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Differentiating diversity among different land cover types in the eastern Amazon

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ABSTRACT

Measurements of biodiversity can be used to assess the scale of anthropogenic impact and predict species loss. A great number of diversity measures exist involving species richness and relative abundance that differ in how they are calculated. The choice of the adequate biodiversity measure to compare biological communities poses a challenge. The aim of this study was to evaluate the ability of 26 diversity measures to differentiate land cover types in the eastern Brazilian Amazon. Diversity was inventoried and quantified in three vertical strata in six locally dominant land cover types: primary and secondary forests, agroforestry systems, oil palm plantations, annual croplands and pastures. No diversity measure was able to differentiate all land cover types in every stratum. Fisher's alpha was able to differentiate cover types in the middle and upper strata, while Smith-Wilson and Jentsch's mixture quotient were able to differentiate in the lower and upper strata, and heterogeneity indices only differentiated in the upper stratum. The distinction and ranking of plant diversity among land covers depended on the diversity measure chosen. The number and types of land cover and vertical strata were a key factor in the ability of the diversity measure to differentiate among them.

KEYWORDS: Amazon conservation; Acará River valley; life forms; Pará state; vertical strata

Diferenciação da diversidade entre diferentes tipos de cobertura do solo na Amazônia Oriental

RESUMO

Medidas da biodiversidade podem ser usadas para avaliar a escala de impactos antropogênicos e prever a perda de espécies. Existem muitas medidas de diversidade envolvendo riqueza e abundância relativa de espécies, que diferem na forma em que são calculadas. A escolha da medida de biodiversidade adequada para comparar diferentes comunidades biológicas representa um desafio. O objetivo deste estudo foi avaliar a capacidade de 26 medidas de diversidade para diferenciar classes de cobertura do solo na Amazônia oriental brasileira. A diversidade foi inventariada e quantificada em três estratos verticais em seis tipos de cobertura do solo localmente dominantes: florestas primárias e secundárias, plantações de dendezeiros, sistemas agroflorestais, áreas de cultivo anual e pastagens. Nenhuma medida de diversidade foi capaz de diferenciar todas as classes de cobertura em cada estrato. O alfa de Fisher foi capaz de diferenciar tipos de cobertura nos estratos médio e superior, enquanto o Smith-Wilson e o quociente de mistura de Jentsch diferenciaram nos estratos inferiores e superiores, e os índices de heterogeneidade apenas diferenciaram no estrato superior. A distinção e a ordenação da diversidade de plantas entre as coberturas dependeram da escolha da medida de diversidade. O número e os tipos de cobertura da terra e de estratos verticais foram um fator chave na capacidade de distinção das medidas de diversidade.

PALAVRAS-CHAVE: conservação da Amazônia; vale do Rio Acará; formas de vida; estado do Pará; estratos verticais

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INTRODUCTION

The study of biodiversity in agricultural landscapes has gained importance with the development of strategies aiming at the sustainability of food production and biological conservation (Balmford *et al.* 2019). Measurements of biodiversity can be used to assess the scale of anthropogenic impacts and predict species loss (Sirami *et al.* 2019), to help environmental policies that incorporate agricultural landscapes as an integral component of conservation programmes (Kok *et al.* 2018). However, measuring biodiversity can be problematic, not only due to the costs related to data collection (Zermeño-Hernández *et al*. 2015), but also because biodiversity estimates often depend on the selection of the ecological metrics used (Gibson *et al.* 2011; Moreno *et al*. 2018).

All biodiversity measures are based on the number of species (richness), species relative abundance (evenness), or the combination of both (heterogeneity) (Magurran 2012), and there has been a rapid evolution of the development of biodiversity indices in recent decades (Newbold *et al.* 2016; Moreno *et al.* 2017) differing in mathematical expression and calculation form (Magurran 2012).

Different metrics may rank samples differently, e.g., in alpha diversity (*sensu* Whittaker 1960) a given measure may indicate that community A is more diverse than B, while another measure may indicate the opposite or similar values. This creates difficulties in choosing measures to compare communities (Beck and Schwanghart 2010), which can compromise comparability among samples or lead researchers to use traditional methods without an adequate methodological or conceptual basis (Moreno *et al.* 2017). Accordingly, many authors choose the most common measures used by their peers in previous studies, which may not always be the most appropriate, particularly when the objective is ultimately to evaluate human impacts on biodiversity (Melo 2008), e.g., when comparing land cover types to assess biodiversity loss in agricultural landscapes.

In the Amazon, species diversity can respond to a wide range of conditions within and among habitats, which can result in a wide range of new species assemblies (Liu *et al.* 2018). Some studies have tried to evaluate plant diversity among agricultural land cover types originating from land use change, but failed to detect subtle differences among vegetation cover measures, e.g., between primary and secondary forest that present a distinct structure and floristic composition (Phillips *et al.* 2017; Do Vale *et al.* 2018) or between tree crops and young secondary forests (Do Vale *et al*. 2018).

When comparing plant diversity, it is important to consider some factors that directly affect measures of diversity, including the vertical structure of the vegetation, as plant communities may or may not be stratified (Do Vale *et al.* 2017). The vegetation strata may be considered as distinct communities due to the variation in biotic and abiotic conditions along the vertical gradient. Factors such as wind speed, temperature, and the amount of sunlight decrease from the canopy to the ground, while the opposite occurs with humidity (Puig 2008). In addition, the characteristics of the vegetation structure, e.g., life forms, stages of plant development and tolerance to shade, also change (Canham *et al*. 1994). Changes in microclimate create complex microhabitats, which consequently influence biodiversity (Nakamura *et al*. 2017).

Although there are some issues to consider, biodiversity measures have been useful to compare plant communities and can be used to test theories about species coexistence and reveal dynamic processes and historical ecosystem determinants (Gibson *et al*. 2011). Nevertheless, when assessing biodiversity among similar habitats for conservation and management purposes, the effectiveness of a biodiversity measure depends on how well it differentiates these habitats (Magurran 2012).

In this context, we evaluated the ability of 26 alpha biodiversity measures to differentiate three vertical strata in several land cover types with distinct structures and land uses in a mosaic of human-modified landscape in the eastern Amazon. Specifically, we analyzed whether a single diversity measure would produce similar behaviors in the different strata when comparing plant diversity among the land cover types.

MATERIAL AND METHODS

Study area

This study was carried out in the Acará River Valley in the northeastern region of the state of Pará, Brazil, including the municipalities of Acará, Bujaru, Tailândia, and Tomé-Açu (Figure 1). This region was colonized by the Portuguese in the 18th century, and native forest cover loss exceeds 60% (Almeida *et al*. 2020a). The region has a hot and humid climate, with a monthly average temperature between 26 and 28 °C, annual average rainfall between 1750 and 3000 mm, and average relative humidity between 80 and 91%. Some areas in this region have an annual period of up to three months without rain, while others do not have a dry period (Andrade *et al*. 2017). The relief is defined by a coastal plateau with a flat top and low altitude (IBGE 2006). Yellow latosol is the predominant soil type, but there are small patches of haplic gleisoil in floodplain areas (IBGE 2015).

Land cover types

Twenty properties (Figure 1) owned by small family farmers were selected based on a socioeconomic study that evaluated the production of labour, income, and food sources in the communities (Costa 2019). Six sampling plots were established on each property, with each plot located within one of the six dominant land cover types on the property. The

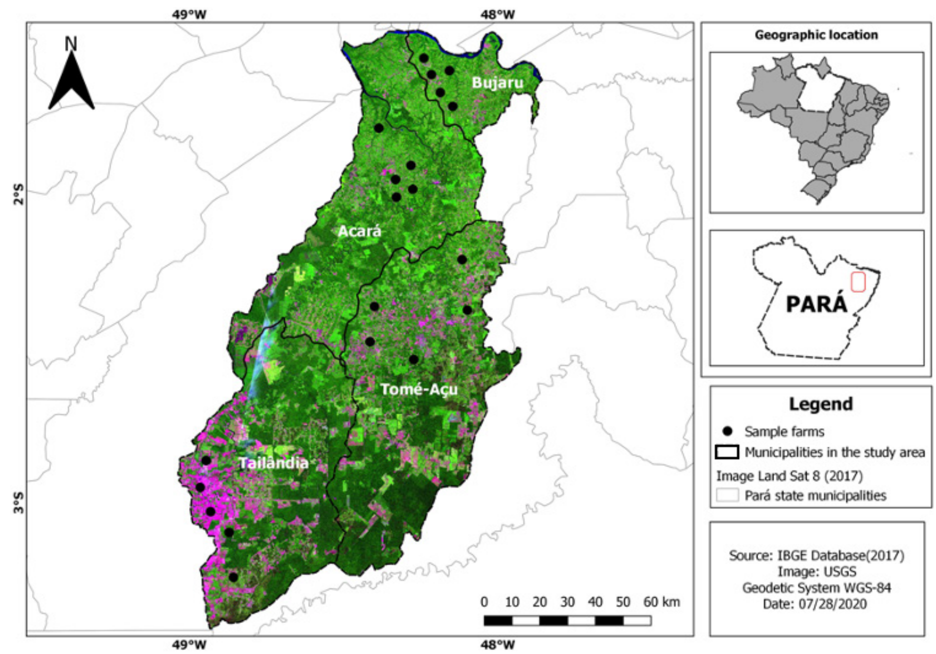

Figure 1. Location of the 20 family farms along the Acará River Valley, in the northeastern region of the state of Pará, Brazil, where sampling plots were established in six different land cover types. This figure is in color in the electronic version.

six dominant land cover classes (LCT) included were primary forest, secondary forest, oil palm plantation, agroforestry systems (SAF), annual cropland, and pasture. The sampling plots on each property were between 100 and 200 m apart from each other.

Primary forest plots were located in fragments of near-primary forest, with no signs of local disturbance, i.e., no large clearings or burnt areas, but these forests are normally used for wood and non-wood product extraction. Primary forests were considered as control areas, as they were the nearest to the original forests that dominated the region. Between 1991 and 2013, approximately 47.7% of these forests were converted to other land uses, with 30% being converted to oil palm plantations (Almeida *et al*. 2020a). Secondary forests were formed by successional vegetation that arose after the abandonment of agricultural areas. It was not possible to specify the time since abandonment. However, based on the structural and floristic criteria established by Salomão *et al*. (2012), we inferred that most secondary forests sampled were in an advanced stage of the succession process.

Oil palm (*Elaeis guinenses* Jacq.) plantations grew 11% in area between 1991 and 2013, and are the main cause of the increase in fragmentation, isolation, and reduction of forest remnants in the region (Almeida *et al*. 2020a). SAF included different spatial arrangements of *Theobroma cacao* L. (cacao), *Theobroma grandiflorum* Willd. ex Spreng. K. Schum. (cupuaçu) and *Euterpe oleracea* Mart. (açai palm), in addition to other non-dominant forest species, such as *Swietenia macrophylla* King (mahogany) and *Carapa guianensis* Aubl (crabwood). Annual croplands included areas for cultivation of *Vigna* sp. (bean), *Oryza* sp. (rice), *Zea mays* L. (maize), and mainly *Manihot esculenta* Crantz (cassava). Pastures were formed by *Urochloa brizantha* (Hochst. Ex A. Rich.) R.D. Webster or *U. humidicola* (Rendle) Morrone & Zuloaga.

If the farm did not include all six LCT described above, the missing LCT were sampled in an adjacent property. In five cases, no oil palm plantation was available, not even on adjacent farms. Therefore, only 15 oil palm plots were sampled, while 20 plots of the other LCT were sampled.

Plant diversity measures

In each sampling plot, the vegetation was surveyed for three strata, as follows: (a) an area of 10 × 50 m was established for the upper stratum (trees with diameter at breast height (DBH) ≥ 10 cm); (b) a sub-plot of 5 × 50 m was established for the middle stratum (trees and shrubs with DBH < 10 cm and height ≥ 2.0 m); and (c) 10 plots of 1 × 1 m were regularly distributed in the centre of the plot for the lower stratum (individuals of all life forms with 2.0 m > height ≥ 10 cm). Only primary forests, secondary forests, and SAF included middle and upper strata. The pre-identification of the species was carried out by a parataxonomist and confirmed by comparison at the João Murça Pires Herbarium at Museu Paraense Emílio Goeldi – MPEG (Belém, Pará).

Initially, vegetation cover was characterised by abundance, specific richness, types of life forms, and shade tolerance (as pioneer or shade-tolerant, according to Do Vale *et al*. 2018), in addition to the number of singletons (species with only one individual per LCT), doubletons (species with only two individuals per LCT), uniques (species detected in only one plot per LCT), and duplicates (species detected in only two plots per LCT). These data help to understand the results since many diversity measures use or are influenced by these indicators.

Subsequently, 26 alpha diversity measures were calculated for each sampling plot (see the equations in Supplementary Material, Table S1), considering three categories: (1) seven richness indices, including: species richness, species density, Fisher's alpha, Gleason, Margalef, Menhinick, and Jentsch's mixture quotient; (2) eight evenness indices, including the McIntosh evenness, Smith-Wilson evenness, Simpson's evenness, Pielou-Simpsons evenness, Gini-Simpson evenness, Buzas-Gibson evenness, Pielou-Shannon evenness (known as pielou index or J), and Heip index; and (3) 11 heterogeneity indices, including the McIntosh index, Simpson, Brillouin, Simpson reciprocal, Gini-Simpson, Berger-Parker, Berger-Parker complement, Berger-Parker reciprocal, Shannon, Shannon exponential, and Shannon maximum index.

Our criteria for the selection of these 26 measures were: (1) to employ measures commonly used in studies at the community-level, such as species richness, species density, Fisher's alpha, Shannon index, Shannon maximum, Pielou-Shannon evenness, and Jentsch's mixture quotient (the latter being more commonly used in forestry); (2) to include measures of different theoretical conceptions; and (3) to include measures with potential to propose improvements over more commonly used measures.

Among richness measures, species richness and species density are the simplest measures of biodiversity, but strongly dependent on sample size and sampling effort; Fisher's alpha (also known as the log series index) and Jentsch's mixture quotient propose to show the relationship between number of species and number of individuals, while the Gleason, Margalef and Menhinick try to reduce the effect of the number of individuals to make the measure more independent of sample size (Palaghianu 2014; Sherwin and Prat I Fornells 2019).

The most important requirement for an evenness measure is that its result is independent of species richness, although the results of the Heip index are less independent of richness than the Smith-Wilson evenness (Smith and Wilson 1996). The Buzas-Gibson evenness is equivalent to the number of equally distributed species (Buzas and Gibson 1969), while the other evenness measures are equivalents of heterogeneity indices, such as the McIntosh evenness, Pielou-Simpsons evenness, Gini-Simpson evenness and Pielou-Shannon evenness.

Among the heterogeneity measures, the McIntosh index is based on geometric analogies where the community is a point in an S-dimensional hypervolume; the Shannon index is derived from information theory, assuming that individuals are randomly sampled from an infinitely large community and that all species are represented in the sample (Shannon exponential and Shannon maximum indices are proposals for improvement of the Shannon index); the Brillouin index is also based on information theory, but assumes that sample randomness cannot be guaranteed; the Simpson index is based on probability theory and calculates the probability that two randomly selected individuals from an infinitely large community belong to the same species (Simpson reciprocal and Gini-Simpson indices are proposals for improvement of the Simpson index); and the Berger-Parker index expresses the proportional importance of the most abundant species and is highly biased by sample size and richness (the Berger-Parker complement and the Berger-Parker reciprocal indices are proposals for improvement of the Berger-Parker index) (Pielou 1975; Magurran 2012). The McIntosh and Simpson indices are considerably more influenced by species equality and less by richness than the Shannon index (DeJong 1975). The Berger-Parker index is recommended to monitor the impairment of biodiversity linked to anthropic disturbances (Caruso *et al*. 2008) as is the case in the biological communities analyzed in this study.

Statistical analysis

The three strata were analysed independently. Diversity was measured in each plot using all 26 diversity measures, and then, to analyse if there were significant differences among LCT, analysis of variance (ANOVA) was performed for each index and stratum separately. The ANOVA models were evaluated using Levene, Shapiro-Wilk and Durbin-Watson tests. If necessary, the data were transformed using the box-cox method of maximum likelihood. If ANOVA assumptions were met, ANOVA analysis was followed by the Fisher's least significant difference (LSD) test for multiple comparison, recommended for situations with sample differences between groups, since there were fewer plots in oil palm plantations ($n = 15$) than in other LCT ($n = 20$). If ANOVA assumptions were not met, the Kruskal-Wallis test (K-W) was applied, followed by Dunn's post hoc test. Significance was set at the 5% probability level (see Supplementary Material, Table S2).

Diversity measures were calculated and analysed using the Paleontological Statistics Software Package for Education and Data Analysis - PAST 3.25 (Hammer *et al*. 2001) and the advi package (Pavoine, 2018) using R 3.6.1 Software (R Core Team 2019).

RESULTS

A total of 25,297 individual plants belonging to 588 species were recorded, of which 436, 330, and 241 species occurred in the lower, middle, and upper strata, respectively. Most of the individuals found in all strata were shade-tolerant trees or shrubs (between 48 and 91% of the individuals), except in the upper stratum of the SAF, where palm trees predominated (48%), and in the lower stratum of the agricultural uses (oil palm plantation, SAF, cropland and pasture), where pioneer herbs predominated (38 to 63%). Most of the species per LCT also were shade-tolerant trees or shrubs (65 to 87%), except in the lower stratum of the agricultural uses, where pioneer herbs and shrubs predominated (36 to 67%). Shade-tolerant tree species were also well represented in the lower stratum of SAF and cropland (24 and 18%, respectively). In pasture, most individuals (48%) were forage species, but they represented only 2.6% of the species (Table 1).

The percentage of singleton and doubleton species in the lower stratum was higher in primary and secondary forests (52 and 43%, respectively) and lower in oil palm plantations, annual croplands, pastures, and SAF (27, 30, 32 and 37%, respectively). This gradient was not observed for unique and duplicate species, since these occurred at high percentages in all LCT (from 62 to 70%). In the middle stratum, SAF had the highest proportion of less abundant species (singletons + doubletons = 63%) and less frequent species (uniques + duplicates = 90%). SAF also had high percentages of less abundant and less frequent species in the upper stratum, ranging from 47% for singletons and doubletons, to 75% for uniques and duplicates (Table 1).

Several indices did not meet ANOVA assumptions, even after data transformation. In the lower, middle, and upper strata, 29, 89, and 75% of the indices were compared using Kruskal-Wallis tests, respectively. The power test was always greater than 0.80, which means that sample sizes were large enough to differentiate small differences, the only exception

Table 1. Individuals and species percentages per life form (LF), e.g., liana, herb, palm, shrub or tree, and ecological group (ST = shade tolerant; P = pioneer) in three strata (lower, middle, upper) of land cover types (PF = primary forest; SF = secondary forest; SAF= agroforestry systems; AC = annual croplands; OP = oil palm plantation; PAS = pasture) in sampling plots in the eastern Brazilian Amazon.

LF	EG	Lower stratum						Middle stratum			Upper stratum		
		PF	SF	SAF	AC	OP	PAS	PF	SF	SAF	PF	SF	SAF
Individuals													
Herb	ST (%)	11.4	15.2	2.0	0.5	0.6	-	-	-	-	-	-	-
	P (%)	0.3	9.7	54.6	59.1	63.2	38.1	-	-	-	-	-	-
Liana	ST (%)	2.1	3.4	0.9	0.3	0.1	-	-	-	-	-	-	-
	P (%)	4.4	10.0	10.8	4.1	2.5	1.6	0.3	0.8	0.2	0.1	-	-
Palm	ST (%)	3.6	4.6	1.2	0.2	-	-	2.2	3.0	48.1	0.7	1.1	34.9
Shrub	ST (%)	12.2	8.5	3.3	2.4	0.2	0.1	4.9	5.0	1.4	-	0.2	-
	P (%)	1.9	3.3	15.0	15.0	22.3	11.2	0.6	4.2	1.9	0.1	1.9	1.1
Tree	ST (%)	59.5	39.9	5.6	4.0	0.9	0.2	86.1	65.4	33.7	83.1	76.9	51.2
	P (%)	4.6	5.3	5.1	5.8	1.5	0.9	5.9	21.6	7.9	15.8	20.0	3.3
Cultivated (%)		-	-	1.6	8.5	8.8	47.9	-	-	6.7	-	-	9.5
Shade-tolerant (%)		88.8	71.7	12.9	7.4	1.7	0.4	93.2	73.4	83.3	83.9	78.1	86.1
Pioneer (%)		11.2	28.3	85.5	84.1	89.5	51.7	6.8	26.6	10.0	16.1	21.9	4.4
Total Individuals		1603	1838	2641	4872	3054	6388	1233	1378	418	669	635	568
Species													
Herb	ST (%)	4.5	4.2	5.6	4.2	2.0	0.0	-	-	-	-	-	-
	P (%)	2.0	3.7	18.1	27.3	36.0	38.5	-	-	-	-	-	-
Liana	ST (%)	4.0	3.7	5.0	4.2	2.0	1.3	-	-	-	-	-	-
	P (%)	4.5	4.2	5.6	11.2	7.0	6.4	0.5	0.4	1.8	0.6	-	-
Palm	ST (%)	2.0	2.6	1.9	2.1	0.0	1.3	1.8	1.3	5.3	1.2	2.6	5.7
Shrub	ST (%)	10.9	11.6	8.8	8.4	3.0	3.8	7.3	8.9	7.0	-	0.9	-
	P (%)	2.5	4.2	18.1	15.4	30.0	28.2	2.3	4.3	7.0	0.6	3.5	3.8
Tree	ST (%)	63.9	57.9	23.8	18.2	8.0	9.0	77.7	71.9	57.9	87.2	79.8	66.0
	P (%)	5.9	7.9	9.4	7.0	6.0	9.0	10.5	13.2	15.8	10.5	13.2	13.2
Cultivated (%)		-	-	3.8	2.1	6.0	2.6	-	-	5.3	-	-	11.3
Shade-tolerant (%)		85.1	80.0	45.0	37.1	15.0	15.4	86.8	82.1	70.2	88.4	83.3	71.7
Pioneer (%)		14.9	20.0	51.3	60.8	79.0	82.1	13.2	17.9	24.6	11.6	16.7	17.0
Singletons (%)		36.1	23.7	21.9	16.1	17.0	26.9	35.0	34.5	40.4	39.5	35.1	37.7
Doubletons (%)		15.8	18.9	15.0	14.0	10.0	5.1	15.9	13.2	22.8	23.8	15.8	9.4
Uniques (%)		49.5	44.2	49.4	46.2	47.0	55.1	42.7	51.9	75.4	50.6	47.4	62.3
Duplicates (%)		18.8	22.6	19.4	16.8	15.0	14.1	18.6	14.0	14.0	20.9	19.3	13.2
Total Species		202	190	160	143	100	78	220	235	57	172	114	53

being Simpson's evenness in the upper stratum, which had a power of 0.49 (Supplementary Material, Table S2).

In the lower stratum, no diversity index was able to differentiate significantly among all LCT (Table 2). Most indices showed no significant difference between primary and secondary forest (78% of the measures), SAF and oil palm plantations (67%), SAF and annual croplands (94%), and oil palm plantations and annual croplands (64%). Some indices did not differ significantly between very different LCT, e.g., Simpson's evenness and Buzas-Gibson between oil palm plantation and primary forest. The Smith-Wilson evenness and Jentsch's mixture quotient were the best in distinguishing LCT, with significant differences among SAF, pasture, primary/secondary forest, and annual cropland/oil palm plantation (Table 2).

In the middle stratum, four evenness measures did not find any significant differences among LCT: Smith-Wilson evenness, Buzas-Gibson index, Pielou evenness index and Heip index (Table 3). Most indices did not differ significantly between primary and secondary forest. Fisher's alpha index was the only one that differentiated primary forests (more diverse) from secondary forests and these from SAFs (less diverse).

In the upper stratum, most measures significantly differentiated among the three LCT, ranking primary forests as the most diverse, followed by secondary forests, and SAF (Table 4). Only Simpson's evenness showed similarity between SAFs and secondary forests, all other measures were able to differentiate SAFs from forests. Six measures indicated similarity between primary and secondary forests, three measures of evenness (Simpson, Buzas-Gibson, Heip) and three measures of heterogeneity (the three variations of the Berger-Parker's index) (Table 4).

Table 2. Values for 26 diversity measures (mean ± standard deviation) in the lower stratum of each of six land cover types (PF = primary forest; SF = secondary forest; SAF = agroforestry systems; AC = annual croplands; OP = oil palm plantation; PAS = pasture) in sampling plots in the eastern Brazilian Amazon. n = sample size. Different letters after the values along lines indicate significant differences between land cover classes according to a Fisher's (*) or Dunn's test.

Diversity measure	PF n = 20	SF n = 20	SAF n = 20	OP n = 15	AC n = 20	PAS n = 20
Richness measures						
Species Richness	27.8 ± 5.70 a	26.4 ± 3.52 ab	20.15 ± 8.21c	20.07 ± 7.47c	22.6 ± 8.05bc	11.40 ± 5.71d
Species density	2.78 ± 0.57a	2.64 ± 0.35ab	2.02 ± 0.82c	2.01 ± 0.75c	2.27 ± 0.8bc	1.14 ± 0.57d
Fisher's alpha *	16.37 ± 5.68a	13.17 ± 2.98a	7.52 ± 2.76b	5.78 ± 2.58b	6.82 ± 2.97b	2.63 ± 1.34c
Gleason *	6.38 ± 1.21a	5.89 ± 0.73a	4.25 ± 1.27b	3.79 ± 1.3b	4.26 ± 1.36b	2.11 ± 0.84c
Margalef*	6.15 ± 1.21a	5.67 ± 0.73a	4.03 ± 1.29b	3.60 ± 1.31b	4.07 ± 1.37b	1.92 ± 0.85c
Menhinick*	3.15 ± 0.61a	2.81 ± 0.42b	1.90 ± 0.5c	1.43 ± 0.47d	1.60 ± 0.54cd	0.78 ± 0.31e
Jentsch's mixture quotient	0.36 ± 0.09 a	0.31 ± 0.08a	0.21 ± 0.12b	0.11 ± 0.04c	0.13 ± 0.07c	0.06 ± 0.04d
Evenness measures						
McIntosh's evenness	0.87 ± 0.06a	0.86 ± 0.07ab	0.76 ± 0.16cd	0.82 ± 0.07bc	0.75 ± 0.1d	0.54 ± 0.19e
Smith-Wilson evenness	0.65 ± 0.09a	0.62 ± 0.09a	0.50 ± 0.13b	0.41 ± 0.1c	0.41 ± 0.12c	0.29 ± 0.08d
Simpson's evenness	0.45 ± 0.11a	0.43 ± 0.15ab	0.37 ± 0.15bc	0.43 ± 0.14ab	0.31 ± 0.14cd	0.28 ± 0.1d
Pielou-Simpson's evenness*	2.47 ± 0.33a	2.51 ± 0.47a	1.81 ± 0.56b	2.03 ± 0.4b	1.79 ± 0.43b	0.99 ± 0.48c
Gini-Simpson's evenness	0.95±0.03a	0.93 ± 0.04ab	0.86 ± 0.14cd	0.91 ± 0.06bc	0.86 ± 0.07d	0.65 ± 0.2e
Buzas-Gibson*	0.65 ± 0.10a	0.54 ± 0.10bc	0.53 ± 0.17bc	0.57 ± 0.11ab	0.47 ± 0.13c	0.39 ± 0.12d
Pielou-Shannon evenness*	0.87 ± 0.05a	0.80 ± 0.06b	0.76 ± 0.13bc	0.80 ± 0.07bc	0.74 ± 0.08c	0.57 ± 0.15d
Heip*	0.64 ± 0.10a	0.61 ± 0,13ab	0.51 ± 0.17cd	0.54 ± 0.12bc	0.45 ± 0.13d	0.32 ± 0.13e
Heterogeneity measures						
McIntosh's index	0.80 ± 0.06a	0.77 ± 0.07a	0.65 ± 0.15b	0.68 ± 0.09b	0.63 ± 0.1b	0.40 ± 0.16c
Brillouin*	2.44 ± 0.20a	2.40 ± 0.22ab	1.97 ± 0.47c	2.18 ± 0.4bc	2.09 ± 0.36c	1.25 ± 0.47d
Simpson's index*	0.09 ± 0.03 a	0.09 ± 0.04a	0.19 ± 0.14b	0.14 ± 0.08b	0.18 ± 0.07b	0.41 ± 0.19c
Simpson's reciprocal index*	12.46 ± 3.77a	11.51 ± 4.66a	6.90 ± 3.01b	8.05 ± 2.34b	6.53 ± 3.05b	3.02 ± 1.52c
Gini-Simpson's index	0.91 ± 0.03a	0.90 ± 0.04a	0.81 ± 0.14bc	0.86 ± 0.08b	0.82 ± 0.07c	0.59 ± 0.19d
Berger-Parker's index*	0.20 ± 0.07a	0.22 ± 0.08a	0.34 ± 0.17bc	0.26 ± 0.11ab	0.34 ± 0.12c	0.56 ± 0.2d
Berger-Parker's complement*	0.80 ± 0.07a	0.78 ± 0.08a	0.66 ± 0.17bc	0.74 ± 0.11ab	0.66 ± 0.12c	0.44 ± 0.2d
Berger-Parker's reciprocal*	5.48 ± 1.54a	5.41 ± 2.37a	3.53 ± 1.31bc	4.37 ± 1.31ab	3.40 ± 1.35c	2.08 ± 0.92d
Shannon index*	2.86 ± 0.27a	2.63 ± 0.25b	2.22 ± 0.5c	2.34 ± 0.42c	2.27 ± 0.39c	1.34 ± 0.48d
Shannon's exponential index*	18.05 ± 4.62a	14.24 ± 3.49b	10.22 ± 4.33c	11.08 ± 3.38c	10.37 ± 4.41c	4.26 ± 2.07d
Shannon's maximum index	3.31 ± 0.21a	3.26 ± 0.14ab	2.92 ± 0.44c	2.91 ± 0.47c	3.05 ± 0.41bc	2.33 ± 0.44d

Table 3. Values for 26 diversity measures (mean ± standard deviation) in the middle stratum of each of three land cover types (PF = primary forest; SF = secondary forest; SAF = agroforestry systems) in sampling plots in the eastern Brazilian Amazon. n = sample size. Different letters after the values along lines indicate significant differences between land cover classes according to a Fisher's (*) or Dunn's test.

Diversity measures	PF n = 20	SF n = 20	SAF n = 20
Richness measures			
Species Richness	32.15 ± 5.5a	29.90 ± 9.55a	4.85 ± 3.83b
Species density	0.13 ± 0.02a	0.12 ± 0.04a	0.02 ± 0.02b
Fisher's alpha *	29.13 ± 8.59a	22.16 ± 10.91b	2.76 ± 2.92c
Gleason *	7.82 ± 1.04a	7.07 ± 1.89a	1.77 ± 1.02b
Margalef	7.57 ± 1.04a	6.82 ± 1.9a	1.33 ± 1.01b
Menhinick	4.11 ± 0.46a	3.61 ± 0.81a	1.13 ± 0.61b
Jentsch's mixture quotient	0.53 ± 0.08a	0.45 ± 0.1ab	0.33 ± 0.25b
Evenness measures			
McIntosh's evenness	0.91 ± 0.05a	0.90 ± 0.05a	0.75 ± 0.26b
Smith-Wilson evenness	0.79 ± 0.06a	0.72 ± 0.08a	0.72 ± 0.24a
Simpson's evenness	0.55 ± 0.16a	0.52 ± 0.11a	0.70 ± 0.25b
Pielou-Simpson's evenness	2.81 ± 0.35a	2.67 ± 0.45a	0.90 ± 0.53b
Gini-Simpson's evenness	0.97 ± 0.02a	0.96 ± 0.03a	0.79 ± 0.24b
Buzas-Gibson	0.75 ± 0.11a	0.71 ± 0.08a	0.78 ± 0.21a
Pielou-Shannon evenness	0.91 ± 0.04a	0.90 ± 0.04a	0.80 ± 0.21a
Heip	0.74 ± 0.11a	0.70 ± 0.09a	0.70 ± 0.26a
Heterogeneity measures			
McIntosh's index	0.86 ± 0.06a	0.83 ± 0.06a	0.50 ± 0.25b
Brillouin	2.58 ± 0.17a	2.50 ± 0.34a	0.81 ± 0.49b
Simpson's index	0.06 ± 0.02a	0.08 ± 0.04a	0.46 ± 0.21b
Simpson's reciprocal index	17.57 ± 5.61a	15.82 ± 7.16a	2.84 ± 1.81b
Gini-Simpson's index	0.94 ± 0.02a	0.92 ± 0.04a	0.54 ± 0.21b
Berger-Parker's index	0.16 ± 0.06a	0.18 ± 0.08a	0.56 ± 0.2b
Berger-Parker's complement	0.84 ± 0.06a	0.82 ± 0.08a	0.44 ± 0.2b
Berger-Parker's reciprocal	7.12 ± 2.57a	6.84 ± 3.07a	2.03 ± 0.81b
Shannon index	3.16 ± 0.21a	3.00 ± 0.39a	1.05 ± 0.59b
Shannon's exponential index	24.00 ± 5.08a	21.59 ± 8.23a	3.42 ± 2.4b
Shannon's maximum index	3.46 ± 0.17a	3.35 ± 0.34a	1.34 ± 0.68b

Table 4. Values for 26 diversity measures (mean ± standard deviation) in the upper stratum of each of three land cover types (PF = primary forest; SF = secondary forest; SAF = agroforestry systems) in sampling plots in the eastern Brazilian Amazon. n = sample size. Different letters along lines indicate significant differences between land cover classes according to a Fisher's (*) or Dunn's test.

Diversity measure	PF n = 20	SF n = 20	SAF n = 20
Richness measures			
Species Richness	20.60 ± 3.19a	15.35 ± 4.94b	5.68 ± 2.71c
Species density	0.04 ± 0.01a	0.03 ± 0.01b	0.01 ± 0.01c
Fisher's alpha	26.54 ± 13.13a	13.93 ± 8.7b	2.46 ± 1.62c
Gleason	5.89 ± 0.77a	4.43 ± 1.3b	1.73 ± 0.76c
Margalef	5.60 ± 0.78a	4.14 ± 1.31b	1.41 ± 0.78c
Menhinick	3.58 ± 0.45a	2.71 ± 0.76b	1.09 ± 0.48c
Jentsch's mixture quotient	0.63 ± 0.1a	0.48 ± 0.13b	0.22 ± 0.11c
Evenness measures			
McIntosh's evenness	0.93 ± 0.05a	0.87 ± 0.11b	0.66 ± 0.24c
Smith-Wilson evenness	0.84 ± 0.06a	0.76 ± 0.09b	0.57 ± 0.22c
Simpson's evenness*	0.68 ± 0.14a	0.60 ± 0.13ab	0.56 ± 0.18b
Pielou-Simpson's evenness*	2.61 ± 0.31a	2.15 ± 0.54b	0.99 ± 0.52c
Gini-Simpson's evenness	0.97 ± 0.03a	0.93 ± 0.08b	0.73 ± 0.24c
Buzas & Gibson evenness*	0.83 ± 0.08a	0.76 ± 0.11a	0.67 ± 0.16b
Pielou-Shannon evenness	0.94 ± 0.04a	0.89 ± 0.08b	0.71 ± 0.2c
Heip*	0.82 ± 0.09a	0.74 ± 0.12a	0.57 ± 0.22b
Heterogeneity measures			
McIntosh's index*	0.88 ± 0.06a	0.79 ± 0.13b	0.46 ± 0.2c
Brillouin	2.19 ± 0.16a	1.90 ± 0.35b	0.98 ± 0.47c
Simpson's index	0.08 ± 0.03a	0.14 ± 0.09b	0.43 ± 0.23c
Simpson's reciprocal index	14.16 ± 4.02a	9.62 ± 4.19b	3.04 ± 1.54c
Gini-Simpson's index	0.92 ± 0.03a	0.86 ± 0.09b	0.57 ± 0.23c
Berger-Parker's index*	0.16 ± 0.07a	0.24 ± 0.14a	0.55 ± 0.21b
Berger-Parker's complement	0.84 ± 0.07a	0.76 ± 0.14a	0.45 ± 0.21b
Berger-Parker's reciprocal*	7.09 ± 2.62a	5.16 ± 2.16a	2.05 ± 0.76b
Shannon index	2.82 ± 0.21a	2.40 ± 0.46b	1.19 ± 0.56c
Shannon's exponential index	17.16 ± 3.56a	12.02 ± 4.76b	3.79 ± 2.01c
Shannon's maximum index	3.01 ± 0.15a	2.68 ± 0.34b	1.61 ± 0.53c

DISCUSSION

None of the 26 diversity measures tested in this study was able to differentiate all vertical strata among the forest and agricultural land cover types analyzed. The differentiation ability was related to the number of land covers analyzed and the magnitude of the difference among them. In the lower stratum, where six LCT were compared, it was more difficult to differentiate among LCT than in the middle and upper strata, where only three LCT were compared. Differences among measures often produce different diversity rankings, and accordingly, conclusions on which LCT is more diverse than the other can ultimately depend on a subjective choice of diversity measure (Butturi-Gomes 2017).

The difficulty in differentiating LCT in the lower stratum may also be related to the greater complexity of life forms and ecological groups in all LCT. Tree and shrub seedlings scattered throughout the landscape can increase diversity similarity among LCT either permanently or temporarily, according to their establishment potential in different habitats (Arroyo-Rodrigues *et al.* 2017; Mestre *et al*. 2019).

In the lower stratum, plant diversity in all agricultural LCT was difficult to separate. Most indices did not differ significantly among SAF, oil palm plantations and cropland, differentiating only pastures. This may be due to the high abundance of pioneer herbaceous plants (weed plants) in all agricultural land covers, but their lower species richness in pasture. Contrary to our results, Do Vale *et al*. (2017, 2018) found that annual croplands in the Palmares II settlement had a similar diversity to pastures; and Almeida *et al.* (2020b) found similar diversity between oil palm plantations and pastures.

It is difficult to differentiate the biodiversity of agricultural land covers due to factors related to the history and intensity of use and management practices, which affect the establishment of plant species (Peres *et al*. 2010; Mukul and Herbohn 2016). In oil palm plantations, for example, the effects on biodiversity depend on the technique used in the initial preparation of the area, herbicide applications and cleaning frequency (Fitzherbert *et al*. 2008).

In the middle and upper strata, SAF were more easily differentiated by most indices. Although SAF seek to reproduce the structure of forest environments, with greater diversity than other agricultural types. When compared to forests, SAFs have lower species diversity. SAF diversity is influenced by management strategies such as selection of species to be planted, mediated by land use history, which results in agroforests with varying habitat potential for species conservation (Valencia *et al*. 2016).

As secondary forests were estimated to be in an advanced stage of succession, they were expected to be similar to primary forests (Chazdon 2012; Coelho *et al*. 2012); however, the response of biodiversity measures varied among vertical vegetation strata, and the ability of the diversity measures to differentiate among primary and secondary forest decreased from the upper to the lower stratum. Vertical stratification is almost never considered in studies of comparative biodiversity, but our results suggest that the inclusion of vegetation strata in the sampling design can highlight differential effects of the distribution of plant life forms and ecological groups in different niches of primary and secondary forests. These results reinforce the great regeneration capacity of secondary forests, as has been previously established by many studies (Arroyo-Rodríguez et al. 2017; Phillips et al. 2017; Lennox et al. 2018; Rozendaal et al. 2019).

The lack of significant differences between primary and secondary forest in the lower stratum were likely influenced by the establishment of shade-tolerant herbs, shrubs, and tree seedlings. In the middle and upper strata, however, species are more specific to each successional stage, leading to a greater dissimilarity between these forests (Chazdon 2012), as was also observed in our samples. This successional divergence was more evident in the upper stratum, since 20 diversity measures were able to differentiate primary forests from secondary forests in this stratum, and less apparent in the middle stratum, where only Fisher's alpha index was able to differentiate between these forest types. This alpha index is based purely on the relationship between the number of species and individuals, so it cannot be used for non-integer measures of abundance, such as biomass, nor detect changes in evenness (Magurran 2012). Its ability to separate secondary and primary forests in the middle and upper strata may be due to the large differences in the number of individuals and species between the two forest types. For this reason, Fisher's alpha index is recommended by ecologists for its ability to differentiate between different habitats, with little bias towards sample size (Magurran 2012).

In agricultural land covers, vertical stratification is limited since the vegetation does not reach high heights in most classes and forest seedlings in the inferior stratum, which are valuable for conservation assessments, can be lost among the weeds typical of croplands and pastures. However, the local pool of forest seedlings that survive the land use change is valuable as an environmental service for future forest regeneration, as well as helping to maintain forest dispersers and pollinators, such as birds and bees, that play an essential role in the productivity and sustainability of agricultural environments (Phalan 2018). Another conditioning factor in agricultural land covers is the weed density and tree seedlings, which is highly variable and dynamic in the inferior stratum, not only among LCT, but also over time and space within LCT, significantly affecting the performance of the diversity measures (Lacerda *et al*. 2013).

CONCLUSIONS

Our results suggest that the ability of diversity measures to differentiate significantly among LCT depends on: (1) the number of LCT being compared; (2) the vertical vegetation stratum considered; and (3) the successional stage of forest types being compared. An increase in the number of LCT increases environmental complexity and makes comparability more difficult. The type and abundance of life forms and ecological groups varies among vegetation strata, altering the characteristics of the plant community of a LCT. The tested metrics seemed to be more sensitive to differences among LCT in the upper stratum compared to the middle and lower strata, possibly due to the absence of the highly dynamic assemblage of weed and tree seedlings and saplings. Meanwhile, secondary forests in an advanced successional stage can have similar plant diversity to primary forests, making more difficult to distinguish between them if species composition is not considered. The results on the diversity metrics analyzed here can assist future comparative studies aiming to assess species conservation in human-modified landscapes.

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DATA AVAILABILITY

The data that support the findings of this study are available, upon request, from the corresponding author [Izildinha Souza Miranda].

SUPPLEMENTARY MATERIAL (only available in the electronic version)

Dias *et al*. Differentiating diversity among different land cover types in the eastern Amazon

Table S1. Name, acronym (in parenthesis), equation and source reference of biodiversity measures used to calculate alpha diversity measures in three vertical strata in sampling plots of six land cover types in the eastern Brazilian Amazon.

Biodiversity measure	Equation	Reference
Richness measures		
1. Species Richness (S)	S = total number of species	McIntosh (1967)
2. Species density (S_d)	S_d = S/area	Magurran (2012)
3. Fisher's alpha (α)	α = (N (1-x))/x where: N = total number of individuals x = number of species that only have one individual	Fisher (1943)
4. Gleason (D_g)	$D_g = \frac{S}{\ln N}$ where: ln = natural log	Gleason (1922)
5. Margalef (D_{mg})	$D_{mg} = \frac{S-1}{\ln N}$	Margalef (1957)
6. Menhinick (D_{mn})	$D_{mn} = \frac{S}{\sqrt{N}}$	Menhinick (1964)
7. Jentsch's mixture quotient (QM)	$QM = \frac{S}{N}$	Förster (1973)
Evenness measures		
8. McIntosh's evenness (M_{ciE})	$M_{ciE} = \frac{N-U}{N-N/\sqrt{N}}$ where: $U = \sqrt{\sum_{i=1}^{S} n_i^2}$ n_i= number of individuals of *i* species	Pielou (1975)
9. Smith-Wilson evenness (E_{var})	$E_{var} = 1 - \left[\frac{2}{\pi \arctan\{\sum_{i=1}^{S} (\ln ni - \sum_{j=1}^{S} nj/S)^2\}/S}\right]$ where: n_i = number of individuals of species i; n_j = number of individuals of species j; S = total number of species	Smith and Wison (1996)
10. Simpson's evenness (E_s)	Es = (1 /D)/S where D = Simpson dominance $D = \frac{\sum_{i=1}^{S} ni\,(ni-1)}{N\,(N-1)}$ where n_i = number of individuals of species *i*; N = total number of individuals; S = total number of species	Williams (1964)

11. Pielou-Simpson evenness (E_{Ps})	$E\text{-}\ln D = \frac{-\ln D}{\ln S}$
	where: D = Simpson dominance;
	ln = natural log;
	S = total number of species
		Magurran (2012)

12. Gini-Simpson evenness (E_{1-D})	$E_{1-D} = \frac{(1-D)}{1-1/S}$ where: D = Simpson dominance; S = total number of species	Simpson (1949); Smith Wilson (1996)
13. Buzas-Gibson evenness (E_{bg})	$E_{bg} = e^H/S$ where e = antilog of H; H = Shannon's exponential index; S = total number of species	Buzas e Gibson (1969)

Table S1. Continued.

Biodiversity measure	Equation	Reference
14. Pielou-Shannon evenness or only Pielou evenness (J)	$J = H'/H'_{max}$ where: H' = Shannon index; $H' = H' = -\sum_{i=1}^{S} pi * \ln pi$ where p_i = relative density of species $i = n_i/N$ n_i = number of individuals of species i; N = total number of individuals; H'max = Shannon maximum = ln(S) S = total number of species	Pielou (1975)
15. Heip (E_{Heip})	$E_{Heip} = \frac{e^{H'} - 1}{S - 1}$ where: H' = Shannon index; S = total number of species	Heip (1974)
Heterogeneity indices		
16. McIntosh's index (M_{ciD})	$M_{ciD} = \frac{N - U}{N - \sqrt{N}}$, where N = total number of individuals; $U = \sqrt{\sum_{i=1}^{S} n_i^2}$ where: n_i = number of individuals of species i; N = total number of individuals;	McIntosh (1967); Magurran (2012)
17. Brillouin (HB)	$HB = \frac{\ln N! - \sum \ln ni!}{N}$ where n_i = number of individuals of species *i*; N = total number of individuals	Brillouin (1951)
18. Simpson's index (D)	D = Simpson dominance	Simpson (1949)
19. Simpson's reciprocal index (Sr)	$S_r = 1/D$ where: D = Simpson dominance	Simpson (1949)
20. Gini-Simpson's index (Gs)	Gs =1-D where: D = Simpson dominance	Simpson (1949); Hurlbert (1971)
21. Berger-Parker's index (d)	$d = N_{max}/N$ where: N_{max} = n individuals of most abundant species; N = total number of individuals	Berger-Parker (1970)
22. Berger-Parker's complement (d_c)	$d_c = 1-d$ where d = Berger-Parker's index	Berger-Parker (1970)
23. Berger-Parker's reciprocal (d_r)	$d_r = 1/d$	Berger-Parker (1970)
24. Shannon index (H')	$H' = -\sum_{i=1}^{S} pi * \ln pi$ where: p_i = relative density of species $i = n_i/N$ ln = natural log; n_i = number of individuals of species *i*; N = total number of individuals	Shannon-Weaver (1949)
25. Shannon's exponential index (H_{exp})	$H_{exp} = e^{H'}$ or exp (H')	Colwell (2016)
26. Shannon's maximum index (H_{max})	$H_{max} = \ln(S)$ where: ln = natural log; S = Total number of species	Pielou (1969)

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Table S2. Parameters for assessing ANOVA assumptions and ANOVA or Kruskal-Wallis test results used to compare 26 diversity measures across six land cover types in three vertical strata (lower, middle and upper) in sampling plots in the eastern Brazilian Amazon. Lambda (λ) was used when necessary to transform the data using the box-cox method of maximum likelihood.

Diversity measure	Test to assess ANOVA assumptions						ANOVA or Kruskal-Wallis		Lambda (λ)
	Shapiro–Wilk		Levene		Durbin Watson				
	W	p	F	p	D	p	F/K-W	p	
					Lower stratum				
Species Richness	0.996	0.984	3.704	0.004	2.305	0.244	43.84	<0.001	0.787
Species density	0.996	0.984	3.704	0.004	2.305	0.208	43.84	<0.001	0.787
Fisher's alpha*	0.985	0.255	0.875	0.500	2.466	0.05	51.53	<0.001	0.343
Gleason*	0.988	0.443	1.666	0.149	2.377	0.124	36.15	<0.001	-
Margalef*	0.989	0.482	1.762	0.126	2.377	0.130	34.97	<0.001	-
Menhinick*	0.990	0.569	1.896	0.101	2.307	0.272	65.83	<0.001	-
Jentsch's mixture quotient (QM)	0.992	0.782	1.969	0.088	1.841	0.186	48.69	<0.001	-0.420
McIntosh's evenness	0.970	0.011	2.148	0.065	1.812	0.230	52.97	<0.001	2.000
Smith-Wilson	0.987	0.336	1.177	0.325	2.051	0.824	33.78	<0.001	-
Simpson's evenness	0.994	0.917	0.850	0.517	1.666	0.020	25.69	<0.001	0.666
Pielou-Simpson's evenness*	0.985	0.236	1.126	0.351	2.083	0.938	30.05	<0.001	-
Gini-Simpson's evenness	0.917	<0.001	5.219	<0.001	1.969	0.538	57.41	<0.001	2.000
Buzas-Gibson*	0.991	0.674	1.396	0.231	1.662	0.022	9.89	<0.001	-
Pielou-Shannon evenness*	0.974	0.037	1.812	0.116	1.768	0.088	21.67	<0.001	2.000
Heip*	0.995	0.976	1.218	0.306	1.667	0.030	14.90	<0.001	-
McIntosh's index	0.970	0.012	0.615	0.638	2.040	0.818	67.78	<0.001	2.000
Brillouin*	0.996	0.992	1.919	0.097	2.818	0.320	25.26	<0.001	1.919
Simpson's index*	0.991	0.723	1.469	0.206	2.041	0.804	29.30	<0.001	-0.220
Simpson's reciprocal index*	0.992	0.743	0.858	0.512	2.064	0.946	27.96	<0.001	0.303
Gini-Simpson's index	0.931	<0.001	4.165	0.001	2.165	0.674	61.74	<0.001	2.000
Berger-Parker's index*	0.992	0.771	0.664	0.652	1.945	0.478	18.07	<0.001	-0.140
Berger-Parker's complement*	0.986	0.279	1.276	0.279	2.023	0.794	19.18	<0.001	2.000
Berger-Parker's reciprocal*	0.986	0.279	1.276	0.279	2.023	0.794	19.18	<0.001	0.141
Shannon index*	0.991	0.664	0.946	0.454	2.320	0.206	33.63	<0.001	1.798
Shannon's exponential index*	0.982	0.129	1.936	0.090	2.229	0.436	28.75	<0.001	-
Shannon's maximum index	0.995	0.965	4.272	0.001	2.385	0.100	43.84	<0.001	2.000
					Middle stratum				
Species Richness	0.972	0.191	3.689	0.031	2.549	0.058	39.45	<0.001	0.464
Species density	0.967	0.081	3.923	0.025	2.536	0.062	39.44	<0.001	0.464
Fisher's alpha*	0.969	0.135	1.845	0.167	2.466	0.096	111.50	<0.001	0.343
Gleason*	0.985	0.685	5.584	0.006	2.473	0.142	137.00	<0.001	0.626

Table S2. Continued.

Diversity measure	Test to assess ANOVA assumptions						ANOVA or Kruskal-Wallis		Lambda (λ)
	Shapiro–Wilk		Levene		Durbin Watson				
	W	p	F	p	D	p	F/K-W	p	
Margalef	0.978	0.383	5.651	0.006	2.504	0.084	39.67	<0.001	0.626
Menhinick	0.972	0.180	4.360	0.017	2.528	0.060	40.87	<0.001	0.828
Jentsch's mixture quotient (QM)	0.923	<0.001	10.03	<0.001	1.933	0.562	14.64	<0.001	-0.670
McIntosh's evenness	0.906	<0.001	12.24	<0.001	2.297	0.346	7.38	0.025	2.000
Smith-Wilson	0.966	0.094	19.78	<0.001	2.160	0.732	4.05	0.132	2.000
Simpson's evenness	0.965	0.079	4.479	0.016	2.261	0.428	8.762	0.012	0.989
Pielou-Simpson's evenness	0.982	0.785	0.603	0.536	2.732	0.010	39.47	<0.001	1.111
Gini-Simpson's evenness	0.821	<0.001	13.54	<0.001	2.310	0.296	14.63	<0.001	2.000
Buzas-Gibson	0.959	0.045	6.908	0.002	2.207	0.572	5.41	0.066	2.000
Pielou-Shannon evenness	0.880	<0.001	10.88	<0.001	2.26	0.454	3.853	0.146	2.000
Heip	0.964	0.078	8.914	<0.001	2.272	0.422	2.271	0.321	2.000
McIntosh's index	0.925	0.001	8.594	<0.001	1.882	0.448	27.98	<0.001	2.000
Brillouin	0.981	0.489	2.886	0.064	2.705	0.008	39.25	<0.001	1.353
Simpson's index	0.987	0.747	0.448	0.641	2.761	0.010	39.47	<0.001	-0.140
Simpson's reciprocal index	0.987	0.748	0.448	0.641	2.761	0	39.40	<0.001	0.141
Gini-Simpson's index	0.923	<0.001	15.050	<0.001	2.458	0.126	39.49	<0.001	2.000
Berger-Parker's index	0.986	0.744	0.277	0.759	2.797	0.004	37.65	<0.001	0.060
Berger-Parker's complement	0.987	0.799	3.232	0.046	2.589	0.040	77.71	<0.001	2.000
Berger-Parker's reciprocal	0.986	0.744	0.277	0.759	2.797	0.004	37.65	<0.001	-0.060
Shannon index	0.970	0.131	2.878	0.064	2.694	0.010	39.64	<0.001	1.434
Shannon's exponential index	0.971	0.156	2.557	0.086	2.714	0.004	39.64	<0.001	0.303
Shannon's maximum index	0.965	0.081	3.923	0.025	2.536	0.052	164.70	<0.001	1.838
Upper stratum									
Species Richness	0.978	0.334	3.979	0.024	2.733	0.012	40.57	<0.001	0.666
Species density	0.977	0.334	3.988	0.024	2.734	0.008	41.04	<0.001	0.666
Fisher's alpha	0.975	0.262	2.551	0.088	2.613	0.026	41.65	<0.001	0.141
Gleason	0.981	0.484	5.576	0.006	2.747	0.006	41.50	<0.001	0.747
Margalef	0.988	0.359	5.515	0.006	2.729	0.012	41.50	<0.001	0.747
Menhinick	0.978	0.359	5.261	0.008	2.715	0.010	42.07	<0.001	0.787
Jentsch's mixture quotient (QM)	0.947	0.012	2.331	0.106	2.462	0.108	39.78	<0.001	-0.828
McIntosh's evenness	0.895	<0.001	5.336	0.008	1.734	0.182	26.18	<0.001	2.000
Smith-Wilson	0.968	0.120	7.653	0.001	1.990	0.780	22.48	<0.001	2.000
Simpson's evenness*	0.991	0.960	0.983	0.381	2.002	0.784	3.46	<0.001	-
Pielou-Simpson's evenness*	0.963	0.066	2.639	0.080	2.389	0.208	61.84	<0.001	-
Gini-Simpson's evenness	0.847	<0.001	8.561	<0.001	1.535	0.026	29.93	<0.001	2.000
Buzas-Gibson*	0.985	0.657	2.867	0.065	2.002	0.836	8.00	<0.001	2.000
Pielou-Shannon evenness	0.910	<0.001	9.001	<0.001	1.639	0.106	25.92	<0.001	2.000
Heip*	0.972	0.199	2.640	0.080	1.920	0.550	13.17	<0.001	2.000
McIntosh's index*	0.969	0.136	2.508	0.091	2.385	0.188	61.60	<0.001	2.000
Brillouin	0.981	0.478	3.437	0.039	2.566	0.044	38.29	<0.001	1.717
Simpson's index	0.972	0.185	1.988	0.146	2.639	0.022	37.60	<0.001	-0.343
Simpson's reciprocal index	0.972	0.185	1.988	0.146	2.639	0.018	37.60	<0.001	0.343
Gini-Simpson's index	0.913	<0.001	8.505	<0.001	1.971	0.702	37.61	<0.001	2.000
Berger-Parker's index*	0.971	0.179	0.635	0.534	2.341	0.284	34.09	<0.001	-0.101
Berger-Parker's complement	0.945	0.009	1.609	0.209	2.254	0.522	34.09	<0.001	2.000
Berger-Parker's reciprocal*	0.971	0.179	0.635	0.534	2.341	0.298	34.09	<0.001	0.101
Shannon index	0.976	0.293	4.192	0.020	2.662	0.012	39.04	<0.001	1.636
Shannon's exponential index	0.980	0.463	3.723	0.030	2.733	0.012	39.40	<0.001	0.505
Shannon's maximum index	0.971	0.177	5.300	0.008	2.615	0.016	41.04	<0.001	2.000