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Lurdes Silva (✉ lurdes.cb.silva@uac.pt)

CIBIO

Diogo Cláudio Pavão

CIBIO

Rui Bento Elias

CE3C

Mónica Moura

CIBIO

Maria Anunciação Ventura

CIBIO

Luis Silva

CIBIO

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Taxonomic, structural diversity and carbon stocks in a gradient of island forests

Lurdes B. Silva ^(1*), Diogo C. Pavão⁽¹⁾, Rui B. Elias⁽²⁾, Mónica Moura⁽¹⁾, Maria A. Ventura⁽¹⁾, Luís Silva⁽¹⁾.

⁽¹⁾ CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Pólo dos Açores, Universidade dos Açores, Rua da Mãe de Deus, Apartado 1422, 9501-801 Ponta Delgada, Açores, Portugal.

⁽²⁾ CE3C/ABG – Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group & University of the Azores, 9700-042 Angra do Heroísmo, Azores, Portugal.

*Corresponding author: (lurdes.cb.silva@uac.pt)

Abstract

Assessment of forest ecosystems and their services is seen as a key action for the advancement of biodiversity objectives, and to inform the development and implementation of related policies and planning. We assessed biodiversity, structure and carbon stocks in a gradient of three forest types (Natural Forest-NF; Exotic Woodland-EW and Production Forest-PF) in three of the Azores islands. We used biodiversity indices and found that NF harbored the highest plant biodiversity levels and PF the lowest. Diversity levels were lower for structural than for taxonomic data, particularly for PF. The highest tree carbon stock was found at EW in one of the islands, while PF consistently exhibited relatively high tree carbon stocks in the three islands. The largest soil carbon stocks were found at EW, while leaf litter carbon stocks were higher at PF. We concluded that NF play a fundamental role as biodiversity hotspots but have lower relevance as carbon stocks. PFs provide economic assets and act as carbon sinks, while EWs play a major role as carbon sinks in soil, but also at tree level in the oldest forests. A full quantification of forest value would also include ecosystem services such as water protection, recreation and aesthetic value.

Introduction

Forests provide a wide range of products and ecosystems services (FES) that are of vital importance to the functioning of the biosphere [1-3] and have become increasingly prominent on the international policy and scientific agenda, receiving attention from scientists in various fields of research and from policymakers [3-5].

Forests support biodiversity maintenance and conservation [6-8], and given the multitude of ecosystem services provided, it is difficult to generalize the overarching role of forests on biodiversity [6,9,10]. Nevertheless, the relationships between forest type, biodiversity conservation and ecosystem services are highly relevant for informing forest policy and management [1,6]. Meanwhile, there is considerable evidence that natural forests may harbor higher biodiversity levels (e.g., natural tropical forests could have between 70 and 300 or more tree species per hectare) than forest plantations (one or two tree species at planting) [11]. Hence the most important characteristics of the tropical and subtropical humid forests are their species richness, heterogeneity, and complex community organization [12,13]. Other research has shown that temperate forests are also biodiversity hotspots with high levels of endemism [5,14,15], being highly diverse in species, including soil organisms, playing a relevant role as carbon sinks [5,14], and providing important ecosystem services globally, regionally, and locally [15]. Recently, there has been much progress on the understanding of the effects of forest biodiversity on single and multiple ecosystem services, with the number of published reviews signaling that this is a very active field of research [6,9,10].

Forests have also an important role as carbon sinks [16] at both regional and global scales [17,18]. The carbon pools and fluxes in forest ecosystems are affected by many different factors, such as species diversity and identity, tree growth, understory

vegetation, leaching of dissolved organic matter, and organic matter decomposition rate [19-21]. According to several studies [22-24], not all forests have the same capacity to capture and store carbon. Madrigal-González et al. [25], sampling of natural forests on five continents, showed that forests located in cold or dry regions, and the abundance of trees, favours the recapture of CO₂. Kendie et al. [26], after comparing biomass and soil carbon stock potential between natural forests, *Eucalyptus* plantations and regenerated secondary forests, concluded that the carbon pool variation was significant, and that natural forests stored a higher amount of carbon, thus playing an important role in climate change mitigation. Others have shown that indigenous forests sequester more carbon in biomass and soil than did 30 to 50-year-old plantations of exotics, but it remains unclear if this was an intrinsic difference between both types or a difference resulting because of insufficient time for soil organic carbon levels in plantations to recover after the clearance of the original indigenous forest [27].

Productivity in terrestrial ecosystems is directly linked to nutrient cycling among the various components of the plant-soil system [28,29]. In forest ecosystems, primary production is usually evaluated through litter production because litter is the main source of soil organic carbon and plant nutrient cycling [30,31]. Litter production and decomposition in forests can vary with forest type, climate, and ecosystem disturbance (e.g., planted species showed a stronger influence on rates of decomposition and soil respiration than indigenous species) [29,31].

To improve our understanding of ecosystem processes and investigate relationships between biodiversity and ecosystem function, islands have been treated as ‘model systems’ [32]. A broad range of ecological studies have used island as models, (e.g., Mauritius, Krakatau, Hawaii, Galapagos, Madagascar, New Zealand, and

Australia), in order to better understand ecological and evolutionary processes [32,33]. Some results indicate that there is a significant relationship between island area and plant species composition [34]. This relationship was found to be a major factor in determining several ecosystem-level properties of these islands, including standing biomass, plant litter decomposition, nitrogen mineralization, terrestrial carbon partitioning, humus accumulation, and plant nitrogen acquisition [32,35].

The Azores archipelago is an interesting region to be used as a model in studies devoted to biodiversity pattern changes, associated with anthropogenic activity, and to the potential ecosystem services originated by different forest types. However, the knowledge of ecosystem services in the Azores is still quite limited and only a few studies have been published. Those studies showed that there is a considerable loss of biodiversity associated with the impact of anthropogenic disturbance across a landcover gradient of community types [36,37]. To quantify forest carbon sequestration in the Azores Islands, some studies have estimated the total carbon stocks for exotic species (e.g., *Cryptomeria japonica*, *Pittosporum undulatum*) [38,39]. A remote assessment of changes in carbon storage on Pico Island (Azores, Portugal), indicated that an increase in carbon stocks (economical value) while protecting biodiversity (environmental value), is possible through adapted and synergic management actions [39]. Other research showed that a considerable amount of woody biomass is available in the Azores islands and private companies are devoting their interest to using this type of forest residues [40-42]. For native forests, studies showed that carbon sequestration was related to productivity and biodiversity [43]. Others quantified socioeconomic benefits from natural forests and demonstrated that nature conservation and biodiversity areas can drastically improve

quality of life and economic self-sufficiency of local populations by the diversification and creation of new skills, products and business opportunities [44,45].

Nevertheless, a comparison of taxonomic diversity values, structural diversity, and carbon accumulation, based on a detailed collection of field data, and addressing the three main forest types in the Azores – production forest (PF), exotic woodland (EW), and natural forest (NF) - has not been attempted. Therefore, the main goal of this research was to determine the ecosystem services presently associated with the forest areas in the Azores, with particular attention to biodiversity and carbon stocks. Based on previous research dedicated to each forest type, we hypothesized that: i) the highest levels of taxonomic diversity would be found in natural forest stands; ii) the diversity levels would be lower for structural than for taxonomic data; iii) tree carbon stocks would be larger in production forests; iv) leaf litter and soil carbon stocks would be larger in natural forests which are less disturbed; and v) larger differences would be found between forest types than between islands. Thus, our specific objectives for the three main forest types were: i) to evaluate the taxonomic diversity; ii) to evaluate the structural diversity using a dendrometric approach; iii) to evaluate the carbon stocks in standing biomass using allometric equations; and iv) to evaluate the carbon stocks in leaf litter and soil using chemical analyses.

Although this study focused on a single region, findings can be used as a model for other forests, regions and small islands given commonalities in size, natural resources, and ecosystems [32,33].

Results

Taxonomic diversity. Globally, the three forest types in São Miguel showed the largest number of taxa, although with the largest proportion of exotic elements, while the forest in Pico showed the highest contribution of endemic and native taxa (Table 1).

For α diversity there was only a significant effect of forest type ($F=152.09$; $p<0.01$), NF differing from EW and PF (Table 2). For the percentage of α diversity, there was no significant effect of island ($F=1.31$, $p=0.28$) and forest type, ($F=4.12$; $p=0.02$) (Table 2). Regarding β diversity, there was a significant effect of island ($F=8.48$; $p<0.01$) and forest type ($F=51.90$; $p<0.01$), with the largest values at NF, particularly in Pico and São Miguel, and with a relatively high value at the EW in São Miguel (Table 2). For the percentage of β diversity no significant differences were found for island ($F=1.31$; $p=0.28$) and forest type ($F=4.12$, $p=0.02$) (Table 2). There was a significant effect of island ($F=5.88$; $p<0.01$) and forest type ($F=151.55$; $p<0.01$) on γ diversity, with the highest values at NF (Table 2). Again, there was a significant effect of island ($F=7.71$; $p<0.01$) and forest type ($F=146.50$; $p<0.01$) on Shannon diversity with the highest values in NF (Table 2). In terms of evenness, there was a significant effect of forest type ($F=42.30$; $p<0.01$), but not of island ($F=1.57$; $p=0.21$), NF showing the highest levels, followed by EW (Table 2).

Concerning hierarchical diversity partitioning, α_1 diversity represented about 9% of the total species diversity, α_2 13%, and α_3 55% (Table 3). According to β diversity results, differentiation among plots within the same forest was relatively low (β_1), while there was an important component of differentiation among forests within the same type (β_2) and among forest types (β_3) (Table 3).

Forest clusters. Based on the value of cophenetic correlation, the best combination of distance metric and agglomeration algorithm corresponded to Hellinger Distance and UPGMA. The NMDS resulting from the projection of Hellinger distances showed the 90 forests assembled into three groups (Fig. 1), each associated with different dominant species: EW - *P. undulatum* and *A. melanoxylon*; PF – *C. japonica* and *H. macrophylla*; NF - *L. azorica*, *I. azorica* and *J. brevifolia*.

Table 1. Species richness at the three types of forests sampled on three islands in the Azores archipelago. Endemic taxa only occurring in the Azores; Native taxa that colonized the Azores without human intervention, also occurring in other regions; and Exotic taxa that were intentionally or accidentally introduced by human activities [46].

Island	Taxa						Total
	Endemic		Native		Exotic		
	N	%	N	%	N	%	
São Miguel	24	30	24	30	32	40	74
Terceira	20	41	17	35	12	24	45
Pico	30	44	26	38	12	18	62

Table 2. Taxonomic diversity found at 90 forests in the Azores, from three islands (Pico, São Miguel, and Terceira) and three forest types (Exotic Woodland, Natural Forest, and Production Forest). Alpha, beta and gamma diversities, Shannon diversity (H) and evenness (E). Mean and standard error for each diversity parameter. For each row, different letters indicate significant differences ($p < 0.05$) according to the results of a Tukey test applied after ANOVA.

Diversity		Exotic Woodland						Natural Forest						Production Forest					
		Pico		São Miguel		Terceira		Pico		São Miguel		Terceira		Pico		São Miguel		Terceira	
α	m	4.78	a	7.08	a	3.83	a	20.58	b	16.78	b	16.3	b	4.2	a	5.68	a	3.43	a
	se	0.54		0.75		0.28		1.23		2.55		0.57		0.49		0.69		0.38	
α (%)	m	0.73	a	0.63	a	0.72	a	0.75	a	0.71	a	0.77	a	0.66	a	0.68	a	0.65	a
	se	0.03		0.03		0.03		0.01		0.03		0.01		0.04		0.05		0.05	
β	m	1.83	a	4.23	bcd	1.58	a	6.93	e	6.43	de	4.90	cde	2.20	ab	3.13	abc	2.38	ab
	se	0.32		0.55		0.26		0.31		0.88		0.22		0.33		0.63		0.52	
β (%)	m	0.27	a	0.37	a	0.28	a	0.25	a	0.29	a	0.23	a	0.34	a	0.32	a	0.35	a
	se	0.03		0.03		0.03		0.01		0.03		0.01		0.04		0.05		0.05	
γ	m	6.60	a	11.3	a	5.40	a	27.5	c	23.2	bc	21.2	b	6.40	a	8.80	a	5.80	a
	se	0.78		1.15		0.43		1.36		3.06		0.53		0.73		1.22		0.85	
H	m	1.50	abc	1.91	c	1.30	ab	2.99	d	2.75	d	2.77	d	1.25	ab	1.60	bc	1.07	a
	se	0.12		0.12		0.08		0.05		0.18		0.03		0.12		0.16		0.12	
E	m	0.81	cd	0.80	bcd	0.79	abc	0.91	d	0.90	d	0.91	d	0.68	ab	0.78	abc	0.68	a
	se	0.03		0.02		0.03		0.00		0.01		0.00		0.03		0.03		0.04	

Table 3. Partitioning of diversity, according to the hierarchical model of additive partitioning. Partition of γ diversity into its α and β components at three spatial scales i) among plots within the same forest; ii) among forests within the same type; and iii) among forest types.

Diversity	α_1	α_2	α_3	β_1	β_2	β_3	γ
Value	10.18	13.91	59.00	3.73	45.08	49.00	108.00
%	9.43			3.45	41.74	45.37	100.00
%		12.88			41.74	45.37	100.00
%			54.63			45.37	100.00

The PERMANOVA confirmed that forest type explained the largest proportion (64%) of the variation while island explained only 2%. The indicator species analysis also confirmed the expected differences between forests (see Supplementary Table S1 online): NF - 17 species with significant indicator value; EW and PF only 2 and 1 indicator species, respectively. *Vaccinium cylindraceum* (95%), *M. africana* (95%) and *I. azorica* (93%) showed the highest indVals for NF. In addition, several indigenous species were present in NF, including trees/shrubs and ferns. The IndVals for *Pittosporum undulatum* (92%) and *Cryptomeria japonica* (99%) were the highest, respectively for EW and PF.

Environment, soil, and leaf litter parameters. There was a significant difference between forest types regarding altitude ($F=68.15$; $p<0.01$), with a tendency for EW being located at lower elevations and NF at the highest (Table 4). There was a significant difference between islands and forest types for mean temperature (TMEA; $F=11.00$, $p<0.01$; $F=59.40$, $p<0.01$), mean relative humidity (RHMEA; $F=10.95$, $p<0.01$; $F=53.72$, $p<0.01$) and mean precipitation (PMEA; $F=8.22$, $p<0.01$; $F=31.18$, $p<0.01$). Lowest temperatures were found at NF, followed by PF (Table 4). Regarding relative humidity and precipitation, this pattern was reversed (Table 4).

Figure 1. Non-Metric Multidimensional Scaling applied to the Hellinger distance matrix, based on species abundances, and applied to all forest types. The three colors represent the three community types obtained by using numerical ecology methods (represented by 1-Natural Forest; 2-Exotic Woodland; 3-Production Forest).

Concerning soil parameters, significant differences between islands and forest types are reported on Table 5. Bulk density was lower in Pico while OM and total N tended to be high in that island (Table 6). The values of pH tended to be the lowest at NF, while Ca, Mg and Na values appeared to be larger in Pico and at EW, the values of P, K and Al appeared to be somewhat irregular (Table 6).

Soil texture was dominated mostly by loam and sandy soils and our results showed that there were no differences between forest types (see Supplementary Fig. S1 online). However, differences were obtained between Pico, where forest soils were mostly composed of basaltic rock and sandy loam, and the other two islands.

Table 4. Environmental variables found at 90 forests in the Azores, from three islands (Pico, São Miguel, and Terceira) and three forest types (Exotic Woodland, Natural Forest, and Production Forest). Mean and standard error for each environmental parameter. For each row, different letters indicate significant differences ($p < 0.05$) according to the results of a Tukey test applied after ANOVA.

		Exotic Woodland			Natural Forest			Production Forest		
		Pico	São Miguel	Terceira	Pico	São Miguel	Terceira	Pico	São Miguel	Terceira
ALT	m	272.40 a	349.80 ab	202.20 a	683.80 de	616.20 cde	711.10 e	491.70 bc	538.30 cde	507.90 bcd
(m)	se	13.69	44,57	37,55	57,72	33.16	33.47	47.88	55.04	35.41
TMEA	m	16.70 d	15.20 bc	16.50 cd	13.80 ab	13.10 a	13.00 a	15.10 bc	13.60 a	14.30 ab
(°C)	se	0.26	0.29	0.37	0.39	0.28	0.21	0.38	0.43	0.21
PMEA	m	2059.10 abc	1644.80 ab	1254.50 a	3117.10 d	2616.50 cd	2695.40 cd	2732.70 cd	2349.50 bcd	2208.60 bc
(mm)	se	214.10	159.71	82.69	267.50	158.86	135.31	249.07	179.77	116.26
RHMEA	m	87.70 a	91.80 b	90.00 ab	95.40 cd	95.80 cd	97.90 d	92.40 bc	95.50 cd	95.80 cd
(%)	se	1.11	0.66	0.94	0.79	0.57	0.31	1.06	0.95	0.33

Table 5. Comparison of soil properties at 90 forests in the Azores, from three islands (Pico, São Miguel, and Terceira) and three forest types (Exotic Woodland, Natural Forest, and Production Forest). Results of a two-way ANOVA. Bold indicates a significant effect ($p < 0.05$).

Parameter	Type		Island		Interaction	
	F	p	F	p	F	p
pH	17.427	0.000	13.213	0.000	1.282	0.284
P ER	6.432	0.003	5.860	0.004	1.805	0.135
K ER	5.301	0.007	14.806	0.000	0.170	0.953
P O	4.503	0.014	5.804	0.004	1.969	0.107
Ca ²⁺	7.153	0.001	10.333	0.000	2.897	0.027
Mg ²⁺	4.036	0.021	12.986	0.000	4.380	0.003
K ⁺	5.065	0.008	2.207	0.117	1.291	0.280
Na ⁺	0.559	0.574	37.686	0.000	1.051	0.386
Al+ H3O ⁺	9.563	0.000	17.006	0.000	2.682	0.037
Electrical conductivity	2.787	0.068	26.357	0.000	4.258	0.004
N total	1.269	0.287	56.308	0.000	1.833	0.131
Coarse sand	1.768	0.177	116.021	0.000	3.304	0.015
Fine sand	7.639	0.001	47.159	0.000	1.466	0.220
Silt	3.519	0.034	135.901	0.000	1.765	0.144
Clay	4.558	0.013	15.642	0.000	6.416	0.000

Concerning leaf litter parameters, significant differences between islands and forest types are reported on Table 7. In general, N values were lowest at PF, K values were highest at EW, Ca, Mg, S values were somewhat irregular, B and Fe values were largest in EW while Zn, Mn and Cu values tended to be lower at PF (Table 8).

Structural diversity. Regarding structural diversity, significant differences between islands and forest types are reported on Table 9. EW tended to show the highest tree density, while PF showed the lowest (Table 10). In general, PF showed the highest basal areas per hectare (Table 10), except for some stands of EW in São Miguel Island. The number of taxa contributing to *BA* (*BA* γ) was much larger at NF, followed by EW (Table

10). Likewise, structural diversity indices for *BA* (*BA H*, *BA E*) were significantly higher in NF, and lowest at PF (Table 10). PF showed the highest average tree heights (Table 10). Mean *AGB* was highest for EW stands in São Miguel Island and lowest for NF. However, PF showed, consistently and for all islands, high values of *AGB* (Table 10).

Carbon stock in the trees. Total carbon storage in the trees (*AGB* and *BGB*) was significantly different between forest types ($F=7.559$, $p<0.01$) and between islands ($F=7.893$, $p<0.01$). The highest value was found at EW in São Miguel while the lowest was found at NF in all three islands (Table 11). For all islands, PF exhibited relatively high values of carbon stocks (Table 11).

Carbon stock in the leaf litter and in soil. Regarding leaf litter, carbon stock was significantly different between forest types ($F=24.83$, $p<0.01$) and between islands ($F=5.98$, $p<0.01$); Pico Island showing higher stocks as well as PF (Table 11). Carbon stocks in soils were significantly different between islands ($F=29.92$, $p<0.01$) but not between forest types ($F=2.55$, $p=0.08$). In general, Pico Island soils showed the lowest values of carbon accumulation (Table 11).

Discussion

Here we discuss taxonomic and structural diversity, and the results obtained regarding the carbon stocks obtained for the different compartments (i.e., trees, litter, soil) in the three types of forests and in the three islands. We finalize by connecting biodiversity and carbon stock services provided by forests to other important roles in water and soil conservation, recreation and leisure activities.

Taxonomic diversity. Biodiversity indices were generated to bring the diversity and abundance of species in different habitats to a similar scale for comparison [47].

Table 6. Soil variables found at 90 forests in the Azores, from three islands (Pico, São Miguel, and Terceira) and three forest types (Exotic Woodland, Natural Forest, and Production Forest). Mean (m) and standard error (se) for each environmental parameter. For each row, different letters indicate significant differences (p<0.05) according to the results of a Tukey test applied after ANOVA.

		Exotic Woodland			Natural Forest			Production Forest		
Parameter		Pico	São Miguel	Terceira	Pico	São Miguel	Terceira	Pico	São Miguel	Terceira
BD	m	0.17 a	0.55 c	0.55 c	0.10 a	0.50 c	0.38 bc	0.22 ab	0.55 c	0.41 c
(g.cm ⁻³)	se	0.02	0.05	0.05	0.02	0.04	0.05	0.03	0.04	0.04
OM	m	286.31 c	142.03 ab	168.53 abc	409.21 d	118.42 a	165.49 ab	247.49 bc	109.54 a	174.03 abc
(g.kg ⁻¹)	se	33.65	13.44	26.85	48.36	20.12	21.30	22.28	11.37	21.00
N	m	11.78 c	5.91 a	6.63 ab	13.61 c	3.97 a	6.63 ab	10.42 bc	4.21 a	6.72 ab
(g.kg ⁻¹)	se	1.28	0.72	0.91	1.26	0.39	0.83	0.75	0.51	0.66
pH H₂O	m	5.66 bcd	6.12 d	5.62 bcd	5.01 a	5.51 abc	5.18 ab	5.80 cd	6.13 d	5.39 abc
	se	0.08	0.10	0.21	0.16	0.11	0.11	0.13	0.07	0.16
P ER	m	17.40 ab	6.90 a	21.24 ab	34.20 c	8.40 a	26.46 ab	10.80 a	7.70 a	6.89 a
(mg.kg ⁻¹)	se	3.88	1.57	4.81	9.23	2.57	8.28	3.37	2.81	1.62
P O	m	12.70 a	15.80 ab	27.80 ab	29.80 ab	10.90 a	37.70 b	11.20 a	12.90 a	16.47 ab
(mg.kg ⁻¹)	se	2.32	2.24	8.23	7.25	2.97	7.86	1.76	2.99	5.22
K ER	m	189.10 abc	396.90 b	169.70 abc	139.90 ab	277.40 bc	59.10 ab	75.20 ab	240.70 abc	46.10 a
(mg.kg ⁻¹)	se	24.85	108.54	19.23	20.66	85.22	5.92	10.16	51.01	3.84
K⁺	m	0.64 a	1.24 a	1.08 a	0.79 a	0.71 a	0.31 a	0.28 a	0.72 a	0.30 a
(cmol _c .kg ⁻¹)	se	0.12	0.43	0.40	0.13	0.17	0.05	0.03	0.13	0.07
Ca²⁺	m	11.44 c	5.73 abc	9.46 bc	11.51 c	3.38 ab	2.70 a	5.59 abc	4.78 ab	3.09 ab
(cmol _c .kg ⁻¹)	se	1.96	1.10	2.18	2.70	0.49	0.44	0.82	0.85	0.37
Mg²⁺	m	6.71 abc	3.44 ab	8.46 bc	10.28 c	2.09 a	2.39 a	5.50 abc	2.05 a	2.70 a
(cmol _c .kg ⁻¹)	se	1.01	0.47	1.63	2.73	0.42	0.48	0.89	0.34	0.60
Na⁺	m	1.12 bc	0.68 ab	0.45 a	1.32 c	0.41 a	0.21 a	1.18 bc	0.49 a	0.31 a
(cmol _c .kg ⁻¹)	se	0.15	0.12	0.18	0.14	0.10	0.06	0.17	0.12	0.07
Al⁺ H₃O⁺	m	0.15 a	0.07 a	0.19 a	0.36 abc	0.24 ab	0.61 c	0.08 a	0.04 a	0.56 bc
(cmol _c .kg ⁻¹)	se	0.02	0.04	0.07	0.08	0.05	0.08	0.03	0.04	0.16

Table 7. Comparison of leaf litter macronutrients and micronutrients at 90 forests in the Azores, from three islands (Pico, São Miguel, and Terceira) and three forest types (Exotic Woodland, Natural Forest, and Production Forest). Results of a two-way ANOVA. Bold indicates a significant effect ($p < 0.05$).

Parameter	Type		Island		Interaction	
	F	p	F	p	F	p
N	42.520	0.000	4.468	0.014	2.465	0.051
K	35.026	0.000	8.871	0.000	7.568	0.000
P	1.762	0.178	0.228	0.796	0.566	0.688
Ca	14.469	0.000	3.657	0.030	6.996	0.000
Mg	15.204	0.000	7.800	0.001	5.889	0.000
S	22.766	0.000	7.095	0.001	0.879	0.480
B	67.766	0.000	3.883	0.025	3.329	0.014
Fe	23.288	0.000	3.525	0.034	1.366	0.253
Zn	33.081	0.000	4.494	0.014	6.739	0.000
Mn	31.775	0.000	10.445	0.000	3.113	0.020
Cu	16.508	0.000	1.311	0.275	0.777	0.543

The high values of diversity indices revealed a high species diversity and abundance in forest areas [48]. This information offered valuable insights about the structure of groups of organisms within the ecosystem [49].

In general, NF plots showed higher species diversity than PF and EW plots. The higher richness and diversity of forest species found in NF agrees with other studies for the Azores region, e.g. [36,37,43,50-52], and for other regions [53-55]. Regarding PF, this forest type generates a considerable decline on taxa diversity [56]. The low plant diversity noted in PF could be explained by the fact that it is dominated by a single species (*Cryptomeria japonica*), a species that contributes with nearly 90% to the total number of trees per plot, originating complete canopy dominance. Under the dense canopy, only ferns and some invasive species that tolerate low levels of light (e.g., *Hedychium gardnerianum*) are found [57].

Table 8. Concentrations of leaf litter macronutrients (N, P, K, Ca, Mg and S) and micronutrients (Cu, Zn, Fe, Mn, and B), found at 90 forests in the Azores, from three islands (Pico, São Miguel, and Terceira) and three forest types (Exotic Woodland, Natural Forest, and Production Forest). Mean and standard error for each environmental parameter. For each row, different letters indicate significant differences ($p < 0.05$) according to the results of a Tukey test applied after ANOVA.

Parameter		Exotic Woodland			Natural Forest			Production Forest		
		Pico	São Miguel	Terceira	Pico	São Miguel	Terceira	Pico	São Miguel	Terceira
N	m	8.56 bcd	10.00 cde	11.63 de	11.53 de	11.83 e	11.53 de	5.05 a	8.07 abc	6.17 ab
(g.kg ⁻¹)	se	0.97	1.02	0.65	0.73	0.77	0.50	0.27	0.70	0.43
K	m	1.80 ab	3.21 b	6.22 c	1.16 ab	1.27 ab	0.89 a	0.43 a	1.03 a	1.11 ab
(g.kg ⁻¹)	se	0.16	0.64	1.11	0.11	0.25	0.08	0.05	0.47	0.11
P	m	0.46 a	0.61 a	0.68 a	0.75 a	0.67 a	0.72 a	0.60 a	0.54 a	0.57 a
(g. kg ⁻¹)	se	0.03	0.06	0.08	0.15	0.06	0.04	0.20	0.06	0.12
Ca	m	15.29 bc	10.50 a	12.37 ab	9.71 a	11.01 a	9.33 a	12.93 ab	11.69 ab	17.03 c
(g.kg ⁻¹)	se	0.58	0.72	0.89	0.62	0.88	0.67	0.76	1.39	1.25
Mg	m	2.85 bcde	3.64 e	3.28 de	1.95 abc	3.01 cde	1.63 a	1.91 ab	2.38 abcd	3.27 de
(g.kg ⁻¹)	se	0.26	0.34	0.19	0.13	0.24	0.12	0.08	0.41	0.21
S	m	0.65 abc	0.79 bcd	0.75 bcd	0.83 cd	0.93 d	0.78 bcd	0.46 a	0.68 abc	0.57 ab
(g.kg ⁻¹)	se	0.03	0.07	0.05	0.06	0.08	0.03	0.03	0.05	0.03
B	m	21.52 cd	22.43 cd	24.30 d	10.85 ab	16.56 bc	9.20 a	10.25 a	12.48 ab	12.10 ab
(mg.kg ⁻¹)	se	1.06	2.35	1.27	0.53	1.81	0.36	0.30	1.77	0.67
Fe	m	999.85 b	902.00 b	843.50 b	848.95 b	479.98 ab	196.60 a	166.97 a	207.43 a	86.40 a
(mg.kg ⁻¹)	se	158.98	179.56	194.20	240.23	108.36	30.26	37.08	35.40	10.75
Zn	m	81.49 bc	79.61 bc	113.70 cd	54.77 ab	142.97 d	59.00 abc	14.08 a	19.74 a	15.02 a
(mg.kg ⁻¹)	se	8.11	14.81	24.52	6.50	18.09	12.73	0.88	2.82	1.00
Mn	m	147.36 ab	131.91 ab	320.00 cd	197.89 bcd	176.75 abc	350.00 d	22.41 a	41.06 a	23.70 a
(mg.kg ⁻¹)	se	17.18	42.75	67.21	35.40	47.38	21.66	3.21	12.06	2.27
Cu	m	6.27 abcd	7.43 cd	7.60 d	5.71 abcd	6.36 bcd	4.80 abcd	3.73 ab	4.27 abc	3.00 a
(mg.kg ⁻¹)	se	0.33	0.61	1.89	0.32	0.61	0.39	0.21	0.27	0.26

Table 9. Comparison of structural diversity at 90 forests in the Azores, from three islands (Pico, São Miguel, and Terceira) and three forest types (Exotic Woodland, Natural Forest, and Production Forest). Tree density (D, trees/ha), Basal area (BA, m²), BA γ (number of taxa contributing to the BA, i.e., those with a diameter at breast height above 2.5 cm), Shannon diversity based on BA (BA H), Evenness based on BA (BA E), aboveground biomass (AGB Mg.ha⁻¹). Results of a two-way ANOVA. Bold indicates a significant effect (p<0.05).

Parameter	Type		Island		Interaction	
	F	p	F	p	F	p
D	18.83	0.000	2.725	0.072	0.464	0.762
BA	79.498	0.000	1.208	0.304	3.636	0.009
BA γ	99.911	0.000	1.985	0.144	0.854	0.495
BA H	61.342	0.000	4.509	0.014	1.300	0.277
BA E	49.223	0.000	3.070	0.052	0.571	0.684
H	254.159	0.000	3.192	0.046	5.088	0.001
AGB	6.089	0.003	7.212	0.001	7.827	0.000

Changes in the species richness, abundance, and composition of an ecosystem may lead to parallel changes in the amount or quality of services provided by that ecosystem, including carbon sequestration, pollination, or pest control, that are indicative of a linear relationship between biodiversity and ecosystem services [58]. In fact, several causes could explain variations in the degree of biodiversity between the plots of the study area, such as soil type, anthropogenic action, and land use change, among others [59-63].

Concerning NF, which isn't under any form of intensive management and has less anthropogenic influence, since it is not easily accessible [64], the disturbances are limited to minor harvesting of non-timber forest products [55].

Table 10. Structural diversity found at 90 forests in the Azores, from three islands (Pico, São Miguel, and Terceira) and three forest types (Exotic Woodland, Natural Forest, and Production Forest). Mean and standard error for each structural parameter. Tree density (D, trees.ha⁻¹), Basal area (BA, m²), BA γ (number of taxa contributing to the BA, i.e., those with a diameter at breast height above 2.5 cm), Shannon diversity based on BA (BA H), Evenness based on BA (BA E), aboveground biomass (AGB Mg.ha⁻¹). For each row, different letters indicate significant differences (p<0.05) according to the results of a Tukey test applied after ANOVA.

		Exotic Woodland						Natural Forest						Production Forest					
Parameters		Pico		São Miguel		Terceira		Pico		São Miguel		Terceira		Pico		São Miguel		Terceira	
D	m	5310.00	c	4040.00	bc	3940.00	abc	3770.00	abc	3110.00	ab	3110.00	ab	2330.00	ab	1970.00	a	2130.00	ab
(trees.ha ⁻¹)	se	734.91		836.55		454.17		366.99		331.14		164.96		202.24		214.50		265.85	
BA	m	0.58	a	0.93	a	0.49	a	0.48	a	0.45	a	0.47	a	1.87	bc	1.84	b	2.64	c
(m ²)	se	0.07		0.16		0.06		0.08		0.07		0.05		0.28		0.30		0.25	
BA γ	m	3.10	b	2.40	ab	2.60	ab	6.50	c	5.30	c	5.40	c	1.20	a	1.30	a	1.30	a
(taxa/plot)	se	0.46		0.43		0.22		0.62		0.56		0.45		0.13		0.15		0.15	
BA H	m	0.60	bc	0.35	ab	0.47	bc	1.14	d	0.67	bc	0.92	cd	0.02	a	0.00	a	0.02	a
	se	0.14		0.13		0.11		0.13		0.10		0.13		0.01		0.00		0.01	
BA E	m	0.48	cd	0.30	bc	0.47	cd	0.62	d	0.43	cd	0.55	cd	0.02	ab	0.00	a	0.02	ab
	se	0.09		0.10		0.09		0.06		0.07		0.07		0.01		0.00		0.02	
H	m	8.79	ab	9.37	b	8.22	ab	5.12	ab	4.60	a	4.67	a	22.81	cd	18.92	c	26.25	d
	se	0.62		0.98		0.72		0.49		0.50		0.26		1.52		1.34		1.68	
AGB	m	7.79	a	266.24	b	9.57	a	6.05	a	7.04	a	6.49	a	47.21	a	58.95	a	86.83	a
(Mg.ha ⁻¹)	se	1.53		91.23		3.31		1.53		1.62		0.65		5.93		16.58		14.63	

Table 11: Carbon stock found at 90 forests in the Azores, from three islands (Pico, São Miguel, and Terceira) and three forest types (Exotic Woodland, Natural Forest, and Production Forest). Mean and standard error for each structural parameter. Carbon stock in the trees, both above and below ground (C|AB, Mg.ha⁻¹), in leaf litter (C|L, Mg.ha⁻¹), and in soil (C|S, Mg.ha⁻¹). For each row, different letters indicate significant differences (p<0.05) according to the results of a Tukey test applied after ANOVA.

		Exotic Woodland			Natural Forest			Production Forest		
		Pico	São Miguel	Terceira	Pico	São Miguel	Terceira	Pico	São Miguel	Terceira
C AB	m	247.72 a	4569.44 b	185.46 a	147.43 a	133.18 a	145.576 a	526.75 a	475.02 a	797.14 a
	se	34.42	1472.26	23.46	34.88	22.88	14.07	56.88	82.39	87.23
C L	m	2.39 bc	1.27 ab	1.87 ab	1.63 ab	1.55 ab	0.86 a	3.57 c	2.13 ab	3.54 c
	se	0.19	0.13	0.31	0.31	0.21	0.40	0.46	0.19	0.42
C S	m	26.41 a	89.50 c	100.00 c	25.78 a	65.30 ab	76.06 c	30.42 a	65.11 ab	78.03 c
	se	2.80	10.13	15.06	5.70	11.29	15.25	3.86	5.03	7.47

However, the effect of an intensive management regime in the case of PF and of the spread and dominance of invasive species in EW, have originated a significant decrease in biodiversity levels [64-68].

Higher values of precipitation and lower values of temperature were found for NF, and an inverse situation for EW, since the remaining NF are mostly found at high elevation sites, at sloped terrain [51], while EW is generally found at low elevation and at places with higher temperatures [69-72].

The area occupied by forest plantations is expected to increase, making it necessary to assess its potentials to fulfil ecological purposes (e.g., biodiversity conservation), in addition to wood production [73]. While plantations are known for high timber productivity, their potential to preserve and harbor biodiversity is very compromising [63]. When ecosystems are managed for only a limited set of goods and services, such as timber (e.g., Thompson et al. [74]), many other ecosystem services may be overlooked and therefore undervalued [21]. However, plantations of economically interesting tree species can preserve a high biodiversity, if conservation is included in their initial management goals [11]. Further enhancement of biodiversity is possible through greater attention to structural diversity [42,52,75], across landscapes and within stands, applying site-specific stand management, using indigenous species, and increasing rotation length [76]. Management of plantations of economically interesting tree species must seek to strike a balance (synergy) between timber production and biodiversity conservation [11]. In the Azores, the new production forests already include a buffer zone with some native elements [73].

Biodiversity within the forest tends to be greater in stands that are structurally diverse in terms of their age, species, patch edge, understory, and deadwood component [21,75,77,78].

Structural diversity. Forest stand structure is a key element to understand forest ecosystems, stand biodiversity [47] and forest ecology, as it is linked to many ecological processes [79,80]. It is also used as a biodiversity indicator since vertically structured forests foster taxonomic diversity [81]. Furthermore, horizontal and vertical structural heterogeneities enhance resistance of forest ecosystems against disturbances [82,83]. Understanding tree composition and structure of a forest is a vital instrument in assessing its sustainability, species conservation, and management [84].

In this study, forest structure differed among the tree types in tree diameter, height, basal area, and density. The structure of PF and EW was mainly influenced by the dominant species *Cryptomeria japonica* and *Pittosporum undulatum*, with the highest basal area and tree density. The structural dominance of *P. undulatum* in exotic woodland confirms the potential of this species to originate almost pure stands [40-42,69,70,85-87]. Regarding *C. japonica*, as mentioned above, this species originates almost pure stands, completely dominating the canopy [73].

NF showed the highest values for structural diversity since a larger number of woody taxa contributed to the canopy. NF are often characterized by greater structural diversity [36,37,51,52,88-90] than managed forests, where silvicultural practices often excessively uniformize their species composition and structure [84,91-94]. Frequently, forests located in nature reserves or national parks, whose structure is largely the result of natural phenomena, are provided as examples of highly structured forests [52,95]. However, long-term studies focused on NF indicate that the natural processes occurring

in them can lead to the development of a simple system in terms of their species composition and structure [93,96,97]. The importance of structurally diverse forests providing a wide range of ecosystem services has been widely recognized [98]. Stand structure relates to the distribution of tree growth or other plant species within a forest stand and can thus reflect the interaction between vegetation growth and environmental conditions [99,100]. Species and structural diversity can also be correlated, as species diversity increases structural diversity when species with different life strategies coexist. Species diversity can also promote tree size and canopy height heterogeneity as well [101], while structural diversity can be a proxy for species diversity [102].

Carbon stock in trees. Biomass production in different forms plays an important role in tree carbon sequestration. These carbon pools are composed of live and dead *AGB* and *BGB*, and wood products with long and short life. *AGB*, *BGB*, dead wood, litter, and soil organic matter are the major carbon pools in any ecosystem. *AGB* estimation is an essential aspect of studies of carbon stocks as it directly relates to the carbon sequestration on the global carbon balance [103,104].

Our study revealed that, in São Miguel, *AGB* was highest in some of the EW stands, which indicates that they correspond to old forests [41], making *Pittosporum undulatum* an important carbon sink, which is in accordance with previous biomass estimations for this species in the Azores [42]. Apparently, aboveground carbon storage increased with tree density and height, but decreased with species diversity. As expected, PF showed high values of carbon storage, consistently, for the three islands, and NF usually had the lowest values of total carbon storage.

Our data and previous analyses of the structure of NF in the Azores, suggests that although with relatively high levels of tree density, forest height is much smaller than for

PF, and larger trees are found only in the more preserved and therefore older forests, such as those in Pico. A total 239.17 Mg.ha⁻¹ has been estimated for Terceira Island, approximately 75%, sequestered by the endemic tree *Juniperus brevifolia*, a value somewhat larger than our average results, but within the same order [43]. Using the values obtained for *AGB* for the Laurisilva in the Canaries islands, and assuming that the sequestered carbon corresponds to 50% of this biomass [105,106], it has been estimated that Laurisilva sequesters about 127.55 Mg.ha⁻¹, a value that is very close to our estimates.

The *Cryptomeria japonica* stands in the Azorean archipelago are mostly pure, exploited under high shaft, with minimum revolutions of 30 years, and with an annual productivity that can exceed 20 m³ha⁻¹year⁻¹ in the best seasons. São Miguel Island presents the oldest and largest *Cryptomeria* stands, with an average value of 32 years [38] and encompassing 70% of the archipelago's populations [107]. The total carbon stock present in the Azorean *Cryptomeria japonica* forest was estimated at 2816 ± 1594 Gg (in a total of 12968 ha), representing about 217 Mg.ha⁻¹ [38], a value close to that found in our detailed study of 30 forests. For example, Fukuda et al. [108], for an area of 4.51 × 10⁶ ha obtained values of 80.79 and 90.11 Mg.ha⁻¹ (years 1990 and 1995, respectively). Similarly, Sasaki & Kim [109] obtained values of 48.7 and 24.3 Mg.ha⁻¹ (year 1966), 76 and 101.6 Mg.ha⁻¹ (year 2012), for natural and planted forest, respectively. Although planted forests have only contributed with a small portion to the total terrestrial carbon balance, their potential to absorb and store carbon has been recognized to play a more important role in climate change mitigation [110]. Planted forests contributed about 80% of the total forest carbon sink increment of China [18]. Secondary successions in temperate forests are characterized by higher rates of biomass production and a great potential for fixation, capture and storage of carbon [111-113]. Secondary forests,

regenerated on abandoned agricultural land such as pastures, or re-established after stand-replacing disturbances, are an important component of terrestrial ecosystems around the world [114,115]. As in many other archipelagos, the primary Azorean forest, which existed before the arrival of human settlers, was largely cut, having been replaced by secondary forest (e.g., *Pittosporum undulatum*, *Cryptomeria japonica*), with the potential to sequester a large amount of carbon because of their rapid regrowth following disturbance [115,116]. However, other studies have revealed positive effects of biodiversity on productivity and a positive relationship between biomass, basal area, tree density and species diversity were observed (e.g., [117-123]). For instance, some studies found a negative effect of size heterogeneity in several monocultures [124,125], and a positive effect of size heterogeneity (and species diversity) in mixed stands [126]. Eventually, more studies analyzing the biodiversity-biomass relationship, could support feasible alternatives for new forest management plans, potentially enhancing ecological sustainability [127,128].

Carbon stock in leaf litter. Regarding the carbon stock in leaf litter, our research showed variation between the different vegetation types [129,130]. The PF, dominated by *C. japonica*, contained higher carbon concentration in leaf litter and greater accumulation of forest floor litter, thus maintaining a high carbon content due to continuous litter production. Other forest types capable of significantly altering soil organic carbon stock in temperate forests have been reported [131,132]. Coniferous litter contains more lignin, which slows down the rate of decomposition leading to more litter accumulation in the forest floor and formation of acidic compounds [133]. In these acidic soils, soil fauna is less active, decreasing the amount of humus mixing through mineral soil and leaving more materials in the forest floor [134]. In addition, conifers have shallower rooting

systems and tend to accumulate more organic carbon in the forest floor [135]. These could be the reasons for the variation on leaf organic carbon among the forest types, as well as the distribution in the soil profile in moist temperate forests [129]. The humus profile is usually thinner in deciduous and sclerophyllous forests than in coniferous forests. Van Wesemael & Veer [136] suggested that the lower rate of decomposition of the leaf litter in *C. japonica* plantations and *Pinus resinosa* forests, compared to those of oak forests may be due to their chemical properties [137,138]. According to Bowden et al. [139] high leaf litter did not increase carbon in soil, but lower litter inputs resulted in rapid carbon soil decline. Root litter may ultimately provide more stable sources of soil carbon. Management activities or environmental alterations that decrease litter inputs in mature forests can lower carbon content in the soil. However, increases in forest productivity and the resulting increased litter production seem unlikely to improve soil carbon sequestration.

Moreover, leaf litter production is low at high latitudes where short growing seasons limit plant growth; it increases towards the equator where plant growth occurs throughout the entire year. However, in a local region with similar temperature and rainfall, the variation in the litterfall is attributed to differences in the physiology and ecology of tree species, physiographic factors (i.e., slope and aspect) and site productivity [140,141].

As the key process and main repository of the nutrient cycle and cycling of terrestrial ecosystems [142], litter is the basic carrier of nutrients from plants to soil. This dynamic exchange can achieve and maintain a balance between soil nutrients and the elemental ratios required for plant growth [143]. The ability to store carbon and the rate

of accumulation and supply of N and P that limit plant growth, are closely associated [144,145].

Chemical composition is one of the main factors controlling the decomposition rate of litter. This was postulated already by Tenney & Waksman [146] and several studies have later stressed the importance of inorganic and organic components in controlling turnover rate of organic matter and release of nutrient elements [138,147-149]. Boring & Hendricks [150] revealed that generally, litter with high lignin and low N concentration has a slower decomposition rate and immobilizes more N, than litter with low lignin and high N content. Information on levels of inorganic and organic components in tree litter is thus of great importance for studying the carbon dynamics in forest ecosystems [138].

Carbon stock in the soil. Soil is recognized as the largest terrestrial carbon reservoir in the global carbon cycle [29,151]. Depending on soil type, tree species, impacts of disturbances in ecosystems, forest type and climate, soil can contribute with a representative part of the total carbon stock in forest ecosystems [17,152]. Soil properties, such as bulk density, carbon stock, nitrogen stock, cation exchange capacity and pH, may differ among forest types [153].

Our study showed a variability in soil carbon stocks associated with the fact that Pico Island soils are relatively young, mostly composed by basaltic rock debris (i.e., leptosols), differing from the other two islands. The Azorean soils are mainly andosols (i.e., soils that have formed in volcanic ash or other volcanic ejecta) [154]. Soils in Pico Island are mostly formed by basaltic rocks (basalts, mugearite, hawaiiite), by pyroclastic materials of basaltic composition or by trachytes and pyroclastic material (cinders, ashes, pumices, tuffs). Hydruclands have developed only in Pico Island (the youngest of the

Archipelago), on pyroclastic materials of basaltic composition. The area occupied by hydrudands is estimated to be about 5500 ha. They show very low bulk density ($0.20\text{--}0.45\text{ g cm}^{-3}$), high water retention at 1500 kPa (between 150 and 437 %), quite high organic carbon content ($>8.3\%$), high contents of Al extractable by oxalate, and extremely high phosphate adsorption capacity, which can reach 52 g P kg^{-1} [155].

In our study, no clear differences between forest types were found regarding soil carbon sink, and a lack of studies that experimentally compare the influence of the dominant tree species on soil carbon has been previously identified [19].

We found a tendency for a somewhat higher level of cations at EW soils, dominated by broad leaved species, what is to be expected since the uptake rates of acids and bases differ between vegetation types, such that the rates of broadleaf forests are higher than those of coniferous forests [153,156].

Soil textures in the three forest types included in this research varied widely from sandy, loam, to silt, reflecting the complex landscape processes. However, there was a tendency for a dominance of sandy loam at the NF, sandy loam and loam at EW and PF, but with a lower content of loam in the latter. Also, the EW and PF at Pico showed a large contribution of sand or loamy sand. As seen above, this might be linked to the type of substrate available at Pico Island. The relatively high contribution of loam at EW in Terceira and São Miguel might also justify the relatively high content in cations mentioned above. Loam soils are medium textured soils having generally more nutrients and humus than sandy soils and have better infiltration and drainage than clay soils [157,158]. Inversely, sandy soils are coarse textured being loose and friable, draining water quickly, with lower fertility, low soil organic carbon, a low cation exchange

capacity, a high risk of nutrient leaching, a low structural stability, and a high sensitivity to erosion and to crusting [159].

Final remarks. To date, the ecosystem services concept has so far received little attention in islands around the globe [160]. These areas, ranging temperate, semi-tropical, to tropical ocean forests, are rich in biodiversity and natural resources, providing a variety of ecosystem services of global and regional importance (e.g., water regulation, erosion control, pollination, pest-control, food supply and recreation) [160]. This translates to a substantial but often unrecognized contribution to local island economies, crucial contributions to the tourism sector, many cultural ecosystem services depending on natural diversity and healthy ecosystems. Ecosystem services assessment attempts will produce the knowledge base for well-informed decision-making to protect vulnerable overseas areas [160]. In fact, forests have an important role in the conservation of water resources and in the refilling of aquifers [161], since the large areas of pastureland tend to have an impermeable layer relatively close to the soil surface, leading to increased water runoff and to decreased infiltration [162], while forests contribute to precipitation and occult precipitation interception, which is very common in the Azores [163,164]. Moreover, this also contributes to avoid soil erosion [165,166] due torrential discharges and earthquakes, which are common in the Archipelago throughout the year [167]. Forests also play an important role as recreation areas for the local population through the network of recreational forest areas [168], but also through the extensive network of hiking trails which crosses different forest types and is an important tourism resource [169]. Finally, the production forest dedicated to *C. japonica* is presently responsible for 1400 jobs, and of a revenue of 12 million euros annually [170].

Conclusion. This research addresses ecological valorization of forests in the Azores, an interesting model region for studies devoted to biodiversity pattern changes, associated with anthropogenic activity. Regarding taxonomic diversity, there was ample evidence that NF harbored the highest biodiversity levels and PF the lowest, thus NF stands play an important role as native biodiversity hotspots. Diversity levels were generally lower for structural than for taxonomic data, particularly for PF. Again, NF showed the highest levels of structural diversity, showing their importance as biodiversity sinks, and eventually affecting other ecosystem functions such as water retention. Regarding carbon accumulation, total carbon stocks were mostly accumulated in tree biomass, with the largest values for PF and the lowest for NF, except for EW, in São Miguel Island, which showed extremely high values associated with old forest stands. PF provides economic assets and could play a role as carbon sink, while EW presently has a major role as a carbon sink, apparently also preserving soil quality. However, its role in biodiversity preservation is globally negative, and could be replaced by PF or NF where possible. Species density, distribution, and population structure analyzed in this study, should be useful to conservation researchers and scientists and to forest managers to develop effective forest management action plans.

Methods

Site description. The study was conducted in the Azores archipelago (between 36°55'N and 39°42'N and 25°00'W and 31°30'W), situated between North America and Europe, about 1500 km west of mainland Portugal. The archipelago has a total area of 2323 km² and comprises nine inhabited islands of volcanic origin (Fig. 2). This research comprised three islands contributing with the largest forest areas: São Miguel Island with 745 km²,

the highest elevation at 1,105 m a.s.l. and an estimated age of 0.79 MY (millions of years) [171]; Terceira Island with 400 km², a maximum elevation of 1,023 m a.s.l. and 0.39 MY [172] and; Pico Island with an area of 447 km², mostly occupied by a volcano reaching an altitude of 2351 m a.s.l., and an approximate age of 0.27 MY [173].

The three types of vegetation included in the study were: (i) Natural Forests, NF, submontane and montane cloud forests, characterized by geographic isolation, relatively homogeneous climatic conditions, a limited number of native woody species but high biodiversity and a high number of endemic species [50,51,90,174], which are dominated by *Ilex azorica* Gand., *Juniperus brevifolia* (Hochst. ex Seub.) Antoine, *Laurus azorica* (Seub.) Franco, *Morella faya* (Aiton) Wilbur and *Picconia azorica* (Tutin) Knobl, relicts of once much more common formations; (ii) Exotic Woodland, EW, mostly dominated by *Pittosporum undulatum* Vent., a woody invader from Australia; and (iii) Production Forest, PF, including *Cryptomeria japonica* D.Don. Other species also present with lesser extent in PF are *Eucalyptus globulus* Labill. (mostly in Terceira) and *Pinus pinaster* Aiton (mostly in Pico). Other types of vegetation common in the archipelago but that were not targeted in this study include intensive and extensive pasturelands, generally above 400 m in altitude, usually installed in sloped terrain where soils are more difficult to cultivate, and orchards and agricultural field crops located at lower elevations [175]. Quantitatively, pastures occupy 43% of the territory, PF represents 22%, NF 13% and EW 22% [36,51, 86, 92,176].

Pittosporum undulatum, is the dominant woody species in the Azores, using about 30% of the forested area, i.e., 23939 ha from a total of 49343 ha occupied by forest in the archipelago [40,86,175]. This invasive species can overgrow the native vegetation by shading the indigenous species and forming pure stands, particularly in sheltered

locations. Its introduction altered the natural transition between the native plant communities, which were found between 300 and 600 m of altitude [91].

Cryptomeria japonica is considered the most important forestry species in the Azores archipelago, not only because of its economic importance, occupying 60% of the area dedicated to production forest, but also because its stands are a structural element of the Azorean landscapes [86,175]. Although, with a global distribution ranging from temperate to subtropical regions, major stands of *C. japonica* are found in subtropical conditions, in which the precipitation values reach 2540 mm annually, generally in pure stands and frequently on steep slopes, with abundant fogs and intense winds. Thus, in conditions similar to those found in the Azores at middle to high elevations.

Sampling and data collection. Field work was carried out on spring/summer of 2017 and 2018. A geographic information system (GIS; QGIS 2.18) was used to map and identify forest stands, based on the data provided by the Azorean Forest Inventory [175]. A total of 90 forest stands were randomly sampled, 30 in each of the three selected islands São Miguel, Terceira and Pico (10 NF, 10 PF and 10 EW) (Fig. 2). At each forest we marked a plot with 10×10 m (100 m^2), divided into 4 (5×5 m) subplots.

Taxonomic diversity. We recorded all vascular plants within each subplot (5×5 m). Species that could not be identified with certainty in the field were collected, following standard herbarium techniques, and later identified at the AZB Herbarium using available literature [46,177-178]. A few dubious specimens were identified to genus level only. The abundance of each plant species was estimated based on the relative abundance according to cover (estimated visually at each subplot) and number of specimens within all the 360 subplots.

Structural diversity. To access forest structure, a total of 2973 trees were recorded from each subplot (5x5 m) in all 90 plots, and the following dendrometric traits were measured: *H*, tree total height (m), using a Vertex IV 360° and Transponder T3, Haglöf Sweden AB; and *DBH*, diameter at breast height (cm), using a tree diameter measuring tape. Only individual trees and shrubs with *DBH* above 2.5 cm were included [40-42,179]. For individuals that branched at breast height or below, the diameter was measured, separately, at each branch.

Leaf litter sampling. To characterize leaf litter biomass, carbon content and macro/micronutrients, the leaf litter layer was collected using a 1 m² frame, at the center of each subplot, in a total of 270 leaf litter samples. All coarse woody debris were removed from the samples prior to collection. The leaf litter samples were transported to the laboratory and weighed immediately, oven-dried at 60°C for 48-72 h and reweighed. The bulk density (g of dry leaf per m² of soil) was calculated and mean value per each 90 plots was used. A duplicate sample was collected and sent to the Soil and Plant Laboratory of the University of Trás-os-Montes and Alto Douro, in Vila Real, Portugal, to determine carbon content and macro/micronutrients.

Figure 2: Location of the Azores archipelago (Portugal) and the distribution of the 90 selected stands, from each forest type (Natural Forest; Production Forest and Exotic Woodland) in the islands of São Miguel (30 stands), Terceira (30 stands) and Pico (30 stands).

Soil sampling. *Bulk density* - For soil bulk density, three subplots were selected randomly, at each of the 90 plots. At the center of each subplot, a 10-cm-depth trench was opened (or to depth at which impenetrable rocks were encountered) and undisturbed soil cores were collected using a volumetric ring with 1 mm of thickness, 8 cm of internal diameter and 10 cm of height. Mean values were used per site and a total of 270 soil samples, were taken. Samples were transported to the laboratory and weighted immediately, and then oven-dried at 60°C for 48-72 h, and reweighted. The bulk density (g of dry soil per cm³ of soil) was calculated. *Soil parameters* - To estimate soil parameters (organic carbon content, pH, macro/micronutrients, and soil texture), a total of 270 soil cores were collected with a soil sampler, taken randomly at each of the 90 plots, to collect the top 30 cm of soil (or to depth at which impenetrable rocks were encountered). Soil samples were sieved and sent to the Soil and Plant Laboratory of the University of Trás-os-Montes and Alto Douro, in Vila Real, Portugal, for analysis.

Statistical analyses

Species diversity. The most used representation of ecological diversity is species diversity, based on the number of species and on the relative abundance of each species found at a certain location [180]. We compared the mean diversity at each forest type using the Shannon index (H'), because it provides an account for both abundance and evenness (E') [88]. It also does not disproportionately favor any species as it accounts all the species according to their frequencies [181].

Diversity Partitioning. Diversity partitioning reveals the scale at which diversity is maximized [182]. The total species diversity/species richness of plants recorded in study sites were divided into diversity components (α , β and γ) at three spatial scales: α -diversity within plots, β -diversity defined as turnover of species among samples/plots at

different localities, and γ -diversity for the whole region (number of species found in the pooled sampling units) [183]. At the lowest sampling level, α_1 is the mean species diversity in a plot, α_2 is the mean species diversity in a forest, α_3 is the mean species diversity in a type of forest. As for β -diversity, $\beta_1 = (\alpha_2 - \alpha_1)$, $\beta_2 = (\alpha_3 - \alpha_2)$, and $\beta_3 = (\gamma - \alpha_3)$. Thus, the total diversity (γ) in the Azores forests can be partitioned as: $\gamma = \alpha_1 + \beta_1 + \beta_2 + \beta_3$. In this study α and γ diversities were measured directly, as numbers of species in the samples, at the different levels. These analyses were performed using the function “adipart” of the “vegan” R package [184].

Structural diversity. We included 2973 trees ($DBH \geq 2.5$ cm) and reported the following forest parameters: tree density (trees/ha; number of individuals divided by sampled area); Maximum height, H ; Diameter at breast height, DBH (recorded for all the branches at breast height per tree); and Basal area, BA (m^2 ; where $BA = DBH^2 \times \pi / 4$, resulting from the sum of all branches per tree). BA is the cross-sectional area of woody stems, and it measures the relative dominance, that is, the degree of coverage of a species as an expression of the space it occupies in a forest. To estimate BA diversity among 90 plots, first we summed all basal areas from all trees of the same species per plot (BA per ha), and a mean value per plot was used to calculate different estimators: Shannon’s index, gamma diversity, and evenness. For tree maximum height, we used mean value per plot and standard deviation.

Forest clustering. To identify patterns in the composition of Azorean forests we calculated Hellinger distance and Unweighted Paired Group Mean Average (UPGMA) as agglomeration schedule, since this was the combination originating the highest cophenetic correlation value between the community distance matrix and the dendrogram [185]. The optimal number of community groups was determined both by using silhouette

widths, that is Rousseeuw quality index, and the optimal number of clusters according to Mantel statistic (Pearson) [186]. We complemented this analysis with an ordination of the forest communities using all pairwise distances represented by a Non-Metric Multidimensional Scaling (NMDS), with the function “metaMDS” of the R “vegan” package, and the application of a PERMANOVA to determine the amount of variance explained by forest type and island [187].

Indicator species. An analysis of the relative indicator species values [188] was performed to determine the specificity (uniqueness to specific sites) and fidelity (rate of recurrence within each site) of each species regarding a particular forest. The indicator value method (IndVal) facilitates the identification of indicator species for a *a priori* established group of forests [189]. In this study the IndVal was based only on within-species comparisons of abundance and has been used to express the importance of species as ecological indicators in community classifications [186]. The level of significance was set at 0.05 and results from a permutation test. Species with significant indicator values above 70% [190,191], were regarded as characteristic indicator species. Indicator Species Analyses were conducted by using the “multipatt2” function of the “Indicspecies” R package [192].

Carbon stock in trees. Aboveground biomass (AGB, kg expressed on a dry-weight basis) of each tree was estimated using allometric equations reported in the literature. Species-specific allometric equations were used for *P. undulatum*, *C. japonica*, *Clethra arborea*, *I. azorica*, *L. azorica*, *Morela faya*, *Phoebe indica* Pax, *Eucalyptus globulus* and *Acacia melanoxylon* [40,42,193-195]. For the remaining species generic allometric equations were used [196,197]. Depending on the species, biomass was estimated from *D*, *H*, *BA* and/or *NB* (number of branches; Supplementary Table S2 online). Although belowground

biomass (*BGB*, kg) in tree roots accounts for a large portion of the total forest biomass and provides an additional important carbon pool, there is still a lack of partitioning data for *BGB*. Thus, *BGB* of each tree was estimated using the standard ratio of root to shoot biomass for temperate oceanic forests, (see Table 4.4, Chapter 4, [198, 199]). After calculating the total biomass (kg per tree) resulting from *AGB* + *BGB*, the carbon stocks (Mg.C.ha^{-1}) per each forest type was estimated as follows: Biomass to carbon conversions were performed pursuant to the guidelines established in the IPCC Guidelines for National Greenhouse Gas Inventories, (see table 4.3, chapter 4, [198]), which assumes carbon content to be 48% for broad-leaved species and 51 % for conifers species, of the *AGB* of each living tree [200-203].

Carbon stocks in soil and leaf litter. Total carbon stock in the soil (Mg/ha) was estimated from organic matter (g/kg) with conversion factor 0.58, so-called Van Bemmelen factor 1.724 [204], multiplied by bulk density (kg/m^3), and considering the mean soil volume available per hectare, depending on soil depth at each site (5 to 10 cm). Total leaf litter carbon (Mg/ha) was estimated from dry biomass per sample (g dry litter/m^2) and considering the amount of carbon by unit of litter biomass (g C/kg dry litter). For soil and leaf litter mean values were used per stand.

Environmental variables. To compare climate on each forest type, we used mean annual temperature, mean annual precipitation, mean annual relative humidity and altitude based on the CIELO Model [205], a raster GIS environment with 100 m spatial resolution that is used to model local scale climate variables relying on limited available data from synoptic coastal meteorological stations [71]. The CIELO model has been calibrated and validated to the Azorean islands and is available through CLIMAAT project (<https://www.climaat.angra.uac.pt>) and in Azevedo & Pereira [72,205].

Statistical tests. Comparisons of all the parameters between forest types and islands was undertaken using two-way ANOVA followed by a post-hoc Tukey HSD test, after verification of the assumptions of their application (i.e., normality, homoscedasticity). Statistical analysis was performed with IBM Corp. Released 2019. IBM SPSS Statistics for Windows, Version 26.0. Armonk, NY: IBM Corp.

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Author contributions

L.B.S. conceptualization, carried out field and lab work, data collection and analysis, writing original draft, writing-review and editing; L.S. funding acquisition, supervision, conceptualization, carried out field work, data collection and analysis, writing-review and editing; D.C.P. conceptualization, carried out field and lab work, data collection and

analysis; R.B.E conceptualization, carried out field and lab work, data collection and analysis, review; M.M. carried out field work, review and editing; M.A.V revised manuscript; All authors have read and agreed to the published version of the manuscript.

Competing Interest

The authors declare no competing interests.

Supplementary information

Taxonomic, structural diversity and carbon stocks in a gradient of island forests

Lurdes B. Silva ^(1*), Diogo C. Pavão⁽¹⁾, Rui B. Elias⁽²⁾, Mónica Moura⁽¹⁾, Maria A. Ventura⁽¹⁾, Luís Silva⁽¹⁾.

⁽¹⁾ CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Pólo dos Açores, Universidade dos Açores, Rua da Mãe de Deus, Apartado 1422, 9501-801 Ponta Delgada, Açores, Portugal.

⁽²⁾ CE3C/ABG – Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group & University of the Azores, 9700-042 Angra do Heroísmo, Azores, Portugal.

*Corresponding author: (lurdes.cb.silva@uac.pt)

Supplementary Table S1. Indicator species analysis. Species that had an indicator value (IndVal>70) and were significant at ($P < 0.05$), are listed in order by descending indicator value within each plant community type.

Forest	Taxa	IndVal
Natural forest	<i>Vaccinium cylindraceum</i>	0.95
	<i>Myrsine africana</i>	0.95
	<i>Ilex perado ssp. azorica</i>	0.93
	<i>Laurus azorica</i>	0.89
	<i>Lysimachia azorica</i>	0.88
	<i>Culcita macrocarpa</i>	0.87
	<i>Hymenophyllum tunbrigense</i>	0.85
	<i>Luzula purpureosplendens</i>	0.84
	<i>Struthiopteris spicant</i>	0.83
	<i>Juniperus brevifolia</i>	0.82
	<i>Athyrium felix femina</i>	0.80
	<i>Selaginella Kraussiana</i>	0.80
	<i>Dryopteris aemula</i>	0.79
	<i>Elaphoglossum semicylindricum</i>	0.76
	<i>Frangula azorica</i>	0.74
	<i>Pteridium aquilinum</i>	0.73
	<i>Erica azorica</i>	0.70
Exotic woodland	<i>Pittosporum undulatum</i>	0.93
	<i>Morella faya</i>	0.73
Production Forest	<i>Cryptomeria japonica</i>	0.99

Supplementary Figure S1. Characterization of soil texture per each forest type (90 stands) and for the three islands.

Supplementary Table S2. Allometric equations used to estimate *AGB* (kg) and *BGB* (kg), were based on diameter at breast height, *DBH* (cm, resulting from the sum of all branches), tree height, *H* (m); number of branches at breast height (1.30 m), *NB*; and basal area, *BA* (cm²; where $BA = DBH^2 \times \pi/4$, resulting from the sum of all branches per tree). Note: *a*, *b*, are scaling coefficients that vary with the variables under investigation.

Species	Allometric equation	References
<i>Acacia melanoxylon</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[1]
<i>Banksia integrifolia</i>	$\ln(AGB) = \ln(a) + b_1 \ln(DBH)$	[2]
<i>Cletra arborea</i>	$\ln(AGB) = a + \ln(DBH^b) + \varepsilon$	[3]
<i>Cryptomeria japonica</i>	$\ln(AGB+BGB) = a + b_1 \ln(DBH) + b_2 \ln(H)$	[4]
<i>Erica azorica</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[5]
<i>Eucalyptus globulus</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[1]
<i>Euphorbia stygiana</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[6]
<i>Frangula azorica</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[6]
<i>Ilex perado</i> subsp. <i>azorica</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[5]
<i>Juniperus brevifolia</i>	$\ln(AGB) = a + \ln(DBH^b) + \varepsilon$	[3]
<i>Laurus azorica</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[5]
<i>Laurus nobilis</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[5]
<i>Myrsine africana</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[6]
<i>Morella faya</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[5]
<i>Ocotea foetens</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[6]
<i>Picconia azorica</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[6]
<i>Pittosporum undulatum</i>	$\ln(AGB) = a + b_1 \ln(BA^2H) + b_2 \ln(DBH^2H) + b_3 \ln(H^2) + b_4 \ln(NB^2) + \varepsilon$	[7]
<i>Psidium littorale</i>	$\ln(AGB) = a + \ln(DBH^b) + \varepsilon$	[3]
<i>Ulmus procera</i>	$(AGB) = 0.0044DBH^{2.438} + 0.0068DBH^{3.001} + 0.1308DBH^{2.271}$	[8]
<i>Viburnum treleasei</i>	$\ln(AGB) = a + b_1 \ln(DBH) + \varepsilon$	[6]

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