrate species (Merrifield and Royce 2002; Panizzo 2011; Scheffers, Phillips et al. 2014; Silva and Piratelli 2014).

### *Survey limitations*

Our study sites are restricted to naturally regenerating secondary forests in an agricultural matrix dominated by pasture. Therefore, we cannot expand our results to other agricultural systems. For example, different taxa (e.g. birds and arthropods) are affected differently in coffee than in oil palm plantations (Edwards, Magrach et al. 2014; Jordani, Hasui et al. 2015). Our results are restricted to secondary forests near a primary forest, thus source-sink dynamics could have improved microhabitat and species recovery (Barlow, Gardner et al.



2007; Gibson, Lee et al. 2011). Whether similar recovery would occur in isolated secondary forests and whether microhabitat recovery would be so rapid in other ecosystems outside of the Tropical Andes, especially in hotter and drier lowlands, are both critical unanswered questions.

## ***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. 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 biodiverse communities, including many species at risk of extinction. While protecting primary forests remains a critical conservation goal (Gibson, Lee et al. 2011), we live in an era of increasingly human-dominated tropics (Lewis, Edwards et al. 2015). The protection or promotion of secondary forest regrowth is often a more economically feasible strategy of protecting microhabitat rich and climate change resilient forests as opposed to preserving primary forests, which retain extremely valuable timber stocks (Fisher, Edwards 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.

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## **References**

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## Table legends

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 complexity 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.

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  $\pm$  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).

Table 1.

Microhabitat	quantile	t value	p value
Bromeliad	90%	2.54	<b>0.01</b>
	50%	3.78	<b>&lt;0.001</b>
	10%	4.79	<b>&lt;0.001</b>
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	<b>&lt;0.001</b>
	50%	2.08	<b>0.04</b>
	10%	2.97	<b>0.003</b>
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	<b>0.005</b>
	10%	1.27	0.20
Composition NMDS axis 1	90%	-4.23	<b>&lt;0.001</b>
	50%	-4.36	<b>&lt;0.001</b>
	10%	-2.82	<b>0.006</b>
Composition NMDS axis 2	90%	-0.94	0.34
	50%	-0.45	0.65
	10%	1.31	0.19

Table 2.

	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	<b>&lt;0.001</b>	458
	Mean	16.46±0.04	16.82±0.04	16.86±0.05	51.39	<b>&lt;0.001</b>	458
	Min	14.21±0.03	14.31±0.03	14.22±0.04	16.39	<b>&lt;0.001</b>	458
	Rate	1.368	1.362	1.140			
Understorey ambient	Max	18.78±0.06 <sup>B</sup>	19.79±0.07 <sup>AB</sup>	20.18±0.09 <sup>A</sup>	57.85	<b>&lt;0.001</b>	2054
	Mean	16.60±0.04	17.29±0.04	16.87±0.05	110.60	<b>&lt;0.001</b>	2054
	Min	14.95±0.04	15.43±0.04	15.58±0.05	61.58	<b>&lt;0.001</b>	2054
	Rate	-	-	-			
Bromeliad	Max	18.00±0.06	19.41±0.07	18.39±0.08	30.64	<b>&lt;0.001</b>	1009
	Mean	16.02±0.04	17.07±0.04	15.85±0.05	36.61	<b>&lt;0.001</b>	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	<b>&lt;0.001</b>	1350
	Mean	15.72±0.04	17.06±0.03	16.70±0.05	120.16	<b>&lt;0.001</b>	1350
	Min	15.02±0.04	16.10±0.03	15.45±0.06	25.95	<b>&lt;0.001</b>	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	<b>0.03</b>	1413
	Mean	15.87±0.04	17.05±0.03	16.92±0.03	175.43	<b>&lt;0.001</b>	1413
	Min	15.18±0.04	16.40±0.03	16.12±0.04	46.44	<b>&lt;0.001</b>	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	<b>&lt;0.001</b>	1384
	Min	15.05±0.04	16.07±0.04	15.67±0.04	20.86	<b>&lt;0.001</b>	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 <sup>B</sup>	14.70±0.01 <sup>B</sup>	15.45±0.02 <sup>A</sup>	9.25	<b>0.009</b>	1384
	Min	14.13±0.02 <sup>B</sup>	14.60±0.01 <sup>B</sup>	15.20±0.02 <sup>A</sup>	11.25	<b>0.04</b>	1384
	Rate	0.124	0.043	0.124			

Figure legends (high resolution files available if accepted for publication)

Fig. 1. (A) Nonmetric multidimensional scaling (NMDS) of microhabitat composition among forest types using microhabitat abundance. 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 ( $p < 0.05$ ).

Fig. 2. Carbon and microhabitat co-benefits for bromeliads (A), tree ferns (B), moss (C), deadwood (D), leaf litter (E), and NMDS axis 1 (F). Quantile regressions of microhabitat abundance data between young (<19 yr old) secondary forest (yellow points), old (19-35 yr old) secondary forest (orange points), and primary forest (light green points). Lines represent 10<sup>th</sup> (bottom line), 50<sup>th</sup> (middle line), and 90<sup>th</sup> (top line) quantiles. Solid lines represent significant relationships ( $p < 0.05$ ). Dash lines represent non-significant relationships.

Fig. 3. Annual temperature variation recorded every two hours (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) along a naturally regenerating young secondary forest (<19 yr; yellow), old secondary forest (19-35 yr; orange), and primary forest (light green) in the Colombian Andes. Error bars represent standard error. Similar superscripts represent no significant differences ( $p < 0.05$ ).

Fig. 1

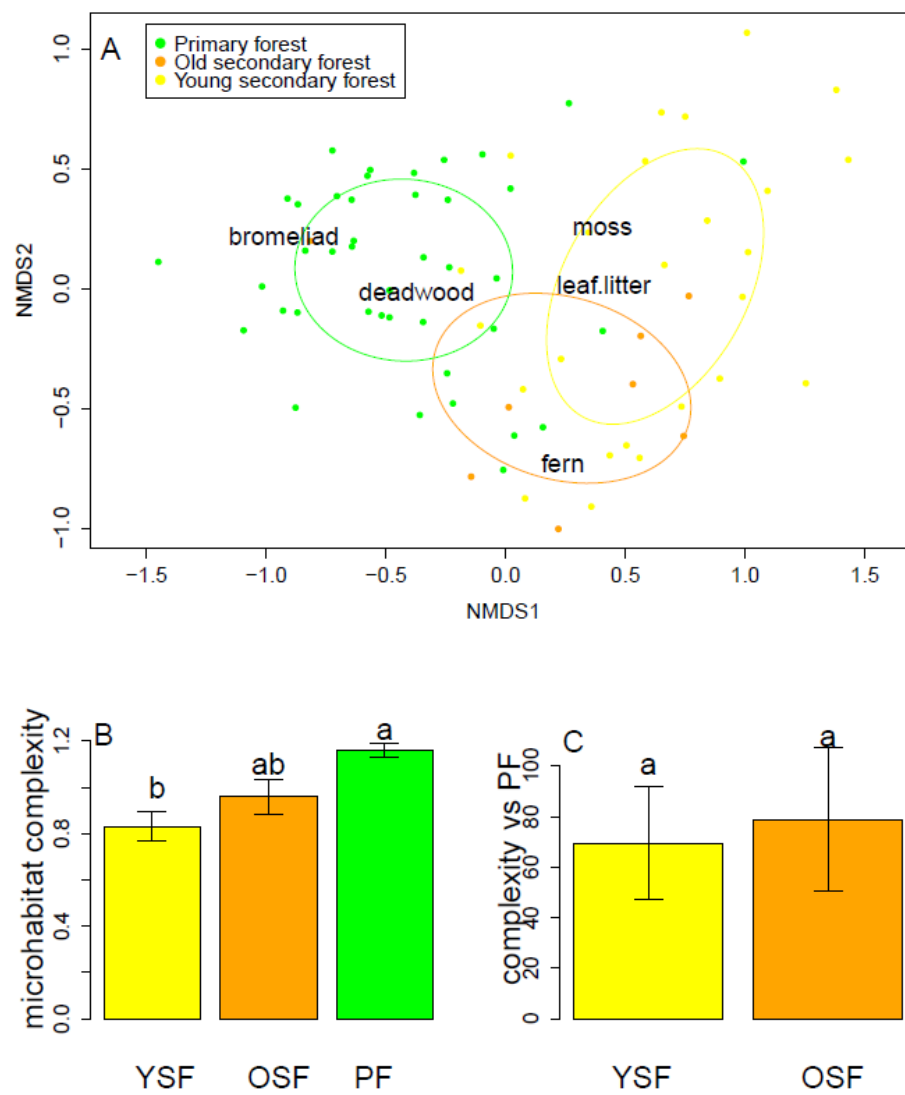


Fig. 2

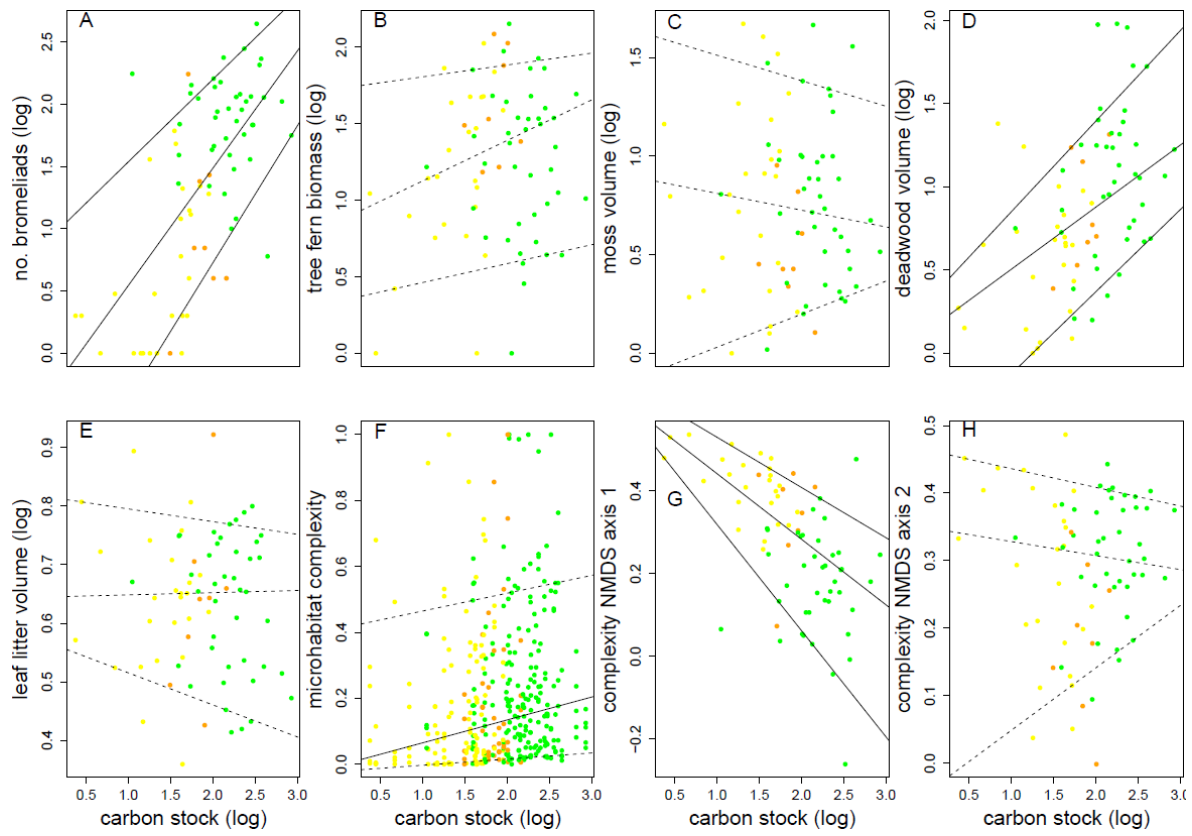
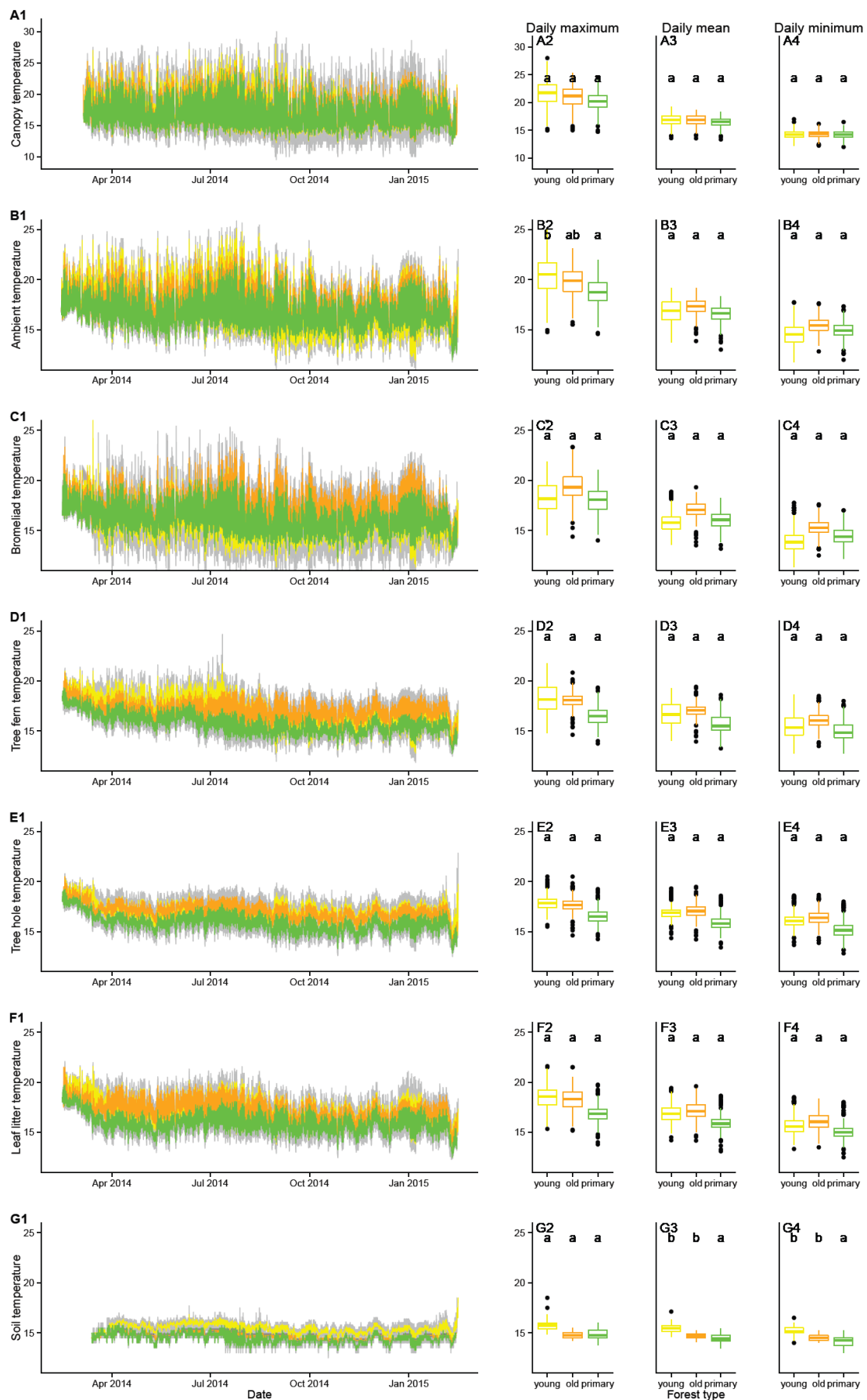




Fig. 3



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