Received: 6 September 2023 | Revised: 28 April 2024 | Accepted: 21 June 2024

DOI: 10.1111/jvs.13289

Journal of Vegetation Science IAVS

RESEARCH ARTICLE

Elevational shifts in tree community composition in the Brazilian Atlantic Forest related to climate change

Rodrigo Scarton Bergamin[1,2,3] | **Vinicius Augusto Galvão Bastazini**[4,5] | **Adriane Esquivel-Muelbert**[1,2] | **Kauane Maiara Bordin**[3] | **Joice Klipel**[3] | **Vanderlei Júlio Debastiani**[6] | **Alexander Christian Vibrans**[7] | **Rafael Loyola**[8,9] | **Sandra Cristina Müller**[3]

[1]School of Geography, Earth and Environmental Science, University of Birminghingdomam, Birmingham, United Kingdom

[2]Birmingham Institute of Forest Research (BIFoR), University of Birmingham, Birmingham, United Kingdom

[3]Laboratório de Ecologia Vegetal, Programa de Pós-Graduação Em Ecologia, Universidade Federal Do Rio Grande Do Sul, Porto Alegre, Brazil

[4]MED – Mediterranean Institute for Agriculture, Environment and Development & CHANGE–Global Change and Sustainability Institute, Institute for Advanced Studies and Research, University of Évora, Évora, Portugal

[5]Rui Nabeiro Biodiversity Chair, University of Évora, Évora, Portugal

[6]Laboratório de Ecologia Quantitativa, Programa de Pós-Graduação Em Ecologia, Universidade Federal Do Rio Grande Do Sul, Porto Alegre, Brazil

[7]Inventário Florístico Florestal de Santa Catarina, Departamento de Engenharia Florestal, Universidade Regional de Blumenau, Blumenau, Brazil

[8]Departamento de Ecologia, Universidade Federal de Goiás, Goiania, Brazil

[9]Instituto Internacional Para Sustentabilidade, Rio de Janeiro, Brazil

Correspondence
Rodrigo Scarton Bergamin, School of Geography, Earth and Environmental Science, University of Birmingham, Birmingham, United Kingdom.
Email: rodrigo.bergamin80@gmail.com

Co-ordinating Editor: Antonio Gazol

Abstract

Question: Climate change induces shifts in species distributions, ultimately changing community composition. Mountains are especially sensitive to climate change, and tree species are predicted to move towards higher elevations, but observed changes are not always unidirectional. The diversity and complexity of tropical and subtropical systems limits our understanding of climate-induced responses of subtropical mountain forests. Here, we investigated migration trends in tree community composition along an elevational gradient, and between the transition from lowland to montane forests in subtropical forests.

Location: Brazilian Atlantic Forest.

Methods: We used thermal affiliations of 627 tree species to calculate community temperature scores (CTS) for different life-history stages of trees in 96 permanent plots. We compared CTS of different life-history stages across space and time.

Results: Most tree communities (58%) did not show a significant difference of CTS between life-history stages, indicating a non-migration trend. On the other hand, 27% of tree communities showed upward migration and 15% downward migration. Upward migration was more common in montane forests, and downward migration in lowland forests. Our temporal analysis shows significant changes in CTS values for juvenile communities with 0.36°C decrease in lowland forests and 0.34°C increase in montane forests.

Conclusions: Contrasting results between lowland and montane forest communities indicate that the transition zone influences migration patterns and may reflect differences in species' thermal limitations, as well as by non-thermal factors such as biotic interactions. Our findings provide the first evidence of climate change-induced community shifts in the Brazilian Atlantic Forest. We demonstrated that upward migration trends were predominantly observed in montane–upper mountain forests, while downward migrations were noted in lowland–submontane forests. The thermophilization of montane forests may suggest an increased risk of reduction for cold-demanding species under climate change scenarios.

KEYWORDS
climate change, elevation gradient, forest dynamics, migration, subtropical forests, thermophilization

1 | INTRODUCTION

Global climate change impacts species' distribution, promoting shifts in community composition that may impact community patterns, reassembly processes, and biotic interactions (Bellard et al., 2012; Lamprecht et al., 2018; Wilson et al., 2021; Watts et al., 2022). As the planet shifts towards a warmer climate, tree species are predicted to move towards cooler latitudes and higher elevations in most regions of the world (Thuiller et al., 2005). Indeed, many shifts towards higher elevations have been observed worldwide (Kelly & Goulden, 2008; Feeley et al., 2011; Morueta-Holme et al., 2015; Rumpf et al., 2018); however, changes are not always unidirectional (O'Sullivan et al., 2021). Studies have also observed downward migrations (Lenoir et al., 2010; Crimmins et al., 2011) and no evidence of range shifts (Zhu et al., 2012), despite changes in climate. There is evidence that higher elevations are warming faster than lowlands (Loarie et al., 2009; Pepin et al., 2022), and thus migration rates could vary along the elevation gradient. As a consequence, upward migrations may be more evident at higher elevations, leading to shifts in community composition towards warm-adapted species. On the other hand, species from lowlands are generally able to tolerate warmer temperatures and can persist at lower elevations (Freeman et al., 2018) without the need to migrate due to rises in temperature. Our knowledge on elevational shifts in tropical and subtropical mountain regions is restricted to few studies focusing on the Andes and in mountain forests in Taiwan (Feeley et al., 2011; Fadrique et al., 2018; O'Sullivan et al., 2021). These regions deserve more attention due to their high levels of species diversity and complexity.

Mountain ecosystems are especially sensitive to climate change given the high climate variation within small spatial distances. In mountain regions tree species are shifting their distribution due to climate warming (Parmesan & Yohe, 2003; Feeley et al., 2013; Steinbauer et al., 2018). This phenomenon is called 'thermophilization' and represents a shift in the relative dominance of species at higher elevations, characterized by an increase of species previously centred at lower and warmer elevations (Duque et al., 2015; Fadrique et al., 2018). Steep climatic gradients across elevation with distinct vegetation types in ecotonal zones may provide early signs of climate-induced changes in tree species distribution (Noble, 1993; Beckage et al., 2008). Thus, ecotonal zones are relevant ecological indicators of shifts in species composition due to the impact of climate change. Ecotones could also act as barriers for species migrations by reducing colonization rates and favouring the stability of existing communities (Lutz et al., 2013; Fadrique et al., 2018). Moreover, elevational shifts may be much slower than expected, particularly in regions with warm climates (Lenoir et al., 2020), resulting in tree distribution changes lagging behind the pace of climate change (Renwick & Rocca, 2015).

Data from species' distribution across the entire elevation gradient are essential to show accurate trends in species migration. Long-term monitoring data can provide accurate responses at local and regional scales, by incorporating sensitivity and adaptive capacity of species to future distribution. If species are changing their distribution, analysis of repeated measures over time can reveal the magnitude of change and direction, as well as differences between elevation ranges in mountains (Feeley et al., 2011). However, these data are still scarce for many biodiversity hotspots, such as the Brazilian Atlantic Forest, limiting our understanding of ecosystem changes associated with shifts in species distribution due to climatic changes. To deal with the lack of temporal data, one can use a space-for-time approach in which the distribution of juvenile and adult trees from the same species are compared. The differences in thermal affiliation between juvenile and adult trees should reflect the migration of species along the elevation gradient due to changes in climatic conditions. This approach can help us to predict the future of tree species' distribution (Lenoir et al., 2009; O'Sullivan et al., 2021), especially if linked to long-term monitoring data to validate the observed spatial trend (Boisvert-Marsh et al., 2014).

The subtropical Brazilian Atlantic Forest has different forest physiognomies across heterogeneous environments. For example, along the mountain elevation gradient, forest physiognomies are composed of Atlantic Moist Forest, divided into different types according to altitude (lowland <30 m a.s.l., submontane 30–400 m a.s.l., montane 400–1000 m a.s.l. and upper montane >1000 m a.s.l.), and the humid temperate mosaics of Araucaria Forest and highland grasslands on the plateau (Veloso et al., 1991). Elevation gradient strongly influences the variation in species composition, with high levels of beta-diversity between forest types (Bergamin et al., 2012, 2017). Species richness decreases along the elevation gradient as most tropical plant lineages are restricted to low and mid-elevations (~400 to 500 m a.s.l.) and are gradually replaced by cold-adapted temperate plant lineages towards higher elevations (Rambo, 1951, 1953; Bergamin et al., 2021). Recent studies predicted that the Araucaria Forest will suffer a drastic reduction in its distribution under future climate scenarios (Bergamin et al., 2019; Saraiva et al., 2021), which may favour the expansion of surrounding tropical formations such as the Atlantic Moist Forest and the Seasonal Forest. Indeed, tree species from lower elevations are already colonizing the understorey of Araucaria Forest (Bergamin et al., 2012). This is in line with recent findings of upward migration of tropical and subtropical species due to increasing temperatures in the Andean forests (Feeley et al., 2011; Duque et al., 2015; Fadrique et al., 2018).

Here, we evaluate the effects of climate change on the distribution ranges and local demographic processes using species' thermal affiliations in tree communities along the elevational gradient in the subtropical Brazilian Atlantic Forest by using two complementary approaches. First, we evaluate migration trends and changes in tree community composition in relation to temperature optimal niche, based on regional abundance data of juvenile and adults in a single-census forest monitoring, distributed along an elevation gradient (2–1160 m) in the Atlantic Moist Forest. As temperature change drives species distribution, we expect juvenile communities to have thermal affiliations to warmer temperatures higher than their respective adult communities as a sign of upward migration. In the second approach, we used long-term monitoring data from permanent plots across the elevation gradient within an ecotonal region between Araucaria Forest and Atlantic Moist Forest to evaluate temporal responses of tree species. We expect an increase in stem abundance and growth of more thermophilic species (i.e., associated with warmer temperatures), as an indicator of currently more favourable conditions to them in comparison to species of colder optimal niches. As migration trends could be heterogeneous along the different ranges of the elevation gradient, we expect that tree communities at higher elevations (above the transition zone between lowland–submontane to montane–upper montane forests) will shift upwards, as species are more temperature-limited to colder conditions. We also expect tree communities of lower elevations will show different migration trends, as species from lowland may be able to tolerate increasing temperature over time.

2 | MATERIALS AND METHODS

2.1 | Study area

The study region is located in the subtropical Brazilian Atlantic Forest (Figure 1). To evaluate migration trends and shifts in community composition, we used two data sets encompassing 96 permanent plots established in natural and unmanaged old-growth forests. By selecting this set of permanent plots with these characteristics, we avoid potential bias that may come from afforestation or thinning processes. The first data set encompasses the number of juveniles and adult trees from the forest inventory plots of the Santa Catarina Forest and Floristic Inventory (hereafter IFFSC). The 88 plots are distributed along an elevation gradient within the Atlantic Moist Forest, systematically located at the intersections of a state-wide 10 × 10 km grid. The plot locations range from 2 to 1160 m of elevation and encompass transitional forests from the lowland Atlantic Moist Forest to montane Atlantic Moist Forest (Figure 1). The second data set includes abundance data based on the number and the basal area of juvenile and adult trees from permanent plots of the Long-term Ecological Research in Subtropical Atlantic Forest (hereafter LERSAF). The eight plots are located across an ecotone between the sub montane Atlantic Moist Forest (~350 m of elevation) and the Araucaria Forest (~950 m of elevation) (Figure 1).

Mean annual temperature has increased in the region by 0.25°C per decade in the last 50 years ($r^2 = 0.56$; $p < 0.01$; Appendix S1). Mean annual rainfall did not change over time ($r^2 = 0.01$; $p = 0.18$; Appendix S2). Climate data were obtained from Climate Research Unit (Harris et al., 2014) at 0.5° spatial resolution from 1970 to 2020.

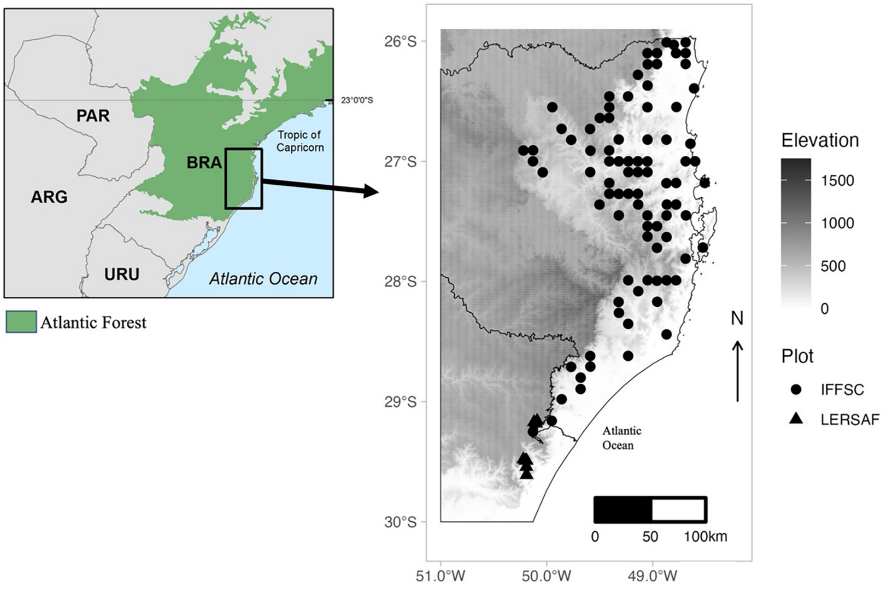

FIGURE 1 Study region in southern Atlantic Forest and the location of the 96 inventory plots across the elevation gradient. Plots from the Santa Catarina Forest and Floristic Inventory (IFFSC) were used for spatial and from the Long-term Ecological Research in Subtropical Atlantic Forest (LERSAF) for temporal analyses.

2.2 | Species temperature affiliation index and community temperature score

To understand the temperature sensitivity of different species we used the temperature affiliation index of each species. Temperature affiliation indices for the 627 tree species occurring in our study was extracted from Klipel et al. (2022). This index represents the species' optimal temperature niche, and it is based on the abundance of the species and the annual mean temperatures across forest sites where the species was registered, in this case, in tree community inventories across the whole Brazilian Atlantic Forest (Klipel et al., 2022). Then, the index is calculated as the weighted mean of the species considering its relative density and distribution along the temperature gradient (Chen et al., 2009; Feeley et al., 2011; Esquivel-Muelbert et al., 2017; Klipel et al., 2022). To characterize each community regarding its temperature affiliation, we calculated the community temperature score (CTS in°C; see Feeley et al., 2013; Duque et al., 2015). The CTS is the community-weighted mean (CWM) based on the temperature affiliation index of all species sampled in the plot, a commonly used approach in trait-based community studies (Ricotta & Moretti, 2011). In our study, we calculated the CTS using either the number of individuals or the stem basal area in the weighted term, and both were represented in the results.

2.3 | Community change analysis based on single-census forest monitoring

We used a single-census forest monitoring to compare the distribution of tree communities considering different life-history stages to infer changes in CTS. We used 88 permanent plots from the IFFSC along distinct mature forests (Vibrans et al., 2020) distributed across an elevation gradient (2–1160 m a.s.l.; Appendix S3 shows the ID of each plot and its distribution along the elevation gradient). Juveniles (from 0.5 to 2 m tall) were sampled within 16 subplots with total area of 0.04 ha within each plot and adult tree individuals (≥10 cm of diameter at breast height [DBH] and ≥8 m tall) within the entire 0.4-ha plots. Here, juvenile communities are used as a proxy of responses to more recent climatic conditions whilst adult communities should reflect former conditions (Lenoir et al., 2009; Zhu et al., 2014; Serra-Diaz et al., 2016; Wason & Dovciak, 2017; O'Sullivan et al., 2021). We assumed that trees with distinct life-history stages have distinct ages and have faced distinct conditions at their critical establishment time.

We calculated the CTS for each plot and life-history stage as described above. Then, we performed a paired *t*-test to test for differences in CTS values between communities of the two life-history stages along the elevation gradient. In all analysis procedure, we conducted a thorough examination of the fundamental assumptions underlying the *t*-test through diagnostic plot analysis, and the data did not show significant departures from the requisite assumptions of normality and homoscedasticity. Additionally, as migration trends may vary along the elevation gradient, we also performed paired *t*-tests to compare the CTS values of the two life-history stages between different forest types. To do this, we divided the data in two groups by forest formation according to the elevation range: (1) lowland and submontane forests (from 0 to 400 m a.s.l., hereafter 'lower–submontane'; $n=46$); (2) montane and upper montane forests (above the 400 m a.s.l., hereafter 'montane–upper montane'; $n=42$).

To test whether the difference in the CTS between the community of juveniles and adults is significantly different from a random expectation, we compared the CTS from these different life-history stages within a community (plot) constructing 95% confidence intervals (CI) under a bootstrap framework (Manly, 1997). This approach considers the position of each community along the elevation gradient. To do so, we kept constant the total number of trees occurring in each plot and in each iteration we randomly draw a bootstrap sample of number of individuals with replacement. The probability of an individual from a given species being randomly drawn was proportional to the observed relative abundance of that species within that community. Based on this new bootstrapped community we calculated a new CTS value for each draw. This procedure was repeated 1000 times, generating bootstrap distribution values of CTS for each community. This distribution allowed us to calculate the bootstrapped mean and the 2.5th (lower limit) and 97.5th (higher limit) quantiles. We considered differences in migration trend within the same community to be statistically significant when 95% CIs of adult and juvenile communities did not overlap. Upward migration was considered when CTS values for juveniles were higher than for adults, as species from lower and warmer distribution range are establishing at higher elevations. On the other hand, downward migration was considered when CTS values for juveniles were lower than for adults, as species from higher and colder distribution range are establishing at lower elevations. Additionally, we extracted the migration direction in each plot by subtracting the bootstrapped mean CTS values for the juveniles from the bootstrapped mean CTS values for adults (ΔCTS). We then applied a linear model to test the relationship between migration directions for each of the 88 plots with elevation gradient. We also performed an ANOVA to compare the ΔCTS between low–submontane and montane–upper montane forests.

2.4 | Community change analyses based on long-term forest monitoring

We investigated changes in CTS over time using data from eight sites with 1-ha permanent plots with a 10-year interval (2008/2009 and 2018/2019). Two permanent plots are in the submontane Atlantic Moist Forest (300 and 350 m a.s.l.) and six are in Araucaria Forest (from 920 to 1000 m a.s.l.). Within each 1-ha site, we monitored 12 permanent sampling units of 100 m^2, randomly placed in the first census, here considered as local communities. Thus, shifts in community composition were observed over time in 24 local communities in the submontane Atlantic Moist Forest and 72 in the Araucaria Forest. Specimens recorded were divided into juveniles (with 1–5 cm of DBH) and adult trees (with ≥10 cm of DBH), and we calculated the CTS for each permanent sampling unit and census. To test differences among CTS of the same life-history stage in the first and last census, we performed a paired *t*-test. We further analysed whether results are not an effect of successional changes due to small-scale disturbances (e.g., natural gaps), by calculating shifts in wood density (WD) of adult tree communities for each census interval (Appendix S4). An increase in WD over time would indicate successional changes in moist forests, as pioneer species are expected to have softer wood in comparison with late-successional species (Poorter et al., 2019, 2021). However, we did not find significant changes in WD between the censuses, meaning no successional changes across the forests. All analyses were performed in R. 4.1.2 (R Core Team, 2021).

3 | RESULTS

3.1 | Community changes based on single-census forest monitoring in the Atlantic Moist Forest

Along the elevation gradient, a total of 37,295 individuals belonging to 603 species were sampled. From these, 466 species and 16,444 trees were found in the juvenile communities and 510 species and 20,851 trees within the adult communities. The plot-level CTS for the juvenile communities ranged from 17.6 to 20.5°C (19.3±0.5) and for adult communities ranged from 17.1 to 20.7°C (19.1±0.6). Across all our data the CTS was on average 0.1°C higher for juvenile communities than adult communities in the same plot ($t_{87}=2.23$, $p=0.02$; Figure 2a). When analysing each forest type according to the elevation range, we did not find differences in the CTS for the lowland–submontane forests ($t_{45}=-0.74$, $p=0.46$; Figure 2b). However, we found that the CTS for juvenile communities was on average 0.27°C higher than for the adult communities for montane–upper montane forests ($t_{41}=4.13$, $p<0.01$; Figure 2c).

Overall, most tree communities (58%) showed a non-migration trend (Figure 3a). In contrast, we also observed 27% of the plots showing an upward migration (abundance of more thermophilic species is higher for juveniles than adult trees) and 15% a downward migration (abundance of more thermophilic species is higher for adults than juvenile trees; Figure 3a). We found a positive relationship between ΔCTS and elevation (Figure 3a) indicating an increase in upward migration as the elevation increases ($r^2=0.17$, $p<0.05$, $\beta=0.0007\pm0.0001$). ANOVA results between forest types showed that tree communities in montane–upper montane forests have a higher ΔCTS then the communities in low–submontane forests (*F*-value = 12.59, $p<0.01$; Figure 3b).

3.2 | Temporal community changes in Atlantic Moist and Araucaria Forest

A total of 86 species were recorded across the two inventories (78 species in the juvenile and 65 species within the adult trees). After 10 years between the first and last census, we observed significant changes in CTS values only for juvenile communities (Figure 4a–d). Considering the number of individuals in the plots for the Atlantic Moist Forest, CTS decreased on average by 0.36°C (from 19.19°C to 18.83°C; $t_{23}=3.54$, $p<0.05$; Figure 4a), however, we did not find significant changes in CTS values when considering the basal area per species ($t_{23}=0.78$, $p>0.05$; Figure 4b). For the Araucaria Forest, we observed an increase in CTS values for juvenile communities over time by 0.34°C (16.02–16.36°C; $t_{70}=-2.99$, $p<0.05$; Figure 4c) considering the number of individuals per species, and by 0.43°C (15.88–16.31°C; $t_{70}=-3.23$, $p<0.05$; Figure 4d) considering the basal area per species.

4 | DISCUSSION

We provide indirect results suggesting species shifts upwards in the subtropical Brazilian Atlantic forests due to global warming. Our results suggest heterogeneous migration trends, which is expected

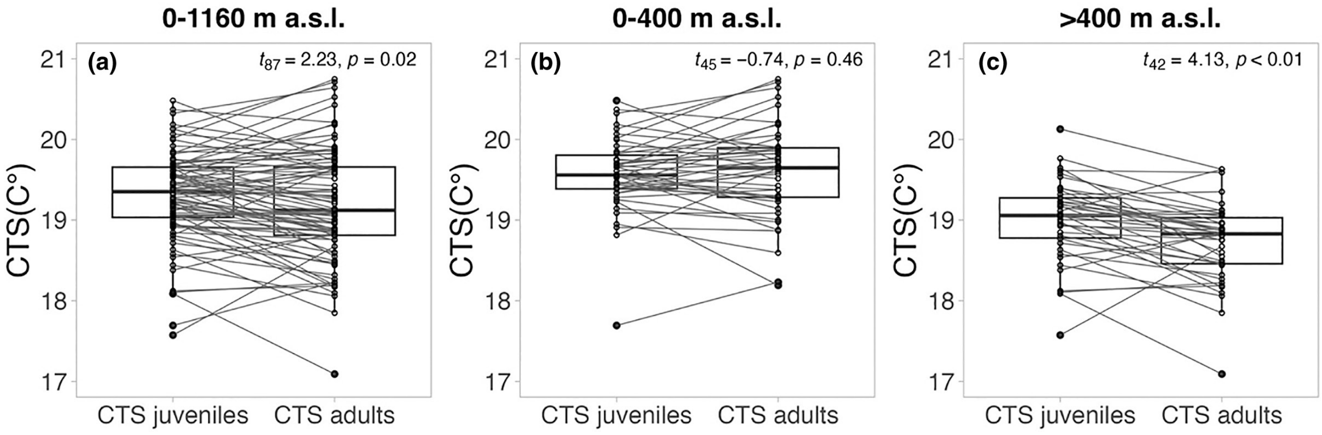

FIGURE 2 Comparisons of community temperature scores (CTS) between juvenile and adult communities. We show the results for: (a) 88 communities along the elevation gradient in the Atlantic Moist Forest (0–1160 m a.s.l.); (b) 46 communities in the lowland–submontane forests (0–400 m a.s.l.); and (c) 42 communities in the montane–upper montane forests (>400 m a.s.l.).

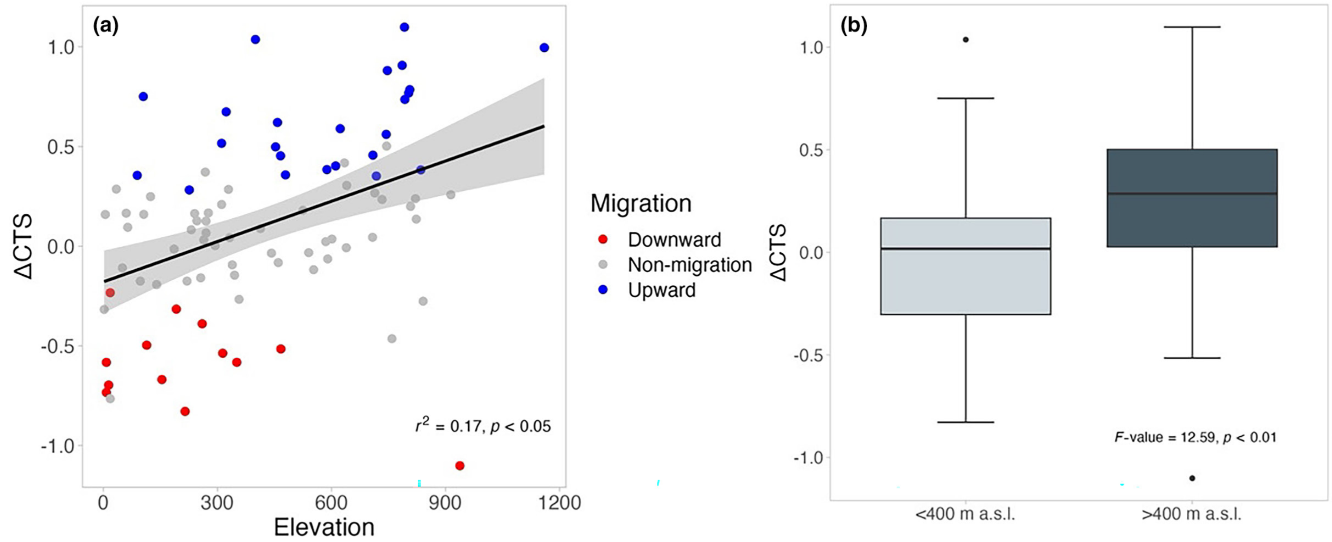

FIGURE 3 Differences between life-history stages across elevation. (a) The relationship between the differences in bootstrapped community temperature scores (ΔCTS) for the juveniles from the CTS values for adults in 88 communities along the elevation gradient in the Atlantic Moist Forest. (b) ΔCTS differences between lowland–submontane forests and montane–upper montane forests.

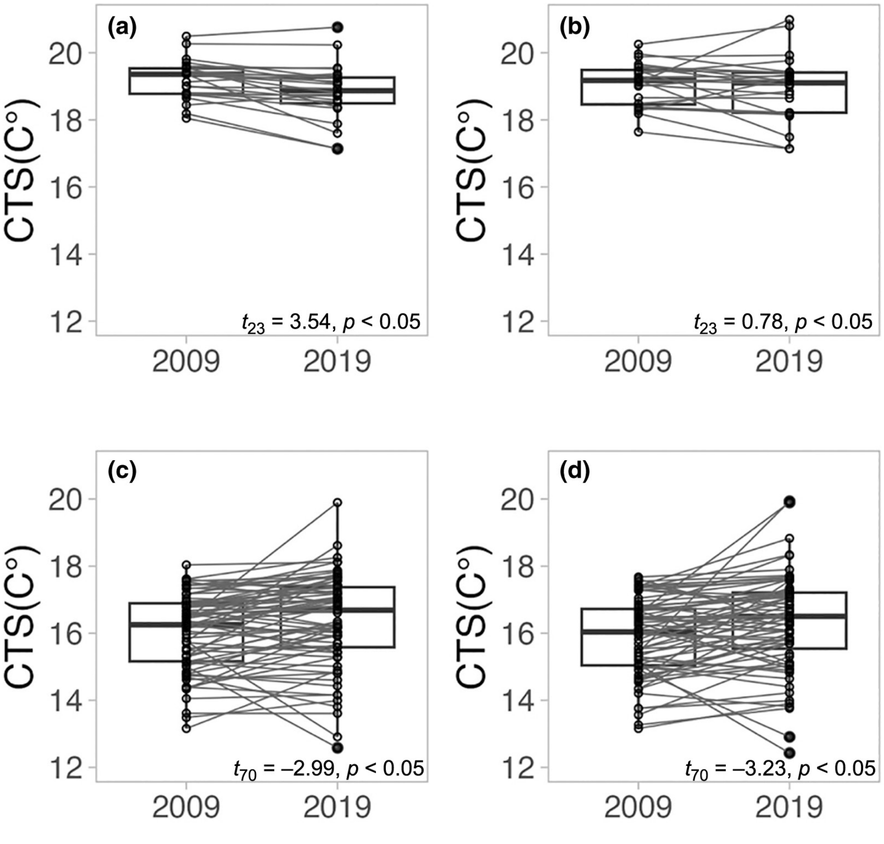

FIGURE 4 Community temperature score (CTS) comparisons of juvenile communities between censuses. Here we show: (a) submontane Atlantic Moist Forest considering the number of individuals per species; and (b) the basal area per species. (c) Araucaria Forest considering the number of individuals per species; and (d) the basal area per species.

for such highly diverse forests. Most communities showed non-migration trends, which may indicate time lags in species' responses to climate change. However, we also observed different migration trends along the elevation gradient considering the forest types. In montane–upper montane forests (above 400 m of altitude), tree communities are more likely to exhibit an upward migration trend, indicating future changes in community composition towards more thermophilic species. On the other hand, downward migration trends were concentrated in lowland–submontane forests (below 400 m a.s.l.). The shifts in composition are consistent with both approaches, when comparing the distribution of juveniles and adults or when comparing communities over a decade of monitoring interval.

Although our results showed a diversity of responses along the elevation gradient with contrasting results between forest types, an important indication of upward migration of tree species is that the CTS values of juvenile communities were higher than values of adult communities for montane–upper montane forests and slightly increased within 10 years of forest monitoring. Plots in montane–upper montane forests tend to have a higher abundance of thermophilic species in younger tree communities, expressing the establishment in more recent and warmer climatic conditions in relation to older tree communities (Lenoir et al., 2009; Woodall et al., 2009; Zhu et al., 2014). In this sense, the upward migration observed in montane–upper montane forest communities at higher elevations is likely a consequence of the rising temperatures over the past years, suggesting that migration may be a common response of species that occur in this part of the elevation gradient in the face of climate change. Indeed, species from higher elevations are generally more temperature-limited (Way & Oren, 2010), and cold-demanding species are more prone to be competitively excluded under warmer temperatures (Alexander et al., 2015) by species with greater affinity to hotter temperatures. Evidence from studies of other mountain regions of South American suggest that changes in the community composition were mainly driven by the upward migration of thermophilic species and the contraction of cold-demanding species'distributions at the rear edges (Feeley et al., 2011; Duque et al., 2015; Fadrique et al., 2018). Studies that used predictive models for the Atlantic Forest have forecasted a retraction in the potential distribution of high-altitude forests for future scenarios of climate change, likely associated with the expansion of a tropical flora from the lowland forests (Bergamin et al., 2019; Saraiva et al., 2021). Our results add more evidence to a limited but increasing knowledge about upward migration and thermophilization of forest communities in tropical and subtropical forests of South America (Feeley et al., 2011; Duque et al., 2015; Fadrique et al., 2018).

While our findings suggest that species from montane–upper montane forest communities are more likely to shift upwards, species from lowland–submontane forests communities showed more idiosyncratic results. These further suggest individualistic species' responses rather than synchronous responses to climate change along the elevation gradient. However, lowland–submontane forest communities were much more likely to show downward migration. Species from lowland are generally able to tolerate warmer temperatures at lower elevations (Freeman et al., 2018), being probably able to display shifts in distribution in both directions. Indeed, climate warming may affect species distribution along elevation gradients through non-thermal factors such as species interactions (Lenoir et al., 2010). Local biotic interactions affect the relative abundance patterns in forest communities, further influencing the establishment and growth of trees. In this sense, downslope migration may be a result of competitive release at the lower margin of the elevational range of species that are migrating upward (Lenoir et al., 2010). The importance of competition in determining the species distribution along elevation gradients decreases as environmental stress increases (Maestre et al., 2009). Therefore, this mechanism may be important in structuring migration patterns in the Atlantic lowland–submontane forests, where tree species richness is higher, and competition plays a major role in community assembly (Klipel et al., 2023).

In ecotonal zones differences in abiotic and biotic factors could act as a barrier for species migration (Fadrique et al., 2018), thus influencing migration patterns. The Atlantic Moist Forest is subdivided into different forest types according to elevation (Veloso et al., 1991), with a sharp transition zone in species composition around 400 m a.s.l. Above 400 m, lower temperatures, greater frost frequency, and cloudier conditions act as environmental determinants, restricting the establishment or the abundance of many tropical lineages (Klein, 1984; Bergamin et al., 2012, 2021). Thus, with the rise in temperatures in recent years, these determinants may become less restrictive at higher altitudes, allowing the migration of more thermophilic species. The shifts in species range vary with elevation as a response to environmental conditions and biotic interactions, and lead to variations in the transition zones and natural boundaries along elevation gradients in mountains around the world (Mamantov et al., 2021). However, as observed here, downward migrations seem be more common from low to mid-elevation forests and upward migrations are more concentrated in montane forests at higher elevations (O'Sullivan et al., 2021).

Despite growing evidence that species are shifting their distribution in response to climate change (Kelly & Goulden, 2008; Lenoir et al., 2009; Feeley et al., 2011), we also detected non-migration trends, which may be a result of migration lags in trees to keep in pace with rapid warming rates (Loarie et al., 2009; Corlett & Westcott, 2013). Migration lags could be associated with the time of ecological processes related to dispersal, establishment, and extinction of long-lived tree species (Svenning & Sandel, 2013; Alexander et al., 2018). In addition, although anthropogenic disturbances associated with deforestation can influence species' distribution shifts by promoting the upward migration of warm-adapted species (Guo et al., 2018), there is evidence that habitat fragmentation increases the potential of migration lags due to long dispersal distance between patches (Honnay et al., 2002; Bertrand et al., 2011; Lenoir et al., 2020), which may occur in the extremely fragmented Atlantic Forest (Ribeiro et al., 2009). Future studies are needed to better understand the causes of tree migration lags in the Atlantic Forest, as our knowledge remains incomplete. Although some limitations exist in the static approach considering the comparison of juvenile and adult trees on a single-census forest monitoring, mainly related to the concept of regeneration niche (Grubb, 1977; Máliš et al., 2016), this framework considering the bootstrap approach may reveal conservative responses of regenerating species to global warming, providing indicatives of future tree species distribution shifts (e.g. Lenoir et al., 2009). In this sense, we have addressed an important knowledge gap for the Atlantic Forest, demonstrating that migration trends in mountains are complex in forests that are rich in biodiversity. Further research considering species identity, traits, climate, and landscape context are needed to have a better picture of tree species response of the Atlantic Forest in the face of future climate change.

5 | CONCLUSION

Our findings provide the first evidence of climate-change-induced community shifts in the Brazilian Atlantic Forest, a remarkable biodiversity hotspot. We show distinct migrations trends coupled with shifts in community composition, in contrast to earlier projections that suggested unidirectional migration towards higher elevation due to a warming climate. We detect contrasting responses between forest communities along the elevation gradient, indicating that the transition zones between forest types influence migration patterns. Although the lowland–submontane forest communities presented idiosyncratic results, downward migrations were more frequent in this part of the elevation gradient and are most likely driven by non-thermal factors such as biotic interactions (e.g., competition). On the other hand, upward migrations were mostly found in the montane–upper montane forests, and it has been considered a common response for tree species that occur at higher elevations. The thermophilization of the montane–upper montane forests observed in the understorey may indicate a greater extinction risk of cold-demanding species under future scenarios of global warming.

AUTHOR CONTRIBUTIONS

Rodrigo Scarton Bergamin, Vinicius Augusto Galvão Bastazini, Sandra Cristina Müller and Rafael Loyola conceived of the research idea. Rodrigo Scarton Bergamin, Joice Klipel, Kauane Maiara Bordin and Alexander Christian Vibrans collected data. Rodrigo Scarton Bergamin, Adriane Esquivel-Muelbert, Joice Klipel, Kauane Maiara Bordin, Vinicius Augusto Galvão Bastazini and Vanderlei Júlio Debastiani performed statistical analyses. Rodrigo Scarton Bergamin wrote the paper with contributions of all authors. All authors discussed the results and commented on the manuscript.

ACKNOWLEDGEMENTS

The authors would like to thank IFFSC for sharing the data and FAPESC for supporting this project. We also thank the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES) – Finance Code 001 for the scholarship of Rodrigo Scarton Bergamin, the *Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul* (FAPERGS; process number 19/2551-0001698-0) and the *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq; grant number 309659/2019-1 to Sandra Cristina Müller) for the partial financial support of the project.

FUNDING INFORMATION

Sandra Cristina Müller and Alexander Christian Vibrans have been constantly funded by CNPq (grants #307719/2012-0 and #309764/2019-0). Rafael Loyola'S research is funded by CNPq (grant #306694/2018-2). Vinicius Augusto Galvão Bastazini is funded by National Funds through FCT – Foundation for Science and Technology under the Project UIDB/05183/2020. Adriane Esquivel-Muelbert was funded by the Royal Society Standard Grant RGS\R1\221115 'MegaFlora', the UKRI/NERC TreeScapes NE/V021346/1 'MEMBRA', the NERC/NSF Gigante NE/Y003942/1 and the FRB/CESAB 'Syntreesys'. This paper is a contribution of the INCT in Ecology, Evolution and Biodiversity Conservation founded by MCTIC/CNPq (grant #465610/2014-5) and FAPEG (grant #201810267000023). Fieldwork in permanent plots of the Rio Grande do Sul was supported by FAPERGS (grants #12/2218-2, # 19/2551-0001698-0) and Rufford Foundation (grant 27666-1), in Santa Catarina by FAPESC (grant 2016TR2524) and IMA/SC (grant 32025/2019).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Tree community data from IFFSC are stored at https://www.givd.info/ID/SA-BR-002 and data from LERSAF are available from https://forestplots.net.

ORCID

Rodrigo Scarton Bergamin https://orcid.org/0000-0002-2405-9977
Vinicius Augusto Galvão Bastazini https://orcid.org/0000-0001-5270-0621
Adriane Esquivel-Muelbert https://orcid.org/0000-0001-5335-1259
Kauane Maiara Bordin https://orcid.org/0000-0003-3871-6293
Joice Klipel https://orcid.org/0000-0003-3936-9692
Vanderlei Júlio Debastiani https://orcid.org/0000-0003-0807-025X
Alexander Christian Vibrans https://orcid.org/0000-0002-8789-5833
Rafael Loyola https://orcid.org/0000-0001-5323-2735
Sandra Cristina Müller https://orcid.org/0000-0002-6316-2897

REFERENCES

Alexander, J.M., Chalmandrier, L., Lenoir, J., Burgess, T.I., Essl, F., Haider, S. et al. (2018) Lags in the response of mountain plant communities to climate change. *Global Change Biology*, 24, 563–579.

Alexander, J.M., Diez, J.M. & Levine, J.M. (2015) Novel competitors shape species' responses to climate change. *Nature*, 525, 515–518.

Beckage, B., Osborne, B., Gavin, D.G., Pucko, C., Siccama, T. & Perkins, T. (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 4197–4202.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity: biodiversity and climate change. *Ecology Letters*, 15, 365–377.

Bergamin, R., Müller, S. & Mello, R. (2012) Indicator species and floristic patterns in different forest formations in southern Atlantic rainforests of Brazil. *Community Ecology*, 13, 162–170.

Bergamin, R.S., Bastazini, V.A.G., Vélez-Martin, E., Debastiani, V., Zanini, K.J., Loyola, R. et al. (2017) Linking beta diversity patterns to protected areas: lessons from the Brazilian Atlantic rainforest. *Biodiversity and Conservation*, 26, 1557–1568.

Bergamin, R.S., Debastiani, V., Joner, D.C., Lemes, P., Guimarães, T., Loyola, R.D. et al. (2019) Loss of suitable climatic areas for

Araucaria forests over time. *Plant Ecology and Diversity*, 12, 115–126.

Bergamin, R.S., Seger, G.D.S., Carlucci, M.B., Molz, M., Mello, R.S.P., Martins, R. et al. (2021) Elevational shifts in phylogenetic diversity of angiosperm trees across the subtropical Brazilian Atlantic Forest. *Austral Ecology*, 46, 486–495.

Bertrand, R., Gégout, J.-C. & Bontemps, J.-D. (2011) Niches of temperate tree species converge towards nutrient-richer conditions over ontogeny. *Oikos*, 120, 1479–1488.

Boisvert-Marsh, L., Périé, C. & De Blois, S. (2014) Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. *Ecosphere*, 5, art83.

Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J.D., Chey, V.K., Barlow, H.S. et al. (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 1479–1483.

Corlett, R.T. & Westcott, D.A. (2013) Will plant movements keep up with climate change? *Trends in Ecology & Evolution*, 28, 482–488.

Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. & Mynsberge, A.R. (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, 331, 324–327.

Duque, A., Stevenson, P.R. & Feeley, K.J. (2015) Thermophilization of adult and juvenile tree communities in the northern tropical Andes. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 10744–10749.

Esquivel-Muelbert, A., Baker, T.R., Dexter, K.G., Lewis, S.L., Ter Steege, H., Lopez-Gonzalez, G. et al. (2017) Seasonal drought limits tree species across the Neotropics. *Ecography*, 40, 618–629.

Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J. et al. (2018) Widespread but heterogeneous responses of Andean forests to climate change. *Nature*, 564, 207–212.

Feeley, K.J., Hurtado, J., Saatchi, S., Silman, M.R. & Clark, D.B. (2013) Compositional shifts in Costa Rican forests due to climate-driven species migrations. *Global Change Biology*, 19, 3472–3480. Available from: https://doi.org/10.1111/gcb.12300

Feeley, K.J., Silman, M.R., Bush, M.B., Farfan, W., Cabrera, K.G., Malhi, Y. et al. (2011) Upslope migration of Andean trees: Andean trees migrate upslope. *Journal of Biogeography*, 38, 783–791.

Freeman, B.G., Lee-Yaw, J.A., Sunday, J.M. & Hargreaves, A.L. (2018) Expanding, shifting and shrinking: the impact of global warming on species' elevational distributions. *Global Ecology and Biogeography*, 27, 1268–1276.

Grubb, P.J. (1977) The maintenanceof species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, 52, 107–145.

Guo, F., Lenoir, J. & Bonebrake, T.C. (2018) Land-use change interacts with climate to determine elevation species distribution. *Nature Communications*, 9, 1315.

Harris, I., Jones, P.D, Osborn, T.J., & Lister, D.H. (2014) Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *International Journal of Climatology*, 34, 623–642.

Honnay, O., Verheyen, J.B., Jacquemyn, H., Bossuyt, B. & Hermy, M. (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters*, 5, 525–530.

Kelly, A.E. & Goulden, M.L. (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 11823–11826.

Klein, R.M. (1984) Aspectos dinâmicos da vegetação do sul do Brasil. *Sellowia*, 36, 5–54.

Klipel, J., Bergamin, R.S., Cianciaruso, M.V., Da Silva, A.C., Jurinitz, C.F., Jarenkow, J.A. et al. (2023) How do distinct facets of tree diversity and community assembly respond to environmental variables in the subtropical Atlantic Forest? *Ecology and Evolution*, 13, e10321.

Klipel, J., Bergamin, R.S., Esquivel-Muelbert, A., De Lima, R.A.F., De Oliveira, A.A., Prado, P.I. et al. (2022) Climatic distribution of tree species in the Atlantic Forest. *Biotropica*, 54, 1170–1181.

Lamprecht, A., Semenchuk, P.R., Steinbauer, K., Winkler, M. & Pauli, H. (2018) Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps. *New Phytologist*, 220, 447–459.

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J. et al. (2020) Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, 4, 1044–1059.

Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E. et al. (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, 33, 295–303.

Lenoir, J., Gégout, J.-C., Pierrat, J.-C., Bontemps, J.-D. & Dhôte, J.-F. (2009) Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986-2006). *Ecography*, 32, 765–777.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, 462, 1052–1055.

Lutz, D.A., Powell, R.L. & Silman, M.R. (2013) Four decades of Andean timberline migration and implications for biodiversity loss with climate change. *PLoS One*, 8, e74496.

Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, 97, 199–205.

Máliš, F., Kopecký, M., Petřík, P., Vladovič, J., Merganič, J. & Vida, T. (2016) Life stage, not climate change, explains observed tree range shifts. *Global Change Biology*, 22, 1904–1914.

Mamantov, M.A., Gibson-Reinemer, D.K., Linck, E.B. & Sheldon, K.S. (2021) Climate-driven range shifts of montane species vary with elevation. *Global Ecology and Biogeography*, 30, 784–794.

Manly, B.F.J. (1997) *Randomization, bootstrap and Monte Carlo methods in biology*. London: Chapman and Hall.

Morueta-Holme, N., Engemann, K., Sandoval-Acuña, P., Jonas, J.D., Segnitz, R.M. & Svenning, J.-C. (2015) Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 12741–12745.

Noble, I.R. (1993) A model of the responses of ecotones to climate change. *Ecological Applications*, 3, 396–403.

O'Sullivan, K.S.W., Ruiz-Benito, P., Chen, J. & Jump, A.S. (2021) Onward but not always upward: individualistic elevational shifts of tree species in subtropical montane forests. *Ecography*, 44, 112–123.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.

Pepin, N.C., Arnone, E., Gobiet, A., Haslinger, K., Kotlarski, S., Notarnicola, C. et al. (2022) Climate changes and their elevational patterns in the mountains of the world. *Reviews of Geophysics*, 60. e2020RG000730.

Poorter, L., Rozendaal, D.M.A., Bongers, F., Almeida, D.J.S., Álvarez, F.S., Andrade, J.L. et al. (2021) Functional recovery of secondary tropical forests. *Proceedings of the National Academy of Sciences of the United Staets of America*, 118, e2003405118.

Poorter, L., Rozendaal, D.M.A., Bongers, F., De Almeida-Cortez, J.S., Almeyda Zambrano, A.M., Álvarez, F.S. et al. (2019) Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nature Ecology & Evolution*, 3, 928–934.

R Core Team. (2021) *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Rambo, B. (1951) O elemento andino no pinhal riograndense. *Anais Botânicos Do Herbário Barbosa Rodrigues*, 3, 7–39.

Rambo, B. (1953) Histo_ria da flora do planalto riograndense. *Anais Botânicos Do Herbário Barbosa Rodrigues*, 5, 185–232.

Renwick, K.M. & Rocca, M.E. (2015) Temporal context affects the observed rate of climate-driven range shifts in tree species: importance of temporal context in tree range shifts. *Global Ecology and Biogeography*, 24, 44–51.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, 142, 1141–1153.

Ricotta, C. & Moretti, M. (2011) CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia*, 167, 181–187.

Rumpf, S.B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J. et al. (2018) Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 1848–1853.

Saraiva, D.D., Esser, L.F., Grasel, D. & Jarenkow, J.A. (2021) Distribution shifts, potential refugia, and the performance of protected areas under climate change in the *Araucaria* moist forests ecoregion. *Applied Vegetation Science*, 24, e12628.

Serra-Diaz, J.M., Franklin, J., Dillon, W.W., Syphard, A.D., Davis, F.W. & Meentemeyer, R.K. (2016) California forests show early indications of both range shifts and local persistence under climate change: early indications of tree range shifts. *Global Ecology and Biogeography*, 25, 164–175.

Steinbauer, M.J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H. et al. (2018) Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556, 231–234.

Svenning, J.-C. & Sandel, B. (2013) Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, 100, 1266–1286.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 8245–8250.

Veloso, H.P., Rangel Filho, A.L.R. & Lima, J.C.A. (1991) *Classificação da vegetação brasileira, adaptada a um sistema universal*. Rio de Janeiro: Ministério da Economia, Fazenda e Planejamento, Fundação Instituto Brasileiro de Geografia e Estatística, Diretoria de Geociências, Departamento de Recursos Naturais e Estudos Ambientais.

Vibrans, A.C., Gasper, A.L.D., Moser, P., Oliveira, L.Z., Lingner, D.V. & Sevegnani, L. (2020) Insights from a large-scale inventory in the southern Brazilian Atlantic Forest. *Scientia Agricola*, 77, e20180036.

Wason, J.W. & Dovciak, M. (2017) Tree demography suggests multiple directions and drivers for species range shifts in mountains of northeastern United States. *Global Change Biology*, 23, 3335–3347.

Watts, S.H., Mardon, D.K., Mercer, C., Watson, D., Cole, H., Shaw, R.F. et al. (2022) Riding the elevator to extinction: disjunct arctic-alpine plants of open habitats decline as their more competitive neighbours expand. *Biological Conservation*, 272, 109620.

Way, D.A. & Oren, R. (2010) Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology*, 30, 669–688.

Wilson, O.J., Mayle, F.E., Walters, R.J., Lingner, D.V. & Vibrans, A.C. (2021) Floristic change in Brazil's southern Atlantic Forest biodiversity hotspot: from the last glacial maximum to the late 21st century. *Quaternary Science Reviews*, 264, 107005.

Woodall, C.W., Oswalt, C.M., Westfall, J.A., Perry, C.H., Nelson, M.D. & Finley, A.O. (2009) An indicator of tree migration in forests of the eastern United States. *Forest Ecology and Management*, 257, 1434–1444.

Zhu, K., Woodall, C.W. & Clark, J.S. (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*, 18, 1042–1052.

Zhu, K., Woodall, C.W., Ghosh, S., Gelfand, A.E. & Clark, J.S. (2014) Dual impacts of climate change: forest migration and turnover through life history. *Global Change Biology*, 20, 251–264.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Graph containing the trends in mean annual temperature in the study region in the last 50 years.

Appendix S2. Graph containing the trends in mean annual rainfall in the study region in the last 50 years.

Appendix S3. Table with plots from the Santa Catarina Forest and Floristic Inventory (IFFSC) used in this paper.

Appendix S4. Brief description and graph regarding wood density analysis.

How to cite this article: Bergamin, R.S., Bastazini, V.A.G., Esquivel-Muelbert, A., Bordin, K.M., Klipel, J., Debastiani, V.J. et al. (2024) Elevational shifts in tree community composition in the Brazilian Atlantic Forest related to climate change. *Journal of Vegetation Science*, 35, e13289. Available from: https://doi.org/10.1111/jvs.13289