Differential responses of soil respiration to warming highlight the sensitivity of tropical Andean tree species to environmental change

Elizabeth Ocampo Montoya
Juan Camilo Villegas Palacio
Andrew Nottingham

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Tutor
Juan Camilo Villegas Palacio, PostDoctor (PostDoc) en Natural resources emphasis
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Facultad de Ingeniería
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ABSTRACT

Tropical forests are the largest terrestrial Carbon sink, they occupy 12% to 15% of the Earth's surface but contain about 25% of the world's Carbon biomass, with soils storing ~1500-2400 PgC. Recent studies suggest that forest soils can go from Carbon sinks to sources in the next decades. In the tropics, most information has been collected in lowlands, leaving tropical highland ecosystems, important Carbon regulators that are particularly vulnerable to warming, relatively understudied. In this study, we explored the temperature sensitivity of soil respiration (R_s) and its autotrophic and heterotrophic components ($R_a$and R_h, respectively) among 14 dominant plant species (inter and intra-specific variation) in an experimental thermosequence in the Colombian Andes. This thermosequence includes a control site at an elevation of 2486 meters above sea level (mean temperature 14ºC) where seedlings were germinated, and two lower sites that represented an average warming of 8ºC (1326 m.a.s.l) and 12ºC (645 m.a.s.l) where some seedlings were transplanted. Soil and water conditions were controlled such that temperature and meteorological conditions were the only source of variation among treatments. At each site, in all the trees that survived after an acclimation period of one year, we measured R_s and its components in four measurement campaigns, spanning an overall measurement period of one year. With this information, we calculated Q_{10} values (the factor by which R_a and R_h increases for every 10-degree rise in temperature). Our results show, as expected, that R_a and R_h both increase with the warming, being highest (and more variable) in the warmest site. Q_{10} values for R_h (Q_{10}=2 and Q_{10}=1.71 for the +8°C and +12°C, respectively) in general were much higher than those for R_a (the species with the highest sensitivity was *Quercus humboldtii* (Q_{10}=3.92) and the lowest was *Tibouchina lepidota* (Q_{10}=0.03)), suggesting that the increase in $R_s$with warming was mostly driven by increased R_h. Importantly, this behavior in Q_{10} highlights the differential effects of temperature in dominant Andean species, which impacts forest composition and function. More importantly, the non-linear sensitivity of R_s to increased temperature, suggests that warming affects the capacity of Andean forests to regulate Carbon fluxes. Overall, our results provide useful information for adapting the management of Andean forests to the impacts of climate change, as well as for the refinement of ecological models that support projections of global environmental change and the Carbon cycle.

Keywords: Carbon cycle, autotrophic respiration, heterotrophic respiration, Andean forest, environmental change, temperature sensitivity, Q10 coefficient.

1. INTRODUCTION

The Carbon cycle is the second-largest biogeochemical cycle, as Carbon is present in all organic molecules, it is an essential element for all living organisms and occurs in all three environmental matrices (atmosphere, water, and soil). Soils are the second largest storage of Carbon, after the ocean, with ~1500-2400 PgC, this is almost twice the amount of Carbon in the atmosphere and vegetation combined (Bradford et al., 2016; Cavicchioli et al., 2019; Crowther et al., 2016). Much of this Carbon stored in the soil comes from the exchange with the atmosphere, making the soil an important regulator of atmospheric Carbon concentrations and, ultimately, the climate system (Crowther et al., 2016). The exchange of Carbon between the atmosphere and the soil starts with CO_2 uptake by autotrophic organisms. Particularly, vegetation transfers atmospheric Carbon to the soil via leaf litter, roots mortality and roots exudation (Poorter et al., 2012; Sokol & Bradford, 2019). The Carbon incorporated by roots is especially important due to its incorporation into more stable soil fractions, and in turn, fuels the metabolism of soil macro and microorganisms. Soil autotrophic and heterotrophic organisms regulate how much Carbon is stored and emitted back to the atmosphere (Cavicchioli et al., 2019) via soil respiration (R_s) from root and root symbionts (autotrophic) and microbial (heterotrophic) respiration. R_s is one of the largest Carbon effluxes from the soil to the atmosphere (Jian et al., 2018; Raich & Schlesinger, 1992; Zhao et al., 2017) as well as one of the largest fluxes in the global Carbon cycle (averaging ~55 PgC/year with large variations among ecosystems) (Adachi et al., 2005; Ramírez & Moreno, 2008; Schlesinger & Andrews, 2000).

Soil respiration can be affected by multiple environmental and ecological factors, such as geographic location, energy and water availability, vegetation composition, temperature, soil moisture content, among others (Kuzyakov & Gavrichkova, 2010; Meir et al., 2008; Tang et al., 2019; Vargas & Allen, 2008). Therefore, it is potentially highly susceptible to global environmental change. R_s varies between different geographic locations (including latitude and altitude) due to particular environmental conditions and species composition associated with resource availability and climate (Lei et al., 2021; Ramírez & Moreno, 2008). Climate conditions (precipitation, solar radiation, humidity, among others), indirectly affect R_s through their effects on biotic processes and thus, the quantity and quality of C inputs and storage in the soil (Engelbrecht et al., 2007; Feeley et al., 2011; García-Palacios et al., 2012; Whitaker et al., 2014). Soil moisture content plays an important role in nutrient availability, leading to constraints on soil C storage (Nottingham et al., 2012), and also affecting soil respiration via constraints on gas diffusion at high contents (Liptzin et al., 2011; Rubio & Detto, 2017) and limitations on decomposition at lower contents (Davidson et al., 2012; Rubio & Detto, 2017). Species composition, which results from climate and environmental factors, plays an important role in R_s, directly through autotrophic respiration (R_a; including plant roots and root symbionts) and indirectly through associations with microorganisms, nutrient cycling, and soil Carbon exchange (Kuzyakov & Gavrichkova, 2010; Rubio & Detto, 2017). In particular, tropical forest soil microbiota provides nutrients for plant growth, especially through the activity of arbuscular mycorrhizal, fungi for phosphorus (P) acquisition, ectomycorrhizal fungi for nitrogen (N) acquisition (Andersen et al., 2017), and bacteria for N-fixation (Batterman, 2018; Hedin et al., 2009). Microbial communities also reinforce the high plant diversity in tropical forests through species-specific interactions between plants and symbiotic or pathogenic microbiota (Lamanna et al., 2017; Mangan et al., 2010).

Many of these factors that affect R_s and its components relate (directly or indirectly) to ambient temperature (Cavicchioli et al., 2019; Jian et al., 2018; Li et al., 2020; Wang et al., 2014), as it determines ecosystem species composition and function, including R_a, with CO_2 fluxes decreasing with elevation (Lopera, 2019). Temperature can also stimulate heterotrophic respiration (R_h) as it induces changes in the metabolism of soil microorganisms, generating an increase in total R_s with increased temperature (Bradford et al., 2016; Carey et al., 2016; Friedlingstein et al., 2014; Li et al., 2020). However, the effects of temperature on R_s and its components differ between colder and warmer regions such that, for the same biome, responses can be different, for example, in lowlands and highlands. Recent studies have suggested that, in response to climate change and deforestation, in future decades lowland tropical forests can switch from Carbon sinks to Carbon sources, with significant implications for the local-to-global terrestrial Carbon dynamics (Gatti et al., 2014; Gatti et al., 2021). However, the effects of temperature variations (associated with climate change) and species composition and structure (associated with deforestation) on R_s in tropical mountain ecosystems, where temperatures are relatively constant throughout the year, but vary in comparison to other tropical ecosystems, are yet to be quantified.

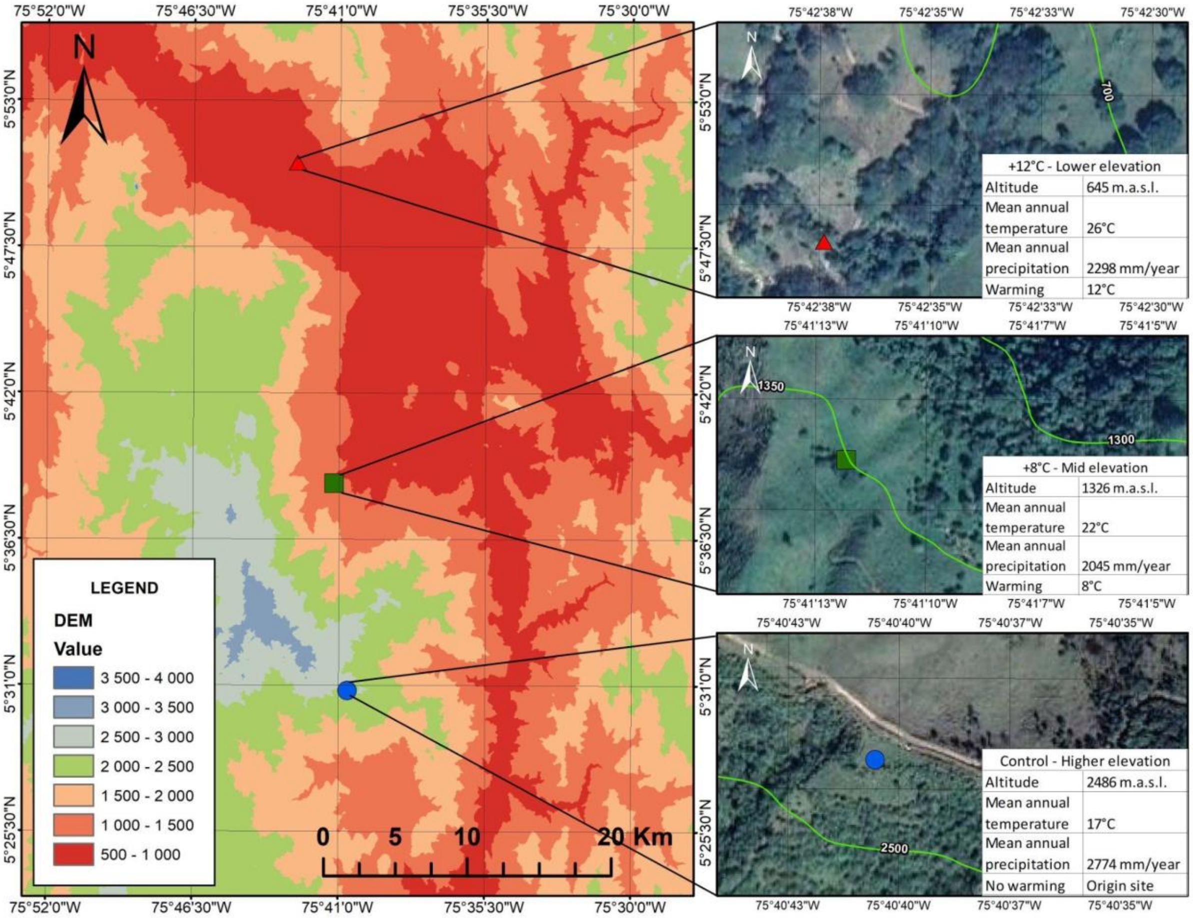
Tropical forests, which only occupy 12% of the earth's land surface, store 40% of global terrestrial Carbon stocks (Beer et al., 2010; Jobbágy & Jackson, 2000; Pan et al., 2011; Rubio & Detto, 2017; Townsend et al., 2011) and of this, 32% is held in soil (Ngo et al., 2013; Pan et al., 2011; Rubio & Detto, 2017). R_s in tropical forests plays an important role in the future concentrations of atmospheric CO_2 (Cox et al., 2013; Rubio & Detto, 2017; Sayer & Tanner, 2010). However, other tropical forests, such as those in the Andes mountains, are also important determinants of regional-to-global biogeochemical functioning, and their sensitivity to future warming has been less studied than in lowland forests (Cavaleri et al., 2015; Nottingham et al., 2015). The Andes are the world's longest mountain range and one of the world´s most important biodiversity hotspots (Duque et al., 2021; Orme et al., 2005). However, its ecosystems are changing at accelerated rates in response to environmental change processes, including land cover and climate change (Báez et al., 2015; Duque et al., 2015) with implications for biodiversity and biogeochemical functioning (Duque et al., 2015; Fadrique et al., 2018). Environmental change is causing changes in species composition and forcing unknown adaptation processes in these forests, potentially resulting in a considerable Carbon loss to the atmosphere (Duque et al., 2021; Fadrique et al., 2018). In consequence, the response of tropical Andean forest soil Carbon to warming is one of the largest sources of uncertainty in current Earth system models (Cavaleri et al., 2015; Cuni-Sanchez et al., 2021; IPCC, 2013).

In this study, we investigate how differences in temperature affect the response of R_s and its components in a group of dominant species, representative of highly diverse Tropical Andean ecosystems. To do so, we measured R_s and its components in a controlled experiment that includes 14 dominant tree species in the Northern Andes, with three contrasting temperature regimes during four campaigns spread through a year. We analyze the sensitivity of R_a and R_h to temperature increases using the Q_{10} temperature coefficient. Which describes the sensitivity of each component to incremental temperature changes. Our results allow us to discuss the potential responses of both R_a and R_h components to warming and how they differ among species, highlighting the importance of species composition in the potential consequences for future ecosystem dynamics in the Andes.

2. METHODS

2.1. Study area

We used the experimental infrastructure of the “Montane-Acclim” project that simulates warming through the transplant of juvenile individuals of dominant Andean tree species grown in a nursery from seeds collected in the forest at the higher elevation site, in to lower elevation sites in an elevation gradient (i.e., an experimental thermosequence). Other environmental factors (such as water availability and soil variability) are controlled, such that only temperature varies in the elevation gradient. The “Montane-Acclim” uses three sites (Figure 1) that represent a natural thermosequence in the Colombian Andes. This thermosequence covers a temperature gradient larger than projected increases. However, the purpose of the project is to evaluate general thermal sensitivity, requiring extreme experimental treatment. Two years after germination, seedlings were planted in the three sites (Figure 2). 24 seedlings of 14 dominant native tree species of the Andean forests (for a total of 336 individuals per site) were planted in 1 m^3 holes, that were all filled with a common soil, extracted from the highest elevation site, and at a distance of 2.5m x 2.5m (Figure 2). The dominant native trees species were: *Chrysochlamys colombiana, Clethra fagifolia, Clusia ducu, Clusia multiflora, Guatteria lehmannii, Hieronyma antioquensis, Ilex laurina, Inga edulis, Inga sierrae, Inga villosissima, Miconia theaezans, Quercus humbodtii, Tibouchina lepidota, Weimannia pubescens*. The highest elevation was 2486 m.a.s.l (Caramanta, Antioquia) with an average temperature of 14 °C, intermediate elevation was 1326 m.a.s.l (Támesis, Antioquia) with an average temperature of 22 °C and lowest elevation was 645 m.a.s.l with an average temperature of 26 °C (Figure 1).

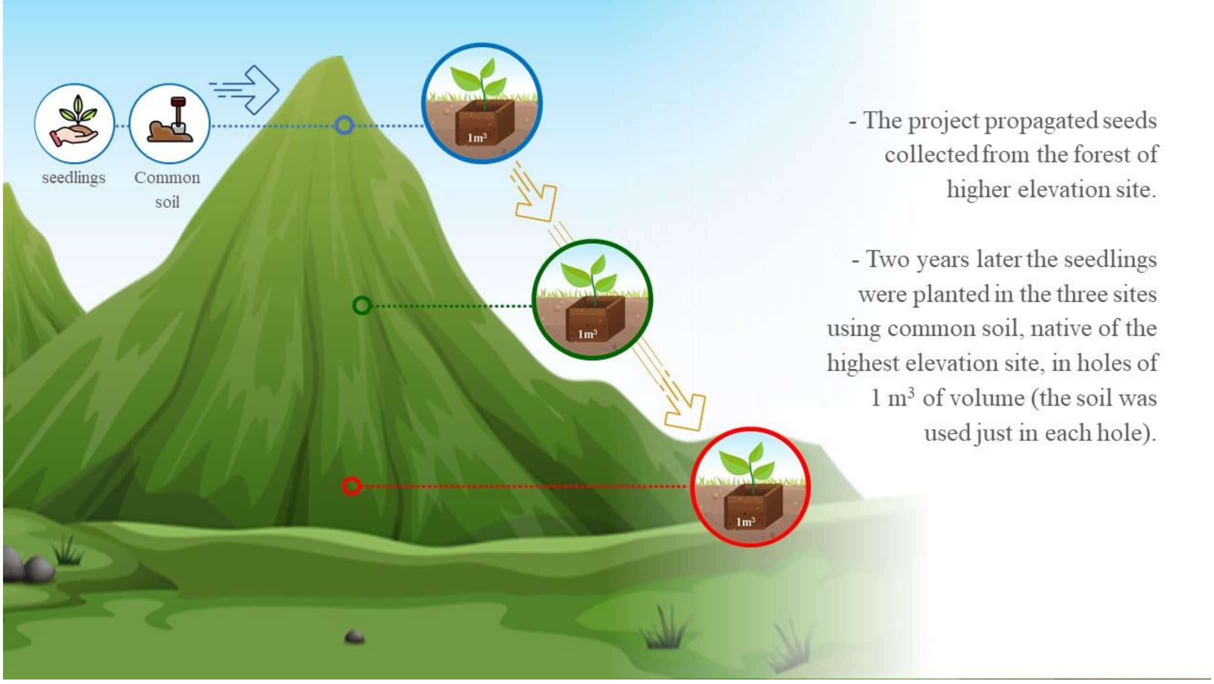


+12°C - Lower elevation	
Altitude	645 m.a.s.l.
Mean annual temperature	26°C
Mean annual precipitation	2298 mm/year
Warming	12°C

+8°C - Mid elevation	
Altitude	1326 m.a.s.l.
Mean annual temperature	22°C
Mean annual precipitation	2045 mm/year
Warming	8°C

Control - Higher elevation	
Altitude	2486 m.a.s.l.
Mean annual temperature	17°C
Mean annual precipitation	2774 mm/year
No warming	Origin site

Figure 1| Geographic location and details of the three sites that are part of the experimental thermosequence.



- The project propagated seeds collected from the forest of higher elevation site.

- Two years later the seedlings were planted in the three sites using common soil, native of the highest elevation site, in holes of 1 m^3 of volume (the soil was used just in each hole).

Figure 2| Methodology schematic explanation.

2.2. Characterization of the spatial-temporal variation of R_s

To characterize the spatial-temporal variation of R_s, we separated it into its components, R_h and R_a ($R_s = R_h + R_a$)(Wang et al., 2014), with measuring campaigns every 3 months during a year (2019-2020): campaign 1 in June 2019, campaign 2 in September 2019, campaign 3 in March 2020 and campaign 4 in July 2020. Ambient temperature was recorded using a meteorological station (Campbell Scientific) during each campaign month and were used to characterize environmental conditions during the campaigns. First, we quantify the total R_s near to the stem in 336 trees in each site (24 trees per species per site). As not all trees survived in all sites, only surviving individuals were measured in +8ºC and +12ºC sites. R_h was measured once for every campaign in 48 polyvinyl chloride plastic (PVC) rings (16 per site) isolated from the roots, and averaged for each site on each campaign. R_a was estimated as the difference between R_s and R_h for each tree on each campaign ($R_a = R_s - R_h$).

We measured the R_s with a portable closed chamber CO2 analysis equipment, with a built-in infrared analyzer (IRGA) model EGM-5 (PP systems, MA, USA), following the measurement protocol proposed by Vesterdal et al., (2012). We flushed the chamber and IRGA for 25 seconds prior to each measurement. Later, we placed the chamber in the soil. The CO_2 efflux is calculated based on the linear increase in the chamber's CO_2 concentrations along the measurement period (1-2 minutes). R_h was measured in soil columns (11 cm of diameter, 50 cm deep PVC rings) isolated from the roots, randomly installed around some of the trees in the experiment. We measured soil temperature inside and outside of the PVC rings to test whether inside conditions of the rings were similar to surrounding soil. Measurements were performed following the protocol in Rubio & Detto, (2017). We first calibrated the IRGA with the new chamber's volume including the empty volume of each PVC ring. To calibrate the volume in the equipment, we calculated the empty volume with the depth between the soil and the end of the tube and the radius of the PVC ring. With this value, we changed the parameters in the IRGA in each ring. We measured all the 16 PVC rings on each site and reported the average value for each site.

2.3. Data analysis

After characterizing R_s and its components, we evaluated how total R_s varies between sites, and which of the components was more likely to cause these variations. We evaluated the differences between sites in each species for R_a and differences between sites for R_h. This was done through a statistical analysis that included a descriptive analysis in which we explored linear associations between variables. We applied Kruskal-Wallis and Tukey tests (as data was not normally distributed) to evaluate differences in R_a between species, among sites (Intra and interspecific differences) and between measurement periods (campaigns). Same was done for R_h (except that it does not include an intra- and inter-specific component), and finally for overall Rs. Individuals from the same species were treated as replicates.

Additionally, we used the temperature coefficient (Q_{10}, which represents the factor by which a process or reaction increases for every 10-degree rise in the temperature) to estimate the sensitivity of R_s (R_a and R_h) to temperature increase. We calculated Q_{10} values, comparing each of the warming treatments (+8ºC and +12ºC) with the control site, for both R_h and R_a Q_{10} is calculated as $Q_{10} = (R_2/R_1)^{(10/T_2 - T_1)}$, where R is soil respiration rate at different treatments (temperature treatments 1 and 2) and T is the temperature at which the reaction rate R is measured in each of the two treatments (temperature information was recorded at each measurement site, for each campaign, using a meteorological station, Campbell Scientific). Ambient temperature is an indicator of climate change for this we used it for Q_{10} . There are more than 10000 published studies between 1961 and 2017 in which they used this climate factor to explain changes in R_s (Bond-Lamberty & Thomson, 2010; García-Palacios et al., 2021; Jian et al., 2021). All statistical analyses were performed using the statistical package R (R Core Team (2020)).

3. RESULTS

3.1. Heterotrophic respiration (R_h)

Our results show that overall R_h values (integrated through all the campaigns) are significantly different ($p \leq 0.05$) among the control site and the other two sites, with higher values in +8°C and +12°C sites (Figure 3). R_h also is more variable at the warmest site (+12°C site). These results suggest an effect of temperature over R_h, potentially through stimulating soil microorganism's metabolism. R_h is higher in the warmest site (+12°C site) than in the control site during most of the campaigns except in the last one, when temperature differences between both sites were more pronounced (Figure 4). In contrast, R_h in the +8ºC site is not consistently different from the other treatments. This means that the rate of increase of emissions by R_h can increase faster with higher warming.

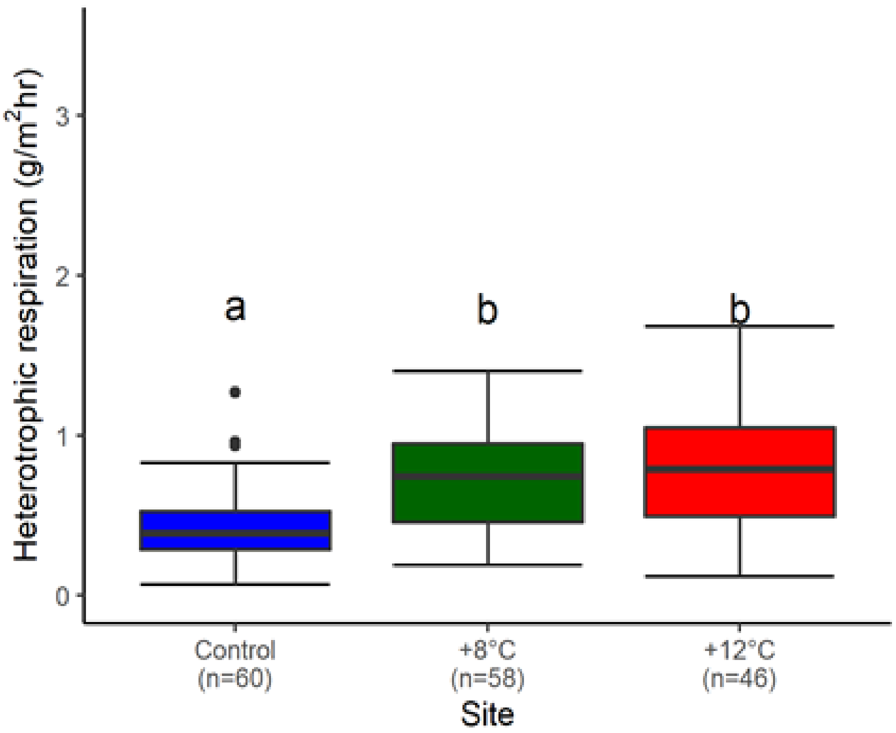


Figure 3| Heterotrophic respiration (R_h) in control and warm sites. Data are measurements from 4 campaigns integrated in a period of one year (June 2019 to July 2020). Differences between control and warmed sites are shown by letters (a, b, and c) where the different letters indicate significant differences ($p \leq 0.05$).

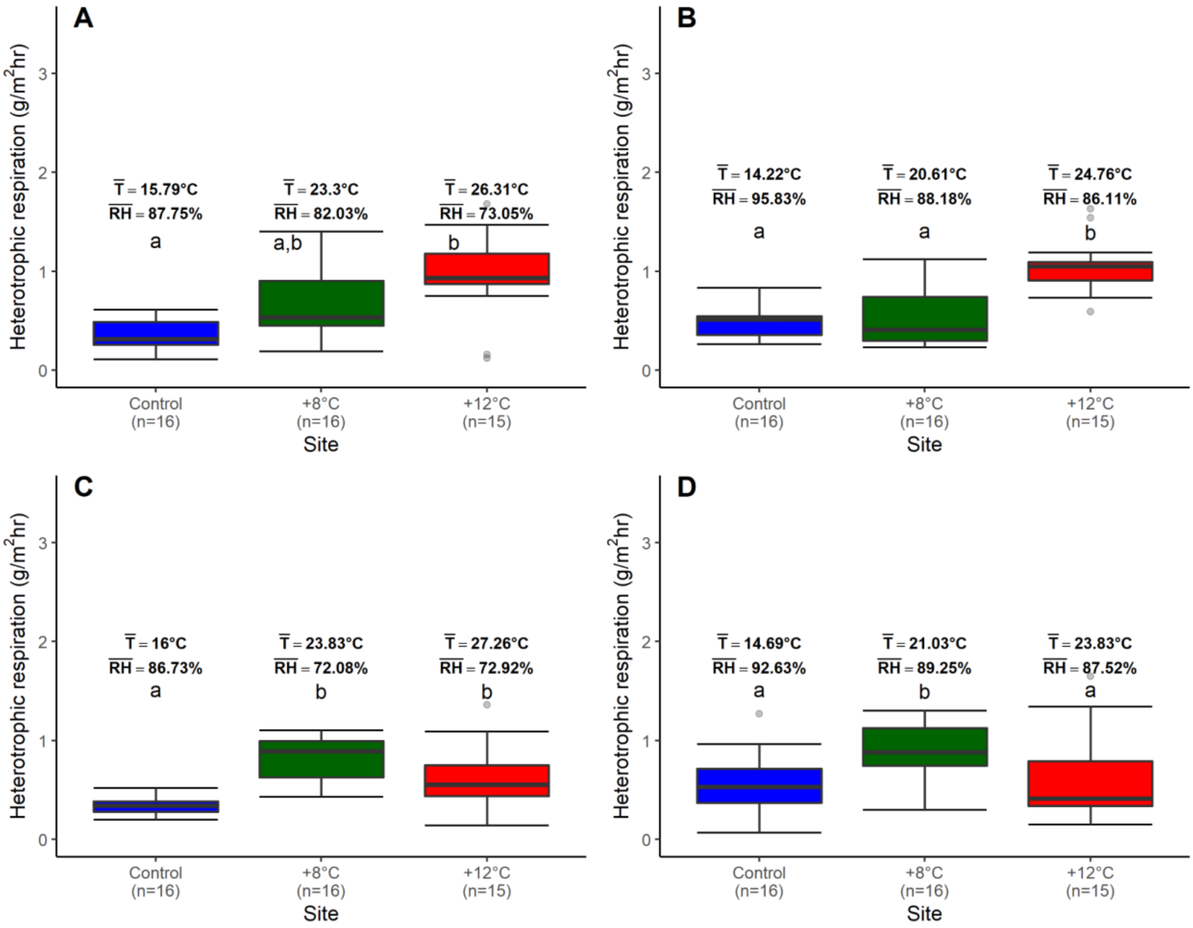


Figure 4 | Heterotrophic respiration (R_h) in control and warmed sites by campaigns. **A**. Campaign 1- June 2019, **B**. Campaign 2- September 2019, **C**. Campaign 3- March 2020, **D**. Campaign 4-July 2020. Differences between control and warmed sites are shown by letters (a, b, and c) where the different letters indicate significant differences ($p \leq 0.05$). The temperature and relative humidity values were calculated for each campaign month.

The results of Q_{10} show a relatively higher effect of +8ºC warming than the +12ºC warming for the entire measurement period (Figure 5, all campaigns). However, this behavior is not consistent through time. In the first two monitoring campaigns, $Q_{10}$is higher for the +12ºC site, whereas it was higher in the +8ºC for campaigns 3 and 4 (Figure 5). Notably, the highest Q_{10} value corresponded to the +8ºC site in campaign 3, which has the highest temperatures overall (temperature values in Figure 4). For Control vs +12°C there is an apparent pattern Q_{10} decline over the successive campaigns, although this pattern cannot be statistically assessed in this study (Figure 5).

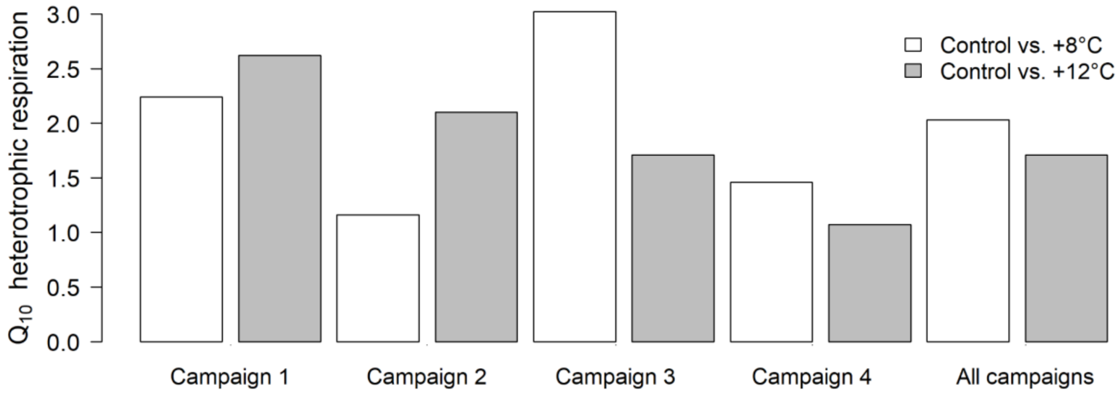


Figure 5 | Q_{10}values calculated from R_h and temperature differences between the sites in the different campaigns and all campaigns together (Campaign 1- June 2019, Campaign 2- September 2019, Campaign 3- March 2020, Campaign 4-July 2020).

3.2. Autotrophic respiration (R_a)

Our results show that R_a is significantly different among all sites (Figure 6) and there is a high variation in R_a values, especially during the campaign 1 and 2 (Figure 6.A-B). Each site has a different n (number of individuals measured) because not all the individuals survive in the warming sites. The highest R_a values occur in the warmest site (+12°C site), indicating that R_a increases with temperature (Figure 6). This is confirmed in a general pattern among all seasons where R_a increases with temperature, but this behavior is more evident in the warmest site (+12°C site, Figure 7). As opposed to R_h where a pattern associated with campaigns and sites emerged, differences in R_a between sites were not consistent among campaigns. The most consistent difference occurs between the control and +12ºC sites (Figure 7). However, there is a large variability in the data, resulting from interspecific differences and potentially differential responses to warming that preclude the emergence of general patterns (as indicated in Figure 8).

The highest $R_a$values are observed in warmer temperatures, for most species (Figure 8). This is particularly evident in the +8ºC site, where most of the interspecific differences occurred (Table 1). Note, however, that the lack of differences in the +12ºC may be associated with the low number of species that survived the entire duration of the experiment. Further, the majority of the record intraspecific differences between sites occurred in campaigns 1 and 4, when temperature differences between sites were more evident (Figure 7 and Figure 8). All of these observations suggest a temperature effect on R_a.

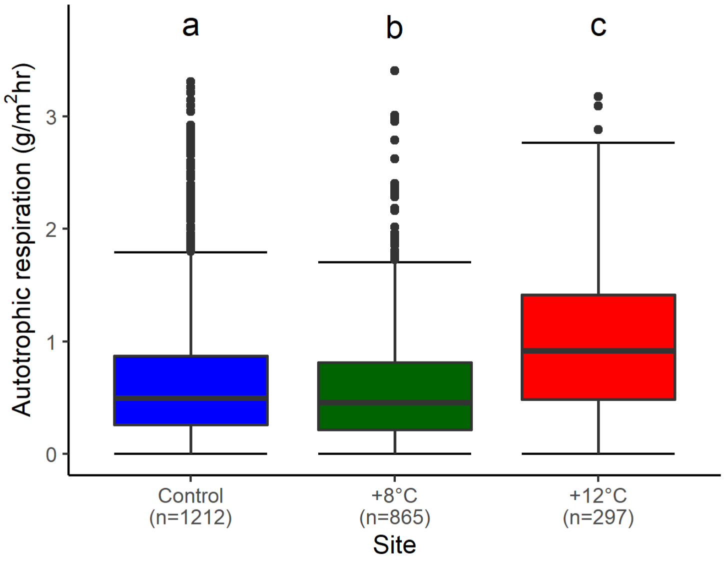


Figure 6| R_a in control and warm sites. Data are measurements from 4 campaigns integrated in a period of one year (June 2019 to July 2020). Differences between control and warmed sites are shown by letters (a, b, and c) where the different letters indicate significant differences ($p \leq 0.05$). Each site has a different n (number of individuals measured) because not all the individuals survive in the warming sites.

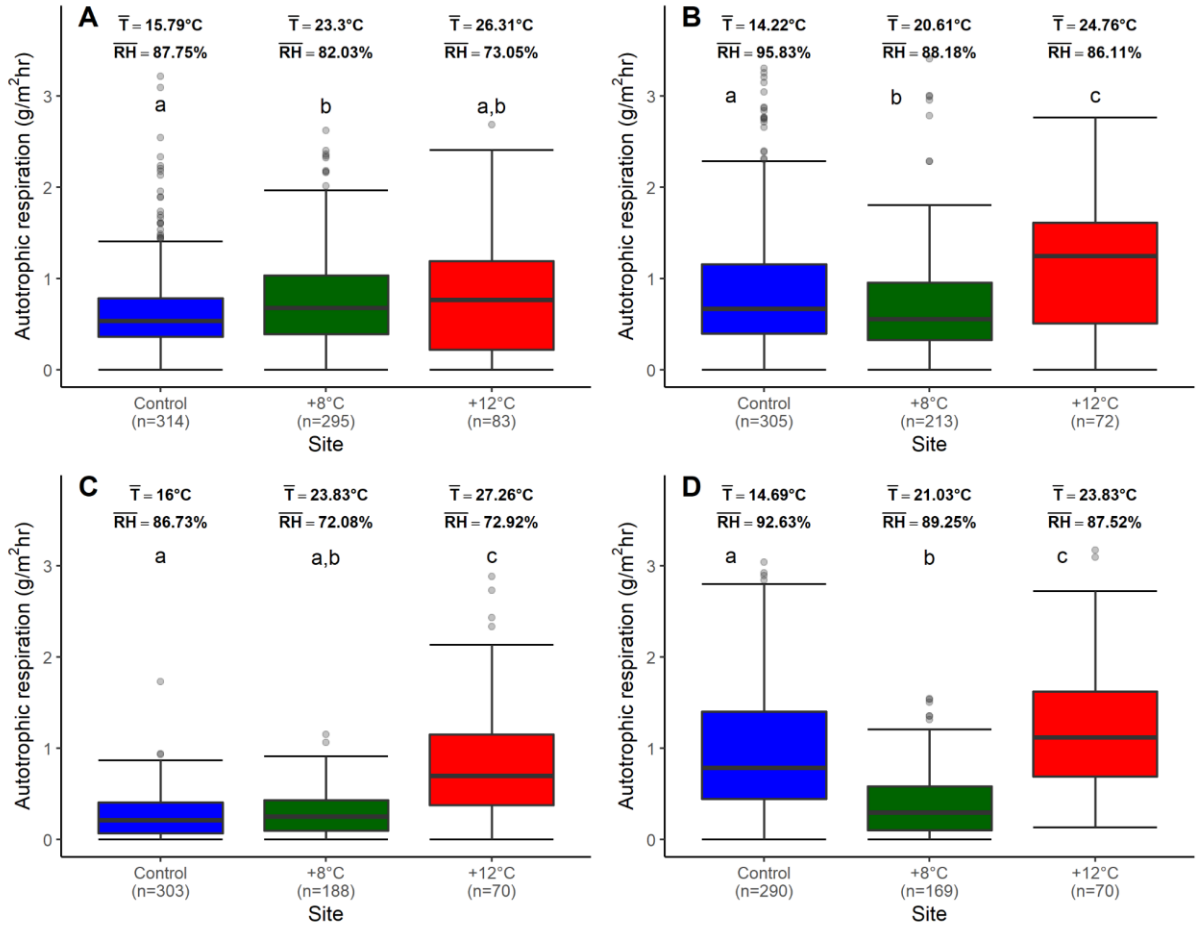


Figure 7 | R_a in control and warmed sites by campaigns. **A**. Campaign 1 - June 2019, **B**. Campaign 2 - September 2019, **C**. Campaign 3 - March 2020, **D**. Campaign 4 - July 2020. Differences between control and warmed sites are shown by letters (a,b, and c) where the different letters indicate significant differences ($p \leq 0.05$). The temperature and relative humidity values were calculated for each campaign month.

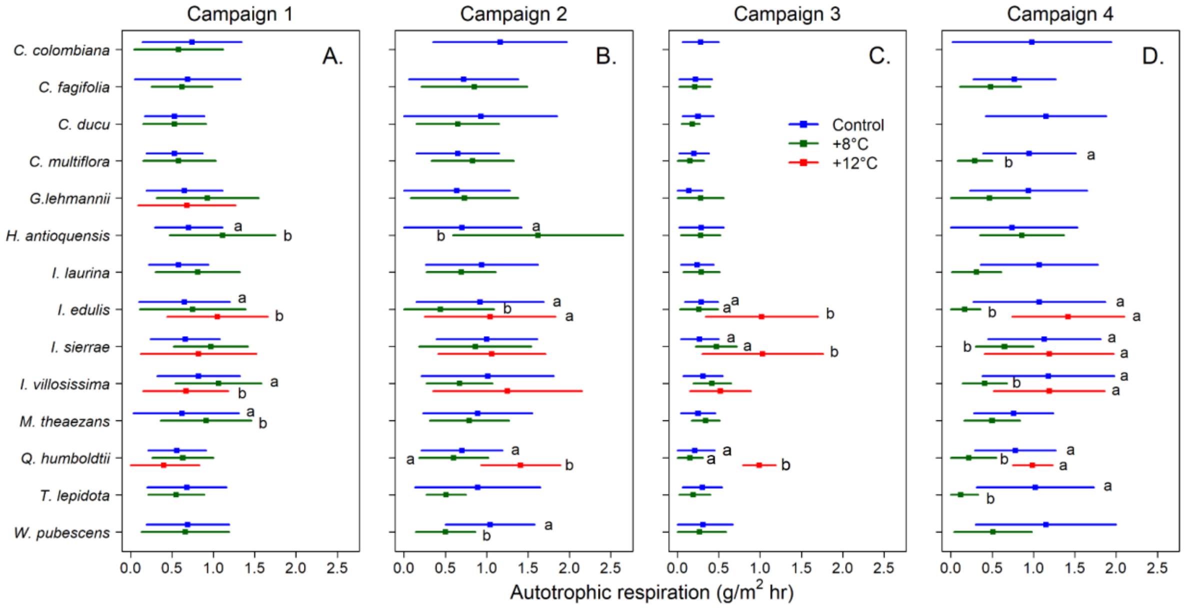
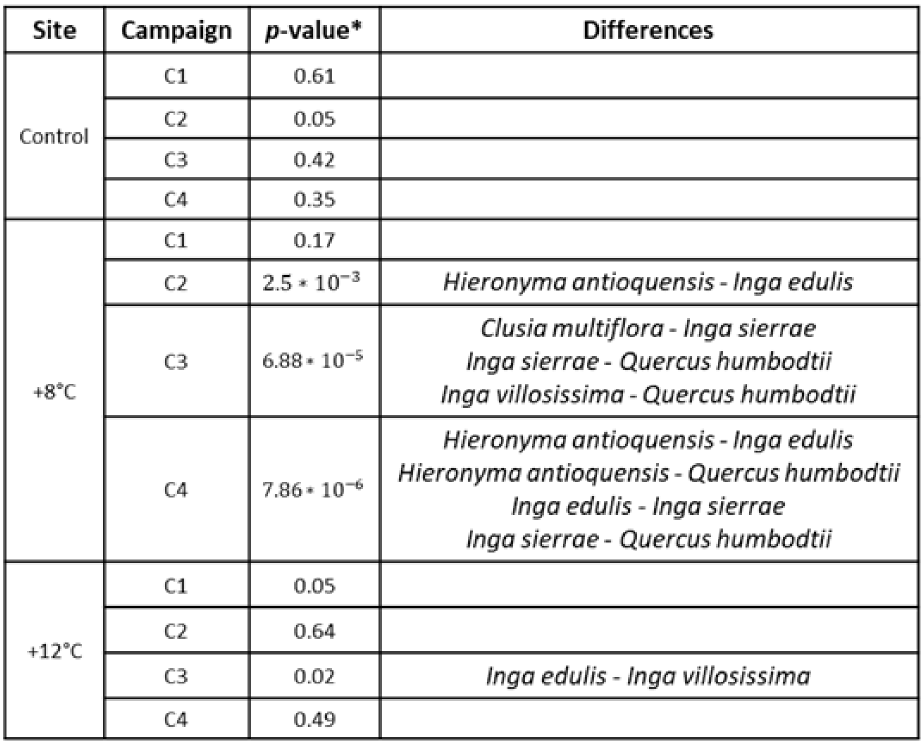


Figure 8 | Average (points) autotrophic respiration (R_a) by species and standard deviation for each campaign (bars). **A**. Campaign 1 - June 2019, **B**. Campaign 2 - September 2019, **C**. Campaign 3 - March 2020, **D**. Campaign 4 - July 2020. Intraspecific variations are shown by letters (a,b, and c) where the different letters indicate significant differences ($p \leq 0.05$). Not all the species survive in the 3 sites, most species did not survive in the warmest site.

Q_{10}values (calculated only for the species that survived on each site) are generally higher in the +12ºC site (Figure 9). This is contrary to what we observe in R_h (Figure 5), highlighting the potentially cumulative negative effect of warming on most species. For some species, however, Q_{10} values were higher in the +8ºC site (Figure 9). These species, mostly in the genus *Inga*, were the group that survived best in the warmest site, suggesting an ecological strategy that favors acclimation in this group. The species with the highest and lowest sensitivity are *Quercus humboldtii* (Q_{10}= 3.92) and *Tibouchina lepidota* (Q_{10}= 0.03), respectively (Figure 9). The highest values of $Q_{10}$is between the control and +12°C site in the campaign 3, that present the highest temperature and the lowest relative humidity (Figure 9).

Table 1| Interspecific variations. Differences ($p \leq 0.05$) between the species in each site and in each campaign (C1: Campaign 1- June 2019, C2: Campaign 2- September 2019, C3: Campaign 3- March 2020, C4: Campaign 4-July 2020).



Site	Campaign	*p*-value*	Differences
Control	C1	0.61	
	C2	0.05	
	C3	0.42	
	C4	0.35	
+8°C	C1	0.17	
	C2	$2.5 * 10^{-3}$	*Hieronyma antioquensis - Inga edulis*
	C3	$6.88 * 10^{-5}$	*Clusia multiflora - Inga sierrae* *Inga sierrae - Quercus humbodtii* *Inga villosissima - Quercus humbodtii*
	C4	$7.86 * 10^{-6}$	*Hieronyma antioquensis - Inga edulis* *Hieronyma antioquensis - Quercus humbodtii* *Inga edulis - Inga sierrae* *Inga sierrae - Quercus humbodtii*
+12°C	C1	0.05	
	C2	0.64	
	C3	0.02	*Inga edulis - Inga villosissima*
	C4	0.49	

*****These differences were determined using the non-parametric method Kruskal-Wallis and Tukey and the differences were $p \leq 0.05$.

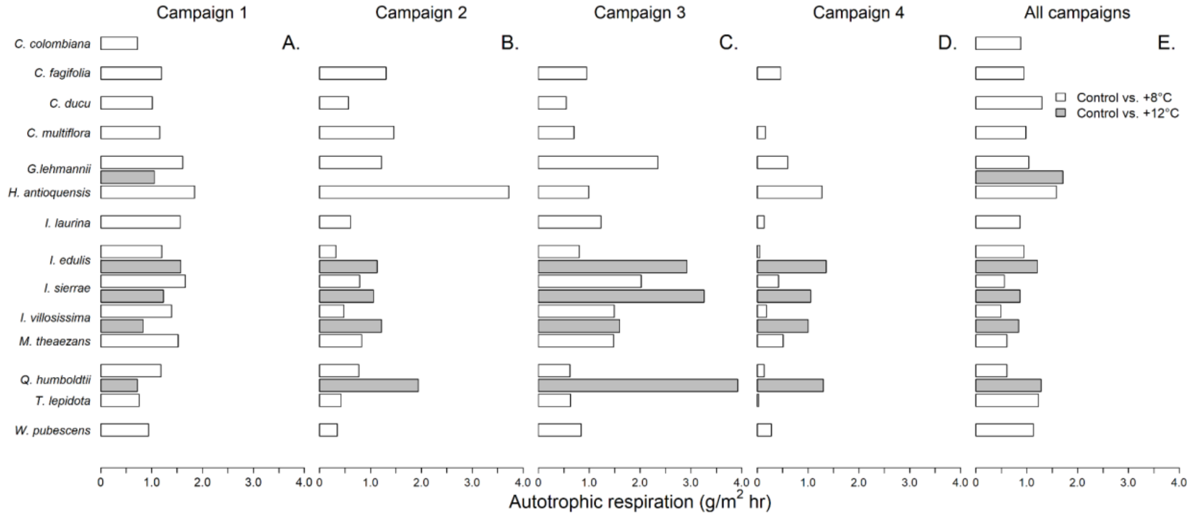
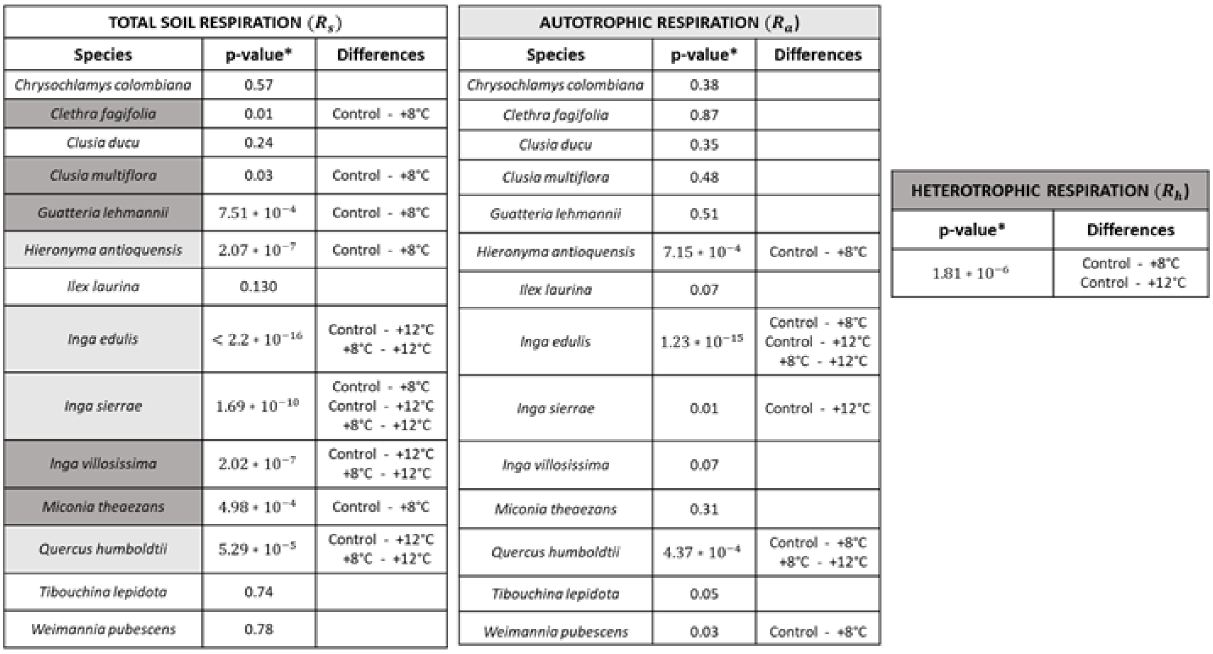


Figure 9 | Q_{10}values calculated from autotrophic respiration (R_a) and differences of temperature between the sites in the different campaigns and all campaigns together (Campaign 1 - June 2019, Campaign 2 - September 2019, Campaign 3- March 2020, Campaign 4-July 2020).

3.3. Total soil respiration (R_s)

Total soil respiration (R_s) varied between sites for 9 out of the 14 species considered in this study (Table 2). For species that survived in warming both treatments (those belonging to the genus *Inga*), R_s was different between the control and +12ºC site in all of them while in only one case (*Inga sierrae)* differences between control and +8ºC treatment were found. However, in most of the species, warming to +8ºC had an effect on R_s (except for *Chrysochlamys colombiana*, *Clusia ducu*, *Ilex laurina*, *Tibouchina lepidota* and *Weimannia pubescens* where no differences between treatments were found) (Table 2-Species without color). When assessing whether these differences relate to the R_a or $R_h$components of R_s, we found, on one hand, that for *Clethra fagifolia*, *Clusia multiflora*, *Guatteria lehmannii*, *Inga villosissima*, and *Miconia theaezans* the differences in total R_s can be explained by R_h, as no warming effect on R_a were found for these species (Table 2- dark color). On the other hand, for *Hieronyma antioquensis*, *Inga edulis*, *Inga sierrae*, and *Quercus humboldtii* the differences in total respiration can be explained by R_a, as changes were larger than those found for R_s (Table 2- light color).

Table 2 | Statistical differences between sites for total soil respiration (R_s), autotrophic respiration (R_a), and heterotrophic respiration (R_h). The colors are associated with the component that explain the differences in total R_s ($R_a$light color, $R_h$dark color and without color the species that no present differences in R_s).



TOTAL SOIL RESPIRATION (R_s)		
Species	**p-value***	**Differences**
Chrysochlamys colombiana	0.57	
Clethra fagifolia	0.01	Control - +8°C
Clusia ducu	0.24	
Clusia multiflora	0.03	Control - +8°C
Guatteria lehmannii	$7.51 * 10^{-4}$	Control - +8°C
Hieronyma antioquensis	$2.07 * 10^{-7}$	Control - +8°C
Ilex laurina	0.130	
Inga edulis	$< 2.2 * 10^{-16}$	Control - +12°C +8°C - +12°C
Inga sierrae	$1.69 * 10^{-10}$	Control - +8°C Control - +12°C +8°C - +12°C
Inga villosissima	$2.02 * 10^{-7}$	Control - +12°C +8°C - +12°C
Miconia theaezans	$4.98 * 10^{-4}$	Control - +8°C
Quercus humboldtii	$5.29 * 10^{-5}$	Control - +12°C +8°C - +12°C
Tibouchina lepidota	0.74	
Weimannia pubescens	0.78	

AUTOTROPHIC RESPIRATION (R_a)		
Species	**p-value***	**Differences**
Chrysochlamys colombiana	0.38	
Clethra fagifolia	0.87	
Clusia ducu	0.35	
Clusia multiflora	0.48	
Guatteria lehmannii	0.51	
Hieronyma antioquensis	$7.15 * 10^{-4}$	Control - +8°C
Ilex laurina	0.07	
Inga edulis	$1.23 * 10^{-15}$	Control - +8°C Control - +12°C +8°C - +12°C
Inga sierrae	0.01	Control - +12°C
Inga villosissima	0.07	
Miconia theaezans	0.31	
Quercus humboldtii	$4.37 * 10^{-4}$	Control - +8°C +8°C - +12°C
Tibouchina lepidota	0.05	
Weimannia pubescens	0.03	Control - +8°C

HETEROTROPHIC RESPIRATION (R_h)	
p-value*	**Differences**
$1.81 * 10^{-6}$	Control - +8°C Control - +12°C

*****These differences were determined using the non-parametric method Kruskal-Wallis and Tukey and the differences were $p \leq 0.05$.

4. Discussion

Our results from a natural thermosequence experiment, support the argument that temperature increases particularly affect R_h (Nottingham et al., 2019) (Figure 10), which was proposed for lowland tropical forests. Although temperature affects both fluxes ($R_h$and R_a), grew faster, suggesting that the effect of temperature on soil microorganism metabolism can be faster and more evident than on R_a. Nevertheless, there is a differential temperature effect on $R_a$with implications on the composition and function of montane ecosystems. The inter and intraspecific differences suggest that the species will have a differential response to temperature increase, showing the highest values in the warmest site (Banbury Morgan et al., 2021; Vesterdal et al., 2012). Temperature showed consistent differences between sites over the campaigns (+8°C and +12°C). Additionally, the sensitivity to temperature increase (Q_{10}) of both soil respiration components ($R_h$and R_a) differs, with R_h showing higher sensitivity sensitivity to an 8°C increase, while for R_a, Q_{10} values are more variables and species-dependent, highlighting that the species have different mechanisms to respond to changes in temperature. These results show the importance of analyzing the two components separately ($R_h$and R_a), because their response to temperature differs (Wang et al., 2014). Our unique plant-species and experimental design provided us the opportunity to analyze both fluxes ($R_h$and R_a), opening future research paths in how different plant-root communities interact with changes in soil Carbon cycling, by changing the microbial community structure and nutrient availability (e.g., presence of N-fixing bacteria and mycorrhizal communities). Further studies with controlled warming can provide further information about particular sensitivity of plant species and more refined knowledge on the effects of smaller temperature increases on soil metabolism.

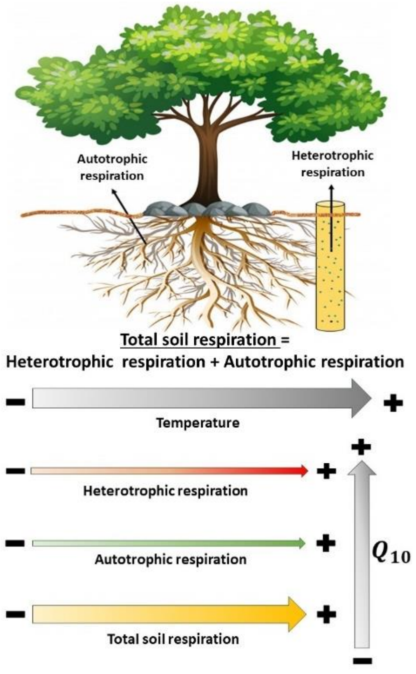


Figure 10| Conceptual synthesis of the effects of warming on soil respiration and its components, as measured by our results. Arrows represent the direction of increase of the different variables. The width of total soil respiration arrow indicates the sum of heterotrophic and autotrophic respiration. The color

in respiration arrows indicates the strength of the relationship with temperature increase, red arrow represents the highest relationship, yellow intermediate relationship and green the weakest relationship.

The R_h results show an increase of this efflux with the highest temperature increase. Our measurements of R_h indicate a higher and consistent sensitivity to warming. Overall, these results suggest that warming may result in positive Carbon-climate feedback (Dacal et al., 2021) where, as temperature increases, CO_2 emission increases too, via R_h(Figure 3 and Figure 10), potentially producing higher warming and reducing the capacity of sequestering Carbon in these ecosystems (yet, for assessing this hypothesis, the other components of NPP need to be quantified). Further, this result suggests the reduced soil Carbon storage due to increased microbial activity in the Andean Forest and this is consistent with data obtained by Bond-Lamberty et al. (2018) for high latitudes. More specifically, soil microorganisms play a pivotal role in tropical forest function, both in biogeochemical cycling and in the maintenance of aboveground plant diversity (Nottingham et al., 2018). Additionally, the Q_{10} R_h results showed the highest values during the warmest campaign highlighting that the positive Carbon-climate feedback can be faster than projected and that the increase in $R_s$with warming was mostly driven by increased R_h.

$R_a$values exhibit a large variation and significant differences between the three sites, this can be associated with the differential response of the species, in terms of R_a fluxes, to temperature increase (Figure 8). Some species did not survive in the warming sites, especially in the +12°C site where only a few survived. This highlights the sensitivity of forest Andean Forest composition to climate change (Fadrique et al., 2018). However, analyzing the results of the species that survived (mostly in the genus *Inga* for the +12°C site), the highest R_a values occurred in the warmest site (Figure 8 and Figure 10), showing an effect of the temperature increase on the $R_a$of these groups. Importantly, most of the interspecific differences occurred in the +8°C site, indicating that the species have different strategies to respond to temperature increases (Fadrique et al., 2018; Malizia et al., 2020). This reinforces what our Q_{10} results show, where a wide range of species sensitivity to temperature is demonstrated. For instance, although R_a in some species appears to be less sensitive to temperature increase, such as e.g., *Tibouchina lepidota* (Q_{10}= 0.03) than others (e.g., *Quercus humboldtii*; Q_{10}= 3.92). However, species survival under increased temperature not only depends on their respiratory metabolism but also on many other ecological and metabolic processes (including age) that need to be further explored to evaluate their potential contributions to the hypothesized positive Carbon-climate feedback.

Our results highlight the importance of advancing our understanding of how warming will affect soil Carbon cycling in tropical mountain forests. In this sense, climate model projections are consistent in reported increase in temperature (IPCC, 2021). The analysis of the two components ($R_h$and R_a) allow tests of how warming affects soil Carbon pools and shows how faster the Carbon from the soil can be lost. This information has been identified as a high priority to better understand the impacts of climate warming in Andean tropical forest ecosystems (Cavaleri *et al.*, 2015; Mitchard, 2018). Collectively, our results are relevant for managing and adapting ecosystems, particularly tropical Andean Forest, and for the refinement of ecological models that support projections of global environmental change and the Carbon cycle (Ye et al., 2019).

5. Conclusions

Our results indicate a challenge in the management of tropical Andean forests because of the high climatic sensitivity of biogeochemical processes, and which can be the future function of these strategic ecosystems in the Carbon cycle. Our results pioneer the exploration of soil metabolic sensitivity to warming. Further refinements are required to more precisely characterize these responses. We suggest the potential for the occurrence of positive Carbon-climate feedback that temperature increase can cause with R_s $(R_h \ and \ R_a)$ as a consequence of climate change and the importance of analyzing its components separately. However, the effects of warming vary depending on the species, highlighting the role of ecosystem composition on biogeochemical regulation. Particularly, the Carbon cycle can be affected by the changes that the temperature increase produce in the soils, in terms of R_s, suggesting an effect on the capacity of andean forest to regulate Carbon efflux. Finally, these results can help to refine ecological models that support projections of global environmental change and the Carbon cycle, through specific parameterization for tropical mountain environments, which have been poorly characterized in their response to environmental change processes.

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