Drivers of carbon stocks in Araucaria forests

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Abstract

Background

Understanding the drivers of variations in carbon stocks is essential for developing the effective management strategies that contribute to mitigating climate change. Although a positive relationship between biodiversity and the aboveground carbon (AGC) has been widely reported for various Brazilian forest types, representing a win–win scenario for climate change mitigation, this association has not been commonly found in Brazilian subtropical forests. Therefore, in the present study, we aimed to evaluate the effects of *Araucaria angustifolia* populations, stand structure and species diversity in shaping AGC stocks in Brazilian subtropical mixed forests. We hypothesized that the effects on the AGC of stand structure and diversity would be mediated by *A. angustifolia*. We also evaluated the expectation of higher carbon stocks in protected forests as a result of their positive correlation with biodiversity conservation.

Results

We found that stand structure, followed by *A. angustifolia* population, played the most important role in shaping the AGC stock. Our hypothesis was partially confirmed, the direct and indirect effects of *A. angustifolia* on stand structure being found to have shaped the AGC. Similarly, our expectation was partially supported, with the higher AGC in the protected area being related not to diversity, but rather to the presence of larger trees, denser stands, and a greater abundance of *A. angustifolia*.

Conclusion

Although the win–win strategy between diversity conservation and carbon storage is not a peculiarity of Araucaria forests, we highlight the potential of these forests as a nature-based climate solution, maintaining high levels of carbon storage in harmony with the provision of keystone resources.

Background

Climate change has caused environmental, economic, and social impacts worldwide and at increasing scales and is associated with industrial activities, land-use change, and deforestation. The role of forests as carbon pools is receiving increasing global attention [1] due to their contribution to the mitigation of planetary climate change through increasing the sinking of carbon dioxide [2]. However, in the current scenario of worsening environmental catastrophes resulting from global change, society has been calling for faster solutions. In response, the best way to manage ecosystems to enhance biodiversity and carbon sequestration, given the intensification of human activities, has become a key topic of investigation [3]. Nature-based solutions, recognized for their effectiveness at addressing global change [4], involve the

appropriate use of nature to generate multiple benefits for society, including biodiversity conservation and climate change mitigation [5].

In general, it is well known that biodiversity can act as a driver of natural forest productivity, enhancing ecosystems functioning [6, 7, 8]. Because productivity and biomass production are positively correlated in forest ecosystems, this biological relationship can also apply to the standing biomass [9] and carbon storage [10]. One of the hypotheses that explains the positive relationship between diversity and biomass is niche complementarity. This concept suggests that species with distinct functional traits use available resources differently, thereby enhancing the net productivity of the ecosystem [11, 12]. On a pantropical scale, biodiversity has a positive effect on carbon storage in temperate and tropical forests along a broad diversity gradient [9, 10, 13]. The biodiversity–carbon relationship is considered a win–win situation in conservation programs because it provides the co-benefits of maximizing biodiversity protection simultaneously with carbon capture [14], making it a key nature-based climate solution [4].

The subtropical mixed forest––also known as Araucaria forest––is a typical southern Brazilian forest type mainly characterized by the presence of the critically endangered conifer *Araucaria angustifolia* (Bertol.) Kuntze co-occurring with other broadleaf species [15, 16]. Due to their ecological, economic, and cultural importance, domesticated landscapes marked by *Araucaria* abundances were created by the activities of pre-Columbian societies, and this influence persists to this day [17, 18, 19]. Currently, Araucaria forests represent an exceptional carbon sink compared to the surrounding forest types, mainly because they contain massive conifers [20]. Niche complementarity can explain the role of Araucaria forests as extensive carbon pools [12]. Conifer and broadleaf species, which have distinct functional traits, cohabit and exploit available resources in different ways [21], increasing the biomass produced in such ecosystems [11]. Therefore, Araucaria forests are becoming a conservation priority due to their high capacity to store carbon [14]. However, negative human impacts have resulted in a loss of diversity and decreased carbon stocks in these forests [22], potentially compromising their role in mitigating the effects of climate change.

Although the diversity–biomass relationship is common in several Brazilian forest types [23, 24, 25], it is less evident in subtropical forests [26], and especially mixed forests, likely due to the dominance of *A. angustifolia* in all successional stages [27]. In addition, the carbon storage capacity and its correlation with biodiversity in subtropical Brazilian Atlantic Forests is information necessary to future conservation efforts that remains poorly understood [14]. Understanding the drivers of variations in the aboveground biomass (AGB) can contribute to the development of management strategies for helping to mitigate climate change by means of enhanced carbon storage [24]. Consequently, in this study, we aimed to evaluate and compare the effects of *A. angustifolia* populations, stand structure and species diversity on shaping the carbon stock in subtropical mixed forests in southern Brazil. We hypothesized that the effects of stand structure and diversity would be mediated by *A. angustifolia* populations because the ecosystems-functioning–diversity relationship can be affected by biomass-dominant species favored by selective successional processes [11]. We also addressed the expectation of higher carbon stocks in protected forests resulting from a positive relationship with biodiversity conservation [e.g., 23].

Material and methods

Study areas

The study was carried out at two sampling sites in the subtropical Atlantic mixed forest in Paraná State, southern Brazil––one site under protected status (national forest), located in Irati city, and the other in an urban forest in Curitiba city (Fig. 1). Both sampling sites were classed as temperate oceanic with cold summers (*Cfb*), with average temperatures of 15 to 17°C and annual rainfall of 1,400 to 1,600 mm [28]. We used inventory data collected from 25 ha of the protected forest in 2017 and from 12 ha of the urban forest in 2015. At both sites, all trees with diameters ≥ 10 cm at 1.3 m above the ground (DBH) were measured in continuous plots of 1 ha each (i.e., 25 and 12 plots, respectively). Detailed information about the sampled sites and the data collection is available in [29] and [30].

Database

To estimate the aboveground carbon (AGC) stock, we initially predicted the AGB at tree-level using the pantropical allometric equation [31]. We obtained the wood specific gravity for each species from data repositories [32] to apply to the pantropical equation. Then, the plot-level AGB was computed, and multiplied by a conversion factor of 0.5 to estimate the AGC stock. At the plot-level, we quantified the relative *A. angustifolia* coverage (AC) in terms of basal area (BA) and *A. angustifolia* diameter structure (AS), as well as the BA and maximum diameter (Dmax) of the stand structure. We also assessed the Shannon diversity index (H') and species richness (S). The shape parameter of the two-parameter Weibull function was computed in order to describe the structure of the *A. angustifolia*. In summary, values close to 1 indicated young populations with more small trees, while values greater than 3.6 denoted old populations with a predominance of larger trees [33]. The Weibull function was calibrated using the maximum likelihood method in the *fitdistrplus* package [34]. The goodness-of-fit was assessed using the Kolmogorov–Smirnov test ($P \leq 0.05$) by comparing the observed and fitted distributions.

Data analysis

Our first objective was to evaluate the effects of *A. angustifolia* populations, stand structure and species diversity on shaping the carbon stock. We computed the Pearson's correlation coefficients (r) in order to examine the relationships between the carbon stock and stand-level predictors (at the 0.05 level), as well as potential multicollinear predictors. The Shapiro–Wilk test was performed to assess the normal distribution for the AGC stock variable. Then, we used regression analysis to examine the bivariate relationships between the AGC stock and individual predictors. Generalized least squares (GLS) models were used to quantify the non-equivalent variances among the sampling sites, including a variance component for each site. The GLS models were fitted using the *varIdent* function in the *nlme* package [35]. We used Akaike's information criterion (AIC), the coefficient of determination (R^2), and the significance of slope coefficients (t-statistics) to examine the goodness-of-fit and identify the potential individual predictors for the AGC. We used the Shapiro–Wilk test for the normality assumption of errors and Levene's test for the homogeneity of variances, both at the 0.05 level.

The effect size was assessed by including all standardized predictors in a full model in order to test their effects on the AGC. We used a model-averaging approach to estimate the coefficients; those predictors with multicollinearity, identified by Pearson's correlation ($r > 0.7$), were excluded. We used the *eta_squared* measure from the *sjstats* package [36] to measure the size effect of the predictors. Then, the predictors' importance was assessed by comparing the standardized coefficients. For the second objective, we tested the hypothesized mediation effects of *A. angustifolia* on the AGC through stand structure and species diversity (Fig. 2).

Structural equation modeling (SEM) was used to examined the direct and indirect effects of *A. angustifolia* population, stand structure, and species diversity in shaping the AGC, based on the conceptual model illustrated in Fig. 2. To assess the mediating effects of *A. angustifolia* populations, we evaluated two paths in the SEM as exogenous variables: 1) using stand structure (BA and Dmax) and 2) using species diversity (H' and S). To test our hypothesis using SEM, we evaluated how the *A. angustifolia* populations (AC and AS) could co-determine the stand structure (Path 1), diversity (Path 2), and AGC (endogenous variable). Thus, we examined the combined effects of *A. angustifolia* population, stand structure, and species diversity on the AGC. All paths in the SEM were assessed using linear regression and correlation analysis. The SEM models were fitted using the *lavaan* package [37], in which the path diagrams were built based on the results provided by the *semPlot* package [38]. The goodness-of-fit was evaluated using the mean of the chi-squared test, *P*-value of SEMabove 0.05 [39], AIC, and coefficient of determination (R^2).

Our final objective was to evaluate the expectation of protected forests being drivers of AGC, with one-way analysis of variance (ANOVA) used to test differences ($P \leq 0.05$) in the AGC and stand characteristics (AC, AS, BA, Dmax, H', and S) between the protected and urban forests. We used the Shapiro–Wilk test for normality and Levene's test for homogeneity of the variances in order to verify the statistical assumptions. Log transformation was applied when an assumption was not achieved. Protection status was also analyzed as a factor in evaluating the bivariate relationships between AGC and stand-level predictors. Principal component analysis (PCA) was applied, using the *factoextra* package [40], to assess the ordination between the drivers of the AGC stocks by sampling site. All statistical analyses were performed in R version 4.1.2 [41].

Results

Evaluation of aboveground carbon drivers

The AGC showed a strong correlation only with BA and a moderate correlation with Dmax and AS (Table 1). Among the predictors, a strong correlation was observed only for H' and S (> 0.7). There was a significant negative effect of AS on AGC (Fig. 3b), whereas BA and Dmax demonstrated a significant positive effect (Figs. 3c and d). Consequently, stocked forests, characterized by the presence of large trees and more abundant and balanced *A. angustifolia* populations, had larger AGC stocks. However, non-

significant changes were observed in the AGC with variations in AC, H', and S (Figs. 3a, e, and f). Therefore, diversity and richness did not directly influence the AGC stock.

Table 1
Pearson's correlation between AGC and *A. angustifolia* population (AC, AS), species diversity (H', S), and stand structure (BA, Dmax)

Variable	AGC	AC	AS	BA	Dmax	H'	S
AGC	1						
AC	0.147	1					
AS	-0.546*	-0.152	1				
BA	0.812*	0.447*	-0.204	1			
Dmax	0.575*	0.178	-0.540*	0.287	1		
H'	0.026	-0.100	-0.128	-0.101	0.018	1	
S	0.010	-0.213	0.172	-0.006	-0.158	0.779*	1

*Significant correlation at the 0.05 level.

Combining all standardized non-collinear predictors into an average model (Fig. 4), BA, Dmax, AS, and AC were significant and supporting the role of *A. angustifolia* populations in shaping the AGC stock. The effect of taxonomic diversity was not significant. In the analysis, only H' was maintained in the model, due to its collinearity with S (Table 1) and its greater support in explaining the AGC (Fig. 3). Therefore, we found no evidence that diversity and richness positively influence the AGC stock. Ultimately, in evaluating the individual and joint effects of the predictors, it was verified that stand structure, followed by *A. angustifolia* population, played the most important role in shaping the AGC stock.

Exploring the hypothesized effects of Araucaria angustifolia

The SEM paths indicated that the AGC was most driven by the direct and indirect effects of stand structure and *A. angustifolia* population (Fig. 5). The SEM for stand structure (Fig. 5a) explained the AGC variation best (R^2 = 0.91, AIC = 504) and was the only accepted model, with a SEM *P*-value greater than 0.05 (P = 0.26). By contrast, the SEM for species diversity (Fig. 5b) had a non-significant overall effect (P < 0.05). The selected SEM explained 91% of the AGC, 30% of the Dmax, and 22% of the BA. The SEM fit results partially confirmed our hypothesis. Although *A. angustifolia* population had a direct effect on the AGC and indirect mediating effects through the stand structure, the indirect effect was not supported for species diversity. The selected SEM (Fig. 5a) also revealed that greater AC resulted in stands with high BAs, while unbalanced *A. angustifolia* populations (greater AS) induced smaller maximum sizes (Dmax).

Assessment of protection status as an aboveground carbon driver

The AGC stock was significantly higher in the protected area (Table 2), in agreement with our expectation. Likewise, this area maintained more abundant and balanced *A. angustifolia* populations (Fig. 3b) and larger trees (Fig. 3d). However, the H' and S did not differ between the protected and unprotected areas. The ordination of the variables by site (Fig. 6) revealed a positive relationship between AGC and Dmax, BA, and AC (Fig. 6a) in the protected area, while there was a positive relationship with BA and a negative relationship with AS in the urban forest (Fig. 6b). The H' and S were not related to the AGC in the study areas, our expectation being partially met. While the AGC was greater in the protected area, this was not related to diversity, but rather to the presence of larger trees, more-stocked stands, and a greater abundance of *A. angustifolia*.

Table 2
Mean values (± standard deviations) for the AGC stock and stand-level predictors between the protected and urban forests

Variable	Protected	Urban	Total
AGC ($Mg.ha^{-1}$)	105.0 ± 9.7^a	95.8 ± 8.6^b	101.9 ± 9.8
AC	0.27 ± 0.07^a	0.25 ± 0.06^a	0.26 ± 0.06
AS	2.57 ± 0.49^b	5.44 ± 0.81^a	5.53 ± 1.44
BA ($m^2.ha^{-1}$)	32.2 ± 2.81^a	31.9 ± 2.98^a	32.1 ± 2.86
Dmax (cm)	100.8 ± 17.2^a	85.3 ± 3.78^b	95.6 ± 13.9
H'	3.35 ± 0.16^a	3.38 ± 0.16^a	3.36 ± 0.16
S	61 ± 5.27^b	66 ± 4.83^a	63 ± 5.36

Values with the same letter were statistically similar in the ANOVA at the 0.05 level.

Discussion

Our findings have provided new insights into the subtropical Brazilian Atlantic Forest, where, unlike other Brazilian forest types, diversity was determined not to be a significant driver in shaping the carbon stock. In subtropical Atlantic mixed forests, *A. angustifolia* plays a more important role than diversity, exerting a positive effect on the stand structure and, consequently, on the carbon stock. Therefore, in the context of global climate change, conservation plans should not only prioritize the maximization of biodiversity protection, but also the enhancement of carbon storage processes [14], considering *A. angustifolia* populations as drivers of carbon stocks [42], including in grasslands and human-modified landscapes where this species dominates [18]. Maintaining *A. angustifolia* in the landscape could be used as a regional nature-based climate solution. In addition to storing a large amount of carbon in old, large, and growing trees, *A. angustifolia* provides several keystone ecological and economic resources.

Assessing the relative importance of aboveground carbon drivers

Species richness and diversity showed strong relationships with AGB at small spatial scales (0.1 ha) because, in smaller areas, the presence of additional species have a significant impact on productivity and forest stock [9, 43]. Thus, our results support the hypotheses proposed by Poorter et al. (2015) and Chisholm et al. (2013), with the effect of diversity on AGC not being observed at larger spatial scales (1 ha). Also in agreement with these hypotheses, we observed strong relationships between AGC and stand structure (BA and Dmax) in the larger plots (1 ha). Additionally, we discovered that the relationship between AGC and *A. angustifolia* population (AS and AC) were also significant at larger spatial scales. Another perspective to consider is that the carbon–biodiversity relationship is conditioned by interactions between multiple stocks and trophic levels [13], including the more visible aboveground portions and primary producers in the forests [3]. The absence of evidence for a link between diversity and carbon might be due to the limitation of our database, which focused only on the aboveground stock and the tree component. Furthermore, the effect of diversity on the AGB is highly dependent on the land-use history [24].

A strong relationship between BA and AGC was expected, since stand basal area is strongly correlated with forest coverage, mean tree size, and tree diameter—the main predictors of carbon stock estimates [9, 44]. Similarly, tree Dmax indicated the effects of large trees, which are an important driver of forest structures and contribute the largest amounts of carbon in forest ecosystems [45, 46, 47, 48]. Also, the positive influence of large trees on AGC has been recognized in subtropical forest types across a wide geographical gradient in southern Brazil [26]. However, our results showed a significant influence of the coverage (AC) and structure (AS) of *A. angustifolia* in shaping the carbon stocks, which has not previously been investigated in Brazilian subtropical forests [42].

Our study had some limitations because ecosystem diversity, structural attributes, and processes can vary along environmental gradients [9]. First, in addition to stand characteristics, other unassessed factors may have influenced the carbon stocks, such as stand age, successional stage, functional and phylogenetic diversity, human disturbance level, land-use history, the surrounding landscape, climate, soil, and topographical aspects [20, 23, 24, 25, 49, 50]. Second, although our sampling area was large, we only investigated two sampling sites—one under protected status (national forest), the other not protected (urban forest). This limitation restricted us in drawing general conclusions about the AGC in subtropical Brazilian mixed forests, since other protected (e.g., strict protected areas) and non-protected forests (e.g., forests in a rural matrix) may contribute differently to the conservation of diversity and the maintenance of carbon stocks [24, 51, 52]. Despite these limitations, our results agree with the findings from other large-scale studies of Brazilian subtropical forests, where (taxonomic, functional, and phylogenetic) diversity was determined as not being significantly related to net carbon changes [14] or carbon stocks [26, 27].

Assessing the direct and indirect effects of Araucaria angustifolia on aboveground carbon

New insights into the absence of a positive relationship between diversity and AGC in subtropical Atlantic Forests [14, 26] and the effect of *A. angustifolia* populations on shaping the carbon stock in Atlantic mixed forests [42] were revealed by our SEM analysis. We found that the species drove stand structure, with abundant populations leading to denser stands and balanced populations to presence of larger trees, both of which resulted in high carbon stocks. These positive effects can be explained by the importance of *A. angustifolia* at the sample sites [29, 30] and its greater accumulation of biomass compared to the co-occurring angiosperms [21]. The absence of evidence for any effects of taxonomic diversity or richness may be related to an ecological filter created by forests with *A. angustifolia* dominated, where only shade-tolerant species can then become established [42, 53]. Therefore, the idea that the most abundant species determines the ecosystem processes, such as biomass production [11], was supported by our findings. In addition, the positive effects of *A. angustifolia* on AGC reveals the role of protected forests, in which abundant and balanced populations are maintained, including large trees that accumulate greater amounts of carbon.

Positive influence of forest protection status on aboveground carbon

Contrary to general expectations [23], the amount of AGC was not greater in the protected areas due to high taxonomic diversity because the H' and S were similar at both sites. This similarity between protected and non-protected areas is a paradox for the conservation of subtropical forests in southern Brazil [54]. However, our results agree with the understanding that one of the essential roles of mature and old-growth subtropical forests lies in maintaining high carbon stocks by supporting large trees [26]. Therefore, protection possibly provides this maintenance function in Araucaria forests by mainly supporting large and abundant *A. angustifolia* trees, which results in stocked stands with high coverage. Maintaining large trees not only ensures higher carbon stocks, but it also conserves a variety of trophic levels [26], especially in *A. angustifolia* trees where old-growth structures provide diverse habitats, such as basal cavities, reiterated trunks, and thick bark [55, 56]. In addition, in mature Araucaria forests, high increases in biomass accumulation are driven by forest growth associated with anthropogenic and natural disturbances [20]. This ensures continuously high levels of carbon sequestration. Furthermore, protecting areas hosting *A. angustifolia* is a paramount strategy for its long-term persistence and conservation [57].

General implications

Our results suggest that fully stocked forests with large trees produce higher AGC stocks, even when diversity is low. However, this may be unfavorable because strategies to maximize the short-term accumulation of carbon may not be as efficient as promoting the long-term growth of forests [2]. This should be a point of attention for forest and environmental managers aiming for long-term carbon-storage outcomes. In addition, forests with fewer species may have less capacity to sustain their productivity in the face of global environmental change [58], thus will likely be more susceptible to climate change [4]. Promoting the long-term regeneration of forests and conserving old growth may be particularly effective in reconciling multiple targets [13, 59]. Another concerning issue is the predicted

decrease in range of *A. angustifolia* due to climate change [60], which may limit its role as a nature-based climate solution, leading to several negative impacts on biodiversity and human well-being [57].

Although the win–win strategy between diversity conservation and carbon storage is not particular to Araucaria forests, we have highlighted the potential of such forests as a nature-based climate solution, maintaining high levels of stored carbon in tandem with providing keystone resources and ecosystem services. This could be a key component in reducing emissions from deforestation and forest degradation (i.e., REDD+), in addition to other forest-related activities as voluntary carbon market. In conclusion, the benefits of climate-oriented management must strike a balance between maximizing AGC and the requirements of biodiversity conservation [10, 13] and human well-being [61] in order to achieve multiple objectives simultaneously. However, conservation and restoration actions are now imperative if the long-term persistence of *A. angustifolia* in landscapes is to be ensured under current global change scenarios [57].

Conclusions

From comparing the direct and indirect effects of various predictors, we found that stand structure played the most important role in shaping carbon stocks. However, this effect was mediated by the structure and coverage of *A. angustifolia* populations. By contrast, taxonomic diversity was not influenced by *A. angustifolia* populations and did not affect the carbon stock. The protected status of one of the studied forests contributed to a higher carbon stock due to large trees being maintained, stands having high coverage, and the *A. angustifolia* populations being more abundant and balanced. Our findings agree with those of recent studies, in which diversity was determined not to be a significant driver of carbon stocks in subtropical Atlantic mixed forests, but underscores the value of Araucaria forests in mitigating climate change through their storing of large amount of carbon, jointly with provision of ecosystem and socio-economic services.

Declarations

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Author contribution

VCC conceptualization, formal analysis, investigation, methodology, writing - original draft; ALP supervision, writing - review & editing, data curation; AFF data curation, project administration. Both authors read and approved the final manuscript.

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Competing interests

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Figures

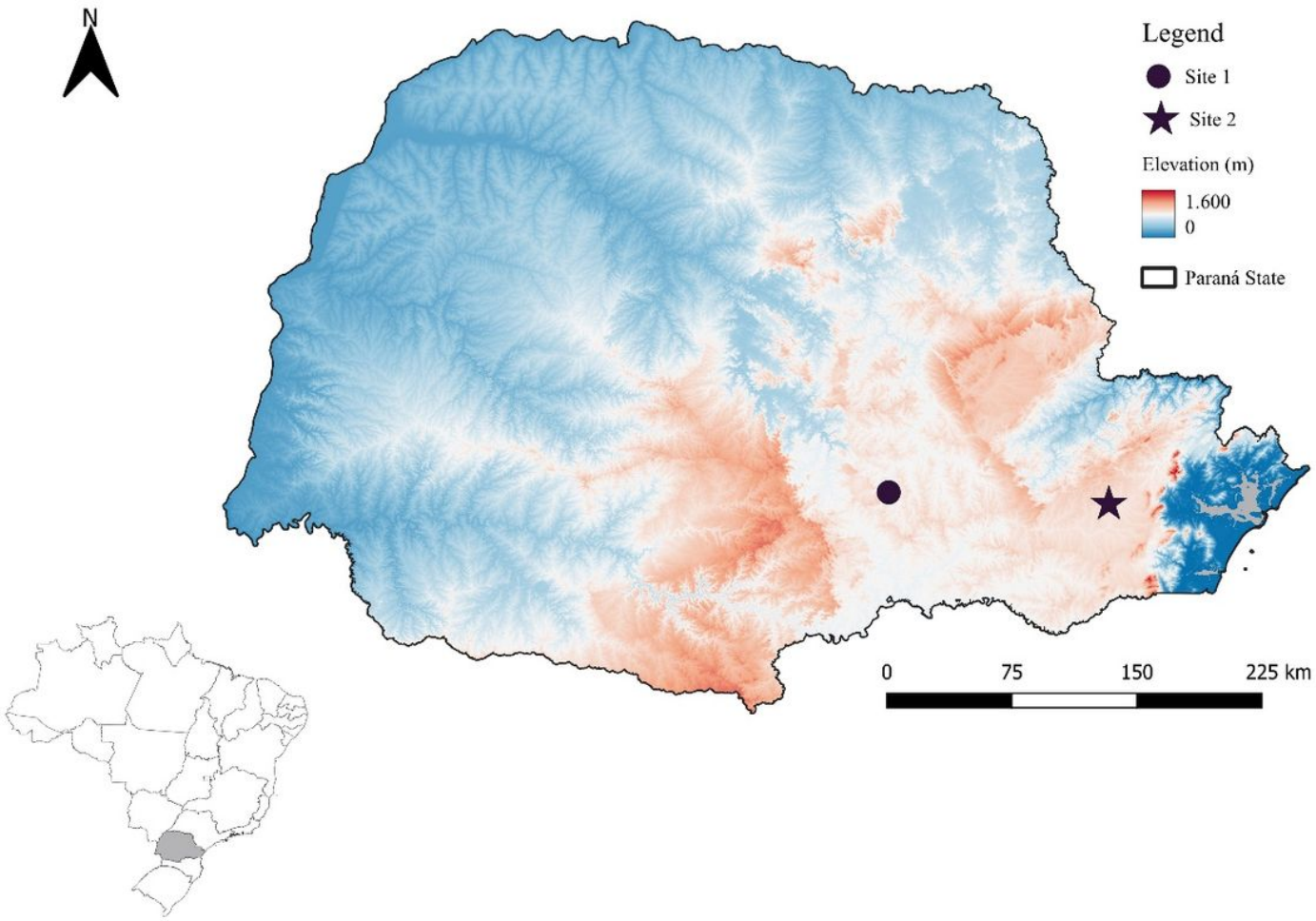

Figure 1

Study sites located in the subtropical Atlantic Forest in southern Brazil. Site 1––protected forest, Irati city; and Site 2––urban forest, Curitiba city

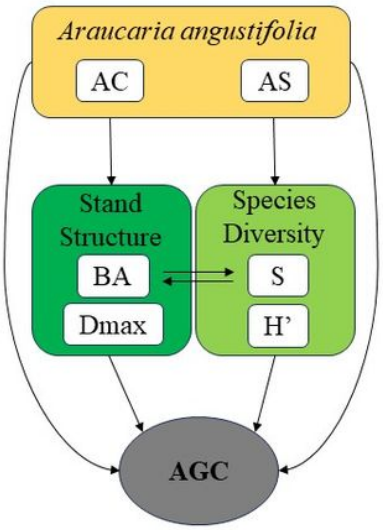

Figure 2

Conceptual model used for testing the hypothesized effects on the aboveground carbon (AGC) stock. AC––*A. angustifolia* coverage; AS––*A. angustifolia* structure; BA––(stand) basal area; Dmax––(stand) maximum diameter; H'––Shannon diversity index; and S––species richness

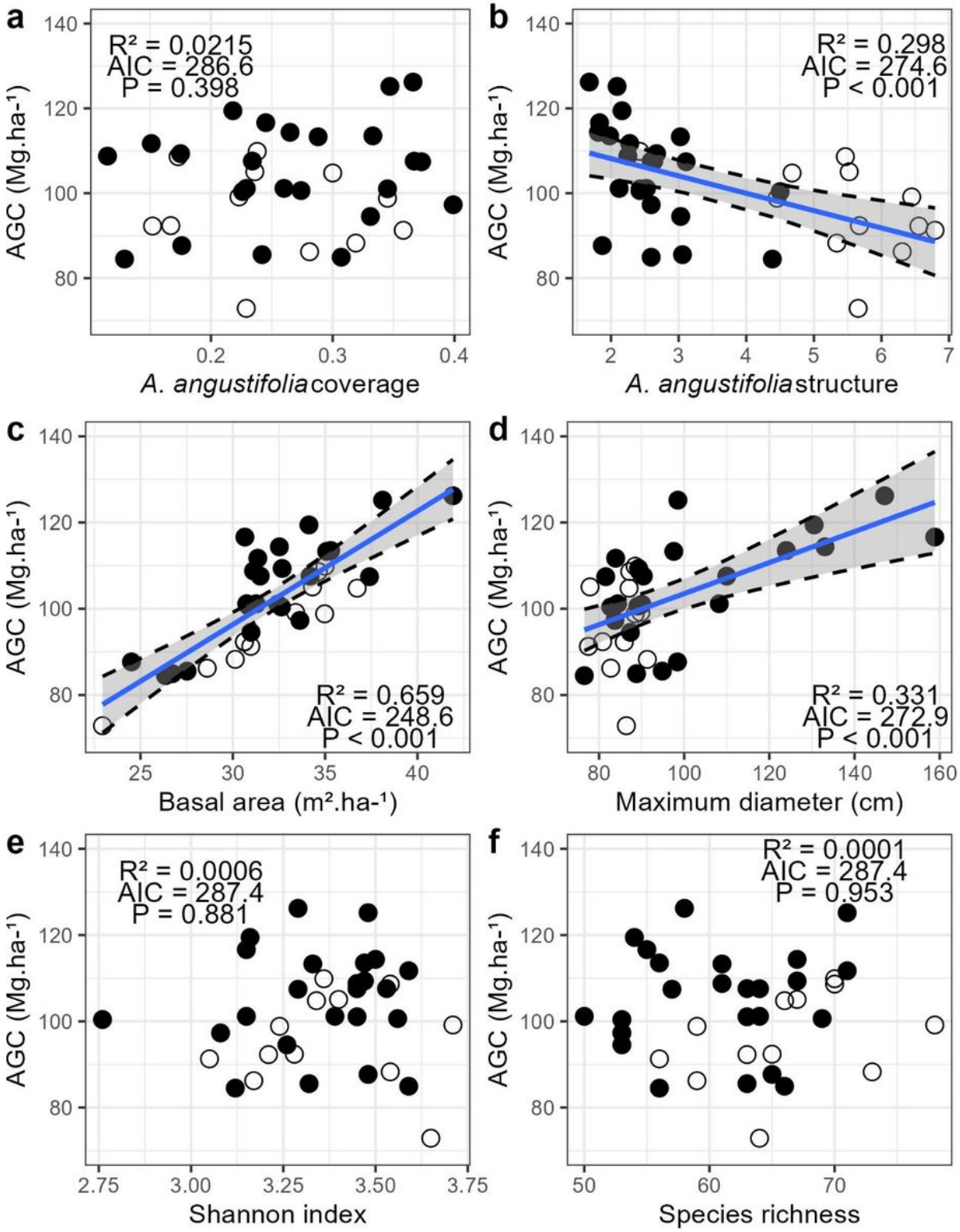

Figure 3

Bivariate relationships between aboveground carbon (AGC) stock and (a, b) *A. angustifolia* populations, (c, d) stand structure, and (e, f) species diversity in protected (empty circle) and urban (full circle) forests. Solid lines––significant effects; and shaded areas––95% confidence intervals

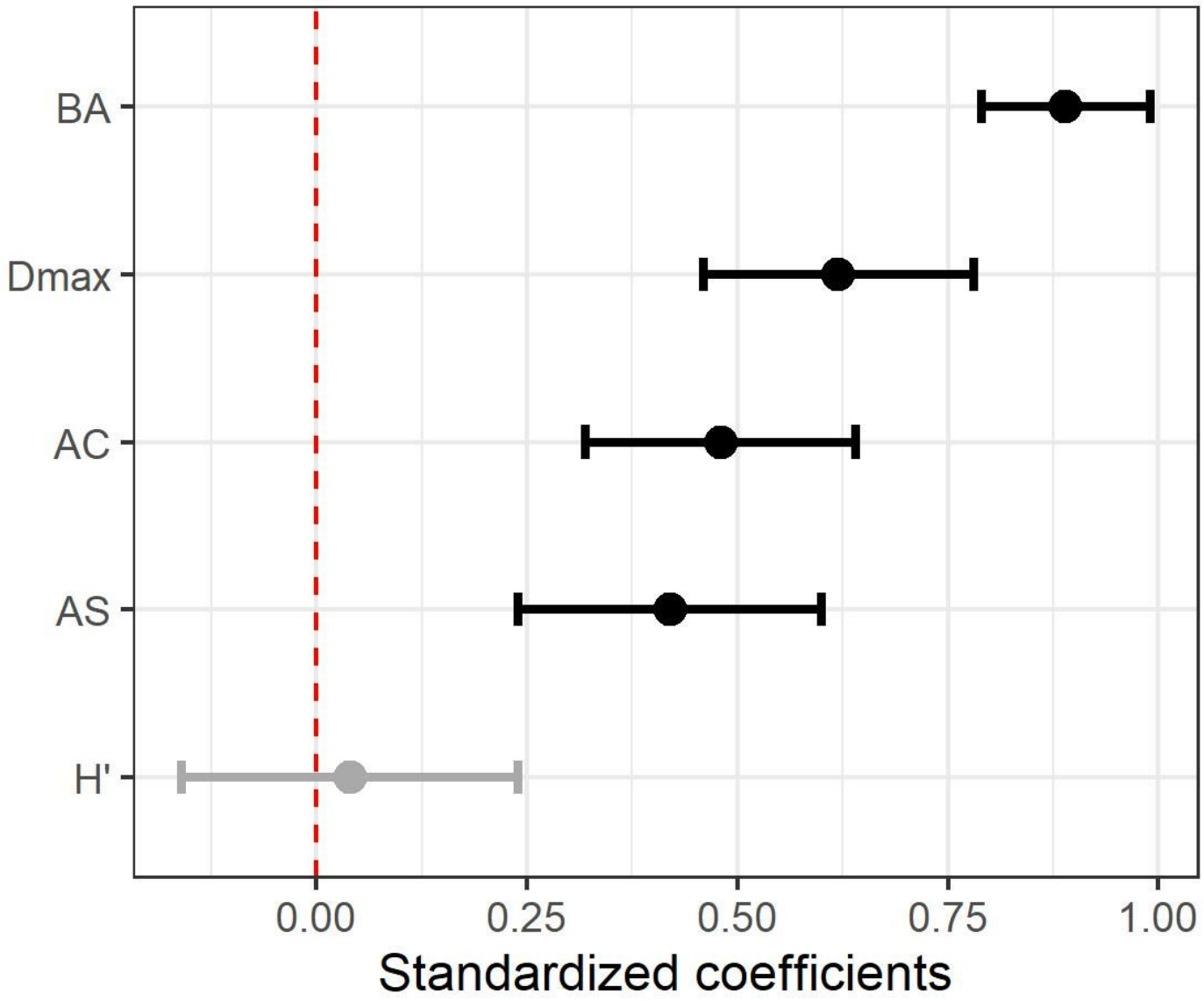

Figure 4

Standardized effect (± standard error) from predictors of the averaged model on the carbon stock. AC––*A. angustifolia* coverage; AS––*A. angustifolia* structure; BA––(stand) basal area; Dmax––(stand) maximum diameter; and H'––Shannon diversity index. Black lines––significant predictors at the 0.05 level; and gray lines––non-significant

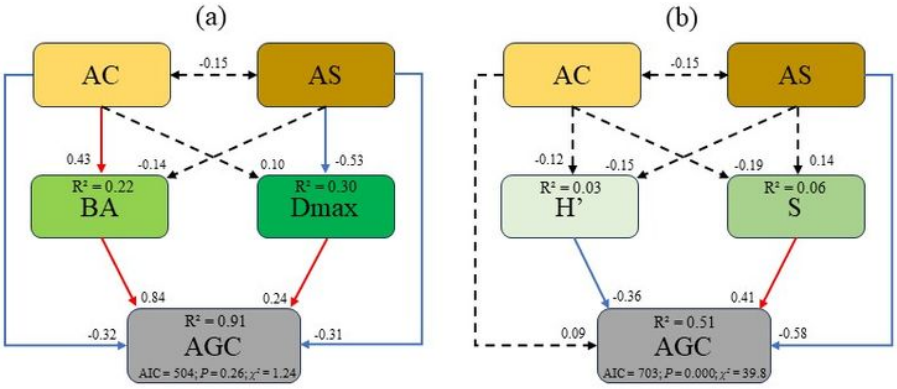

Figure 5

SEMs for testing the hypothesized mediation effects of *A. angustifolia* on (a) stand structure and (b) species diversity in shaping the aboveground carbon (AGC) stock. AC––*A. angustifolia*coverage; AS––*A. angustifolia* structure; BA––(stand) basal area; Dmax––(stand) maximum diameter; H'––Shannon diversity index; and S––species richness. Red solid arrows––significant (P ≤ 0.05) positive effects; blue solid arrows––significant (P ≤ 0.05) negative effect; and black dashed arrows––non-significant (P ≥ 0.05) effects

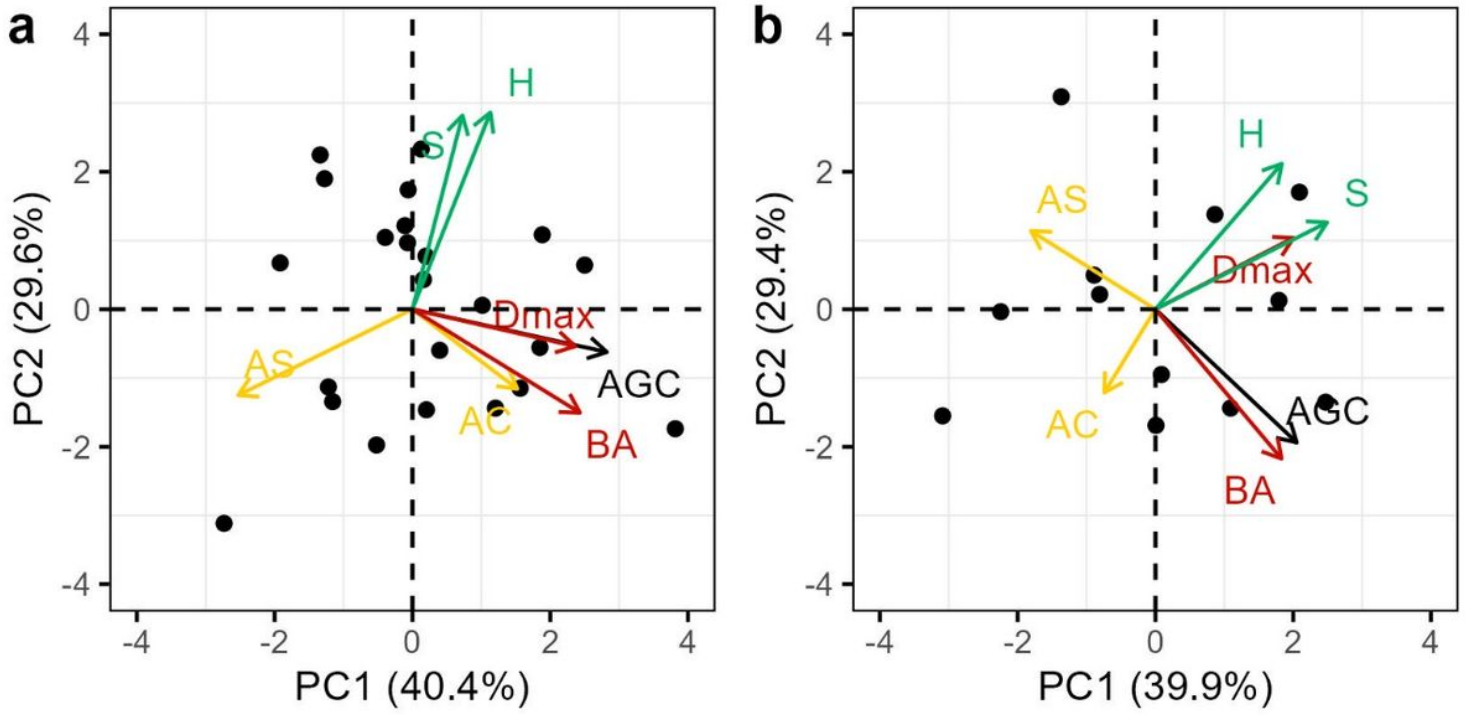

Figure 6

PCA summarizing the relationships between the AGC stock and stand-level predictors in the (a) protected and (b) urban forests. Black dots––sampling plots; colored arrows––types of variables (black––AGC; yellow––*A. angustifolia* populations [AC, AS]; red––stand structure [BA, Dmax]; and green––species diversity [H', S])