Human pressure drives biodiversity–multifunctionality relationships in large Neotropical wetlands

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Many studies have shown that biodiversity regulates multiple ecological functions that are needed to maintain the productivity of a variety of ecosystem types. What is unknown is how human activities may alter the 'multifunctionality' of ecosystems through both direct impacts on ecosystems and indirect effects mediated by the loss of multifaceted biodiversity. Using an extensive database of 72 lakes spanning four large Neotropical wetlands in Brazil, we demonstrate that species richness and functional diversity across multiple larger (fish and macrophytes) and smaller (microcrustaceans, rotifers, protists, and phytoplankton) groups of aquatic organisms are positively associated with ecosystem multifunctionality. Whereas the positive association between smaller organisms and multifunctionality broke down with increasing human pressure, this positive relationship was maintained for larger organisms despite the increase in human pressure. Human pressure impacted multifunctionality both directly and indirectly through reducing species richness and functional diversity of multiple organismal groups. These findings provide further empirical evidence about the importance of aquatic biodiversity for maintaining wetland multifunctionality. Despite the key role of biodiversity, human pressure reduces the diversity of multiple groups of aquatic organisms, eroding their positive impacts on a suite of ecological functions that sustain wetlands.

Human activities are causing biodiversity to decline worldwide[1,2], which has led to an interest in how biodiversity loss might alter the functioning of ecosystems[3]. Most studies have revealed positive and saturating effects of biodiversity on single ecosystem functions[4]. Empirical evidence suggests that species are ecologically unique and can play complementary roles in natural systems, thus varying in their contributions to different functions[3-5]. As a consequence, the effect of biodiversity on ecosystem functioning is stronger – and the relationship is non-saturating – when multiple functions are considered (hereafter 'multifunctionality')[5-8]. Therefore, it has been increasingly recognized that biodiversity and multifunctionality are strongly associated. This recognition has led to the prediction that as biodiversity declines in human-dominated ecosystems, their ability to sustain multiple ecosystem functions is impaired, ultimately altering the biodiversity-multifunctionality relationship[3,9-13]. Current evidence supporting the anthropogenic impacts on biodiversity-multifunctionality relationships are scarce and comes mostly from experimental manipulations of single trophic levels[10-13]. It is possible that these studies under-estimate human impacts on biodiversity and ecosystem multifunctionality since natural systems are comprised of multiple organismal groups of varying trophic levels, and different trophic levels may combine to have stronger impacts on multifunctionality[5-7]. Further research applying a multitrophic perspective is needed to develop a more mechanistic understanding of the consequences of human pressures for biodiversity-ecosystem functioning relationships in natural systems worldwide.

Here, we used a unique dataset from 72 lakes distributed across four large Neotropical wetlands of Brazil (Amazon, Araguaia, Pantanal and Paraná) to test how the cumulative effect of multiple human pressures impacts the relationship between biodiversity and multifunctionality. These four wetlands provide a unique opportunity to test the influence of human pressures across broad spatial scales as the lakes span a 3,700,000 km^2 gradient of distinct human activities (Fig. 1). We quantified human pressure on the wetland using the Human Footprint (HFP) index[14], which was extracted for each lake individually (see Methods). The HFP is a recently developed index that incorporates eight different human pressures: (i) built environments, (ii) crop land, (iii) pasture land, (iv) human density, (v) night-time lights, (vi) railways, (vii) roads, and (viii) navigable waterways into a standardized cumulative index of human pressure[14]. This index provides an interesting opportunity to understand how human pressures are affecting biodiversity-multifunctionality relationships in natural to human-dominated systems.

We compiled data on the species richness and functional diversity of seven taxonomic groups, including fish, aquatic macrophytes, microcrustaceans, rotifers, phytoplankton, ciliates, and testate amoebae. These data comprised 1,465 plant, animal, and microbial species. Because biodiversity-multifunctionality relationships can be multi-dimensional[6-7], we also used measures of multidiversity (joint diversity of all organismal groups, both for species richness and functional diversity)[15]. Studies considering multidiversity have found strong biodiversity-multifunctionality relationships[6-8]. To estimate functional diversity, we focused on a core set of independent organismal traits that mediate the species response to human pressures (Supplementary Table 1): body size, resource-use (e.g., feeding groups, growth forms, and mixotrophy), and mobility (e.g., migration ability, propagation method, and cell motility) traits. These traits are often linked to multiple ecosystem functions in wetlands. For instance, body size, feeding groups, and migration ability are related to metabolism, multitrophic biomass production, and nutrient cycling[16-17]. We further quantified ecosystem multifunctionality by using a set of 11 variables that included nutrient concentrations (*in situ* measurements of N and P water concentrations), metabolism (daily changes in water O_2 concentration), biomass at multiple trophic levels (algae, herbivores, carnivores, detritivores, and omnivores), microorganism abundance (bacterial cell densities), availability of photosynthetically active radiation (light availability underwater), and variation in habitat complexity under water (variation in plant above-bottom cover). Together, these variables measure environmental characteristics that are directly linked to ecosystem functions. A detailed rationale for each variable is provided in Supplementary Table 2. We quantified multifunctionality using three common approaches: (i) the averaging multifunctionality index, (ii) the multi-threshold multifunctionality index, and (iii) multiple single functions. The averaging approach takes the average of the standardized values of each single function. In contrast, the multi-threshold considers the number of functions that simultaneously surpass a range of thresholds, which are expressed as a percentage of the highest observed level of functioning (here, 1-99%). These three approaches are complementary, and when taken together, they provide a robust estimation of how multiple functions (averaging and multi-pillar approach), as well as single functions, respond to biodiversity enhancement[5-8,18].

Because no studies have examined the broad-scale relationships between biodiversity and ecosystem multifunctionality across wetlands, we first established whether species richness and the functional diversity of the seven organismal groups were, in fact, related to multifunctionality as previous narrow-scale evidence suggests[17,19]. For this, we employed multiple linear mixed models considering species richness and functional diversity as predictors and multifunctionality as the response. After confirming a consistent relationship, we also used linear mixed model to determined how human pressures alter these biodiversity-multifunctionality relationships. Lastly, we used structural equation models (SEMs) to investigate the direct and indirect biodiversity-mediated pathways by which human pressure can influence multifunctionality in wetlands.

Results and discussion

Across four hyperdiverse Neotropical wetlands, we found significant positive relationships between the diversity of single groups of aquatic organisms and the multidiversity of all groups with ecosystem multifunctionality (Figs. 2 and 3, and Supplementary Table 3). This finding was consistent for both species richness and functional diversity (Figs. 2 and 3). Our model averaging procedure revealed that the biodiversity of organismal groups was best predictors of multifunctionality, even after accounting for influence of other well-known drivers of multifunctionality such as space, climate (precipitation and temperature), and aquatic properties (conductivity, pH and water level (Supplementary Table 4). The positive association between aquatic biodiversity and multifunctionality persisted regardless of how the measures of multifunctionality were weighted (Supplementary Figs. 1 and 2). The multi-threshold approach provided additional evidence showing that the mean minimum threshold at which the species richness of organismal groups had its strongest effects on multifunctionality averaged 57% (range 5-92%, Supplementary Fig. 3). Similarly, the mean minimum threshold at which functional diversity had its strongest effects on multifunctionality was 91% (range 70-99%, Supplementary Fig. 4). The diversity of aquatic organism groups was also positively associated with most of the individual ecosystem functions, although each organismal group was more closely associated with specific functions (Supplementary Tables 5 and 6). Here, fish diversity was strongly related to multitrophic biomass, macrophyte diversity was most strongly related to light availability and habitat complexity, whereas microorganism diversity was most related to nutrient concentrations and ecosystem metabolism (Extended Data Figs. 1 and 2). Finally, aquatic biodiversity had stronger effects on multifunctionality than other multifunctionality drivers (Extended Data Figs. 3 and 4; SEM: total effect of composite species richness on multifunctionality 0.79, total effect of composite functional diversity on multifunctionality 0.72). Collectively, our broad-scale dataset revealed strong and consistent associations between the diversity of multiple groups of aquatic organisms and ecosystem multifunctionality. These results underline the important role of multiple elements of biodiversity in driving the ecosystem functioning in Neotropical wetlands[15-16,18], as in other ecosystem types such as drylands[8] and forest[7].

The close association between biodiversity and multifunctionality, suggests that biodiversity loss might impact the ability of wetlands to maintain their functioning[4-8]. Analysis of the relationship between HFP and biodiversity revealed a decline in species richness and functional diversity with increasing HFP (Supplementary Figs. 5 and 6). To test how this affected the relationship between biodiversity and multifunctionality, we examined how interaction HFP x biodiversity influenced the slope of biodiversity-multifunctionality relationships. While the isolated effect of species richness on multifunctionality was positive for most organismal groups, the interactive HFP x species effect was negative (Fig. 4a). Similarly, the isolated effect of functional diversity on multifunctionality was positive, but the interactive HFP x functional diversity effect was strongly negative (Fig. 5a). This suggests that human pressure can alter the relationship of both species' richness and functional diversity with multifunctionality. By decomposing the effect of biodiversity on multifunctionality through low, medium, and high HFP intensity, we found that the positive effect of species richness and functional diversity on multifunctionality declined from low to high HFP intensity (Fig. 4b and Fig. 5b). In particular, the effect of the diversity of smaller organisms (such as microcrustaceans, testate amoebae, ciliates, and rotifera) on multifunctionality shifted from positive at low HFP intensity to neutral or negative at high HFP intensity (Figs 4 and 5). By contrast, the positive effect of the diversity of larger organisms (such as fish and macrophytes) on multifunctionality was maintained despite increased HFP. These results illustrate how the ability of smaller organisms to promote multifunctionality is sensitive to human pressure and simultaneously highlight the importance of larger organisms for maintaining ecosystem functioning in a human-dominated world[20].

The changes in the magnitude and direction of the relations between and biodiversity and multifunctionality suggest that such relationships can be context-dependent in wetlands[21]. This is more evident for smaller groups of aquatic organisms as their effects on multifunctionality changed from positive at low HFP intensity to negative at high HFP intensity. Using a structural equation model, we disentangled the direct and biodiversity-mediated, indirect pathways by which human pressures affect multifunctionality. We demonstrate that the direct effect of HFP on multifunctionality was consistently negative across all wetlands (Fig. 6a, Supplementary Tables 8-10). This is consistent with the fact that the studied wetlands cover regions with intensive human activities (Fig. 1). Most of the studied wetlands cover areas of simultaneous crops of soy and sugarcane, and pasturelands grazed by cattle[22-25] and Paraná wetland is located downstream of one of the most populated areas on the planet[22]. Consequently, multiple human pressures can jointly affect the integrity of these wetlands by decreasing biodiversity and ecosystem multifunctionality (Supplementary Fig. 7).

Beyond their direct negative effect on multifunctionality, HFP had large indirect negative effects on the multifunctionality mediated by declining species richness and functional diversity (Fig. 6). Although indirect negative effects of human pressure were driven by the decline in the diversity of most organismal groups, these effects were strongly mediated by fish diversity (Fig. 6b,d). This is consistent with the fact that fish diversity has greatest influence on functioning of wetlands[16,17], and loss in fish diversity is known to impact multiple ecosystem functions[26]. The negative indirect biodiversity-mediated effects of human pressure on multifunctionality were also consistent across wetlands (Supplementary Table 11). Combined with the fact that the positive effects of biodiversity on multifunctionality decreased with increasing HFP (Fig. 4), our results highlight that, if the human pressures continue to increase[27], preservation of biodiversity for maintaining multifunctionality will not be sufficient unless they are accompanied by a reduction of human pressures. Seen in the light of the increasing human influence on natural landscapes, our results illustrate the importance of considering multiple pathways through which human pressures can influence ecosystem multifunctionality.

Conclusion

We have provided the first empirical evidence of a positive broad-scale relationship between the diversity of multiple groups of aquatic organisms and the multifunctionality of wetland ecosystems. We demonstrate that a positive association between aquatic biodiversity and multifunctionality occurs for both single metrics of diversity as for those combined into a multidiversity. These positive relationships are also apparent for the seven groups of aquatic organisms, although larger organisms are more strongly linked to multifunctionality than smaller organisms. Collectively, our findings highlight the importance of aquatic biodiversity for maintaining ecosystem multifunctionality and their associated services[28]. It is imperative that biodiversity conservation be a key management priority in wetlands[29] and that ecosystem management targets the joint conservation of multiple components of aquatic biodiversity, from vertebrates to plants and microorganisms. We have also shown that human pressures degrade the positive relationship between biodiversity and multifunctionality, which occur both directly and indirectly as human pressures reduce the biodiversity needed to maintain numerous ecosystem functions. These findings demonstrate that human pressures are degrading multifunctionality through multiple pathways. Consequently, conserving the functioning of wetlands will be a major challenge as human pressures continue to increase in these ecosystems worldwide[29-30]. More broadly, reducing human pressures must be addressed urgently in wetlands as these systems rank among the most diverse and productive ecosystems globally, providing a suite of functions and services essential for human well-being.

Methods

Study sites and data collection. The study comprised the four largest South American wetlands – Amazon, Araguaia, Pantanal, and Paraná – encompassing a subcontinental spatial area of approximately 3,700,000 km² and 72 lake ecosystems (Fig. 1). These wetlands are subject to distinct intensities of human pressure. Amazon is a global biodiversity hotspot and is more preserved than Araguaia and Pantanal that are both subject to moderate human pressure (Fig. 1). Paraná includes 150 constructed dams[31] and faces the strongest human pressure among the four wetlands. The climate ranges from subtropical to tropical, with a mean annual temperature of 16 - 29ºC and a mean precipitation of 1,300 - 2,000 mm year-1[32]. The field data were collected between August and May 2011 and 2012. The wetland lakes were surveyed under the Brazilian program "National System for Research in Biodiversity" (Sisbiota Brazil). The field surveys were designed to include lakes representing a wide range of climate, human pressure, and environmental conditions. They followed a standardized sampling protocol and the sampling effort was the same in all lakes[32]. In order to provide a comprehensive assessment of aquatic communities, we performed one sampling during the dry season and another during the wet season in each lake. The sampling included fish, aquatic macrophytes, microcrustaceans (cladocerans and copepods), rotifers, phytoplankton, testate amoebae, and ciliates. A detailed sampling protocol for each taxon is available in the Supplementary Methods.

Diversity measure. We quantified the species richness of the seven taxonomic groups of aquatic organisms in all 72 lakes. After identifying each individual to species level, we determined 325 fish species, 87 macrophyte species, 99 microcrustacean species, 124 rotifer species, 598 phytoplankton species, 124 testate amoebae species, and 108 ciliate species. Sample coverage was equal for all wetlands, but the locations differed in total number of individuals present. Therefore, we calculated estimated species richness as the Chao index with abundance-based data using the R package iNEXT[33], which is based on rarefaction and extrapolation of Hill numbers and provides an unbiased estimate of asymptotic species richness and enables comparisons among wetlands with different numbers of individuals. We used the Chao species richness because richness is the most commonly used and simplest metric of biodiversity[5-8]. We also measured the key functional traits for all organismal groups. We focused on the traits that are known to govern the patterns of spatial distribution and individual fitness, and which also influence ecosystem processes[16,34]. These traits fall into the three broad categories: (i) body size (maximum body length for animal taxa or cell volume for phytoplankton), (ii) resource and habitat use traits (feeding groups for animal taxa, growth form for macrophytes, nitrogen fixation or mixotrophy for microorganisms), and (iii) mobility traits (dispersal ability for animal taxa, propagation means for macrophytes, and cell motility for microorganisms). The literature sources used for functional classification and the predicted impact of each trait on ecosystem functions can be found in Supplementary Table 1. In order to determine the functional diversity (FD) of each organismal group, we calculated functional dispersion – i.e., the mean distance in multidimensional trait space of the individual species to the centroid of all species[35]. This measure provides a robust estimate of functional diversity. Because the relationship between biodiversity and ecosystem functioning can be multi-dimensional on both the predictor (biodiversity) and response side (multifunctionality)[6-7], we also estimated a multidiversity index including the diversity of the seven organismal groups[15]. We first standardized the diversity values of each organismal group between 0 and 1 (species richness or functional diversity) by scaling them to the maximum observed value, and then we average these standardized diversity values[15]. This procedure ensures that the diversity of each organism group contributes equally to the multidiversity of the wetlands. We calculated separately the multidiversity index for species richness and functional diversity. The multidiversity index has been widely used because it reflects very well the biodiversity-multifunctionality relationships in multitrophic ecosystems[8,11,15,17].

Assessing ecosystem functions and properties. In each lake, 11 ecosystem variables regulated by aquatic organisms and belonging to a wide range of ecosystem functions and properties were measured (see Supplementary Table 2). These functions and properties included: (i) nutrient concentrations represented by *in situ* measurements of total phosphorous (mg L^{-1}) and total nitrogen (mg L^{-1}) available in the water. Total phosphorus and nitrogen cover all fractions of these nutrients, including nitrate, nitrite, ammonia, particulate phosphate, dissolved organic phosphate, and orthophosphate. We took water samples in each lake and in the laboratory, nitrogen was quantified according to Mackereth et al.[36], while phosphorus was quantified following[37]. (ii) Ecosystem metabolism represented by the daily variation of dissolved oxygen in the water (mg L^{-1} day^{-1}), which was measured from dawn to dusk in each lake using a digital oximeter portable YSI aid (Digimed). We use the mean of daily oxygen variation as it represents the change in the metabolic underwater regime[38]. (iii) Multitrophic standing biomass was represented by the biomass of algae, carnivorous fish, omnivorous fish, herbivorous fish, and detritivorous fish. Algae standing biomass was quantified using biovolume (individuals per mm L^{-1}) of identified algae species. Biovolume was estimated by multiplying the abundance of each species by their mean volume[39]. Fish were classified into trophic groups using information from feeding trials and gut content analysis[16,32]. Afterwards, the fish counts within each trophic group were converted to biomass (g m^{-2}) using published species-specific length–weight relationships[40]. (iv) Availability of photosynthetically active radiation represented by light availability under water (m). We quantified light availability under water by the depth of the euphotic zone, which represents the depth (m) of the lake where there is sufficient light incidence for autotrophs. The euphotic zone was calculated as Secchi depth multiplied by 1.7, where 1.7 is a correction factor for estimating the light available under water[32]. (v) Microorganism abundance (cells mL^{-1}) was quantified using bacterial abundance. To record the accumulative abundance of bacteria, we took water samples at the subsurface (approximately 30 cm below the air-water interface) at the central, deepest region of each lake using polyethylene flasks. Bacteria were analyzed from water samples treated with a fixative solution composed of alkaline Lugol's solution, borate buffered formalin, and sodium thiosulfate that was filtered through black Nuclepore filters (0.2 and 0.8 μm, respectively) and stained with fluorochrome DAPI (4,6- diamidino-2-phenylindole[41]. Bacterial quantification was done with an epifluorescence microscope at a magnification of ×1000 (Olympus BX51). (vi) Variation of underwater habitat complexity was quantified based on variations in the above-ground cover of aquatic plants (m^{-2}). We estimated the area of all leaves and culm of each plant species. We then summed the area of all leaves and culm to obtain the above-ground area cover by each individual. We calculated the standard deviation of the above-ground area cover between all plant species and used this standard deviation as a proxy of variation in the above-ground vegetal cover.

Pairwise correlation between ecosystem functions. To assess the potential for a trade-off between individual ecosystem characteristics, we calculated Pearson correlation coefficients between each pair of individual standardized functions. Of the possible 45 combinations of pairwise functions, we found only seven strong correlations ($r = 0.5$; Supplementary Fig. 8). To remove any bias in our multifunctionality index, the highly correlated functions were down-weighted in its calculation (Supplementary Fig. 9), as described in Manning et al.[42]. Ecosystem functions were grouped into clusters according to their correlations. This weighted approach indicated three different clear clusters: (1) aboveground plant cover, (2) available N and P, light availability underwater, daily oxygen variation, and algal biomass, and (3) carnivore biomass, omnivore biomass, detritivore biomass, omnivore biomass, and bacterial abundance. Weighted multifunctionality was then calculated as the average of all variables within each cluster. For instance, each function within cluster 2 was weighted with a weight of 0.2. These functions were then averaged into a standardised variable. We repeated the analyses of the relationship between biodiversity and multifunctionality for the weighted multifunctionality to determine whether the results differed between weighted and non-weighted multifunctionality (see ref.[42]).

Assessing ecosystem multifunctionality. To obtain robust and quantitative multifunctionality indexes for each lake, we used three multifunctionality approaches: (1) the averaging multifunctionality index, (2) the multi-threshold multifunctionality index, and (3) the multiple single functions index[18]. To obtain the averaging ecosystem multifunctionality index, we standardized all 11 ecosystem functions between 0 and 1 (rawFunction − min(rawFunction) / (max(rawFunction) − min(rawFunction)) and then calculated their means. The averaging ecosystem multifunctionality index is the most commonly used index in the multifunctionality literature[5,18], but has the limitations that the number of functions with high performance are impossible to obtain and it does not allow for potential trade-offs between functions. To take these limitations into account, we used the multi-threshold index. This index calculates how many functions simultaneously exceed a predefined percentage of the maximum observed value of each individual function. Because the selection of any threshold is arbitrary, analysing multiple thresholds of maximum functioning is recommended[18]. We analysed the effect of the diversity of each organismal group on multifunctionality across the full range of thresholds from 1% to 99%. We used the mean of the three largest values of each ecosystem variable across all lakes as the observed maximum to reduce the impact of potential outliers.

Assessing the Human Footprint on wetlands. We used the global Human Footprint (HFP) map as a surrogate of the cumulative human-induced pressure on the wetlands[14]. This map is constructed from an ensemble of eight human pressure: (i) the extent of built environments, (ii) crop land, (iii) pasture land, (iv) human population density, (v) night-time lights, (vi) railways, (vii) roads, and (vii) navigable waterways. To facilitate comparison among pressures, each pressure was weighted (details on the weightings are provided below). The pressures were weighted according to their relative intensity[14]. For example, (i) constructed environments are areas related to urban settlements such as buildings and urban areas. The pressure of built environments was assigned a score of 10 (i.e., a score of 10 is assigned if there are built environments, otherwise a score of 0 is assigned). (ii) Crop land is characterized by monocultures with high inputs of pesticides and fertilizers. In terms of HFP, the crop land pressures received a score between 0 and 7, where 7 indicates intensive agriculture and 0 indicates the absence of crop lands. (iii) Pasture land includes some of the major land uses worldwide and is characterized by cattle and sheep farming. The pressure of pastures on wetlands was assigned a score of 4, which was scaled from 0 to 4 using the %pasture for each 1 km^2 pixel. (iv) Human population is an important underlying driver of the global change of natural ecosystems. Human density was mapped using gridded population downscaled to match the 1 km^2 resolution. All areas with a population above 1,000 people/km^2 were assigned a pressure score of 10. For less populated areas, the pressure score is logarithmically scaled using the following estimation: Pressure score = 3.333 x log (population density + 1). (v) Night-time lights include electric infrastructure related to more rural areas that are not part of built environments. To calculate the pressure of night-time lights, the areas were divided into 10 quantiles of increased night-time light intensity associated with scores between 1 and 10, while areas with no lights were assigned a zero score. (vi) Railways are essential human infrastructures that influence natural ecosystems. The direct pressure of railways was assigned a score of 8 for a distance of 0.5 km on either side of the railway. (vii) Likewise, roads modify the landscape where they are built. The direct and indirect pressure of roads on wetlands was assigned a score of 8 for 0.5 km (direct impact), while nearby areas up to 15 km received a score value that decayed exponentially on either side of the road (indirect impact). (viii) Navigable waterways act as conduits for people to access nature, resulting in impacts on wetlands. The pressure of navigable waterways was assigned a score of 4, which decayed exponentially out to 15 km away from the water banks. For full details of HFP estimation see refs[2,14].

The average HFP of the 1 km^2 pixels (cell-size resolution) overlapping each lake was extracted to derive the cumulative pressure, and this average HFP ranged between 0 and 50 (cumulative sum of all individual human pressures). The average HFP was extracted using the 'raster' R package[43] through a global HFP map that was available for the year 2009. The eight human pressures are not mutually exclusive, and may co-occur in the same wetland or vary among and within wetlands. The HFP was initially developed to represent human pressures in terrestrial systems[14], but most of these human pressures extensively affect wetland ecosystems. For instance, Brazil has experienced rapid expansion of urban areas[44]. Along with the increase in human populations in the vicinity of wetlands, there has been an increased pressure on these ecosystems from sewage, cattle and sheep pastures, railways, roads, and navigable waterways[45]. We found negative correlations between the individual human pressures with biodiversity and multifunctionality, which suggest that the use of the HFP in our study is robust (Supplementary Fig. 7).

Statistical analyses. *Linking aquatic biodiversity to multifunctionality*. First, to determine the direct link between aquatic biodiversity and average multifunctionality across four wetland ecosystems, we fitted a series of linear mixed effects models (LMMs) to the surveyed data. Specifically, we tested the relationship of (i) species richness and (ii) functional diversity of single organismal groups, and (iii) multidiversity with the ecosystem multifunctionality. The models were run using the function lme in the 'nlme' package[46]. We included wetlands and two sampling periods as our random structure, and allowed the intercept and slopes to vary by wetland. The assumptions of normality, linearity, and homoscedasticity were verified using graphical diagnostics (QQ plots and residual plots). To determine the importance of other biotic and abiotic variables besides biodiversity for multifunctionality, we included other well-known drivers of multifunctionality such as space (distance from equator), climate (temperature and mean annual precipitation), and aquatic properties (pH, conductivity, and water level; see Supplementary Methods). We performed a model averaging procedure that calculated all possible subset models and chose from this set those subset models with the lowest values (ΔAICc ≤ 2) of the Akaike Information Criterion corrected for small sample size (AICc). This analysis was conducted using the R-package MuMIn[47].

Using LMMs we also assessed the relationship of species richness and functional diversity of single organismal groups and multidiversity with each of the 11 individual ecosystem functions. This allowed us to compare the multifunctionality results to the performance of individual functions. Priori to these analyses, we standardized all individual ecosystem functions (z-scored: mean-centred and divided by the SD) to better meet model assumptions. Even so, for some functions, the residuals were highly heteroscedastic. We then modelled the variance using the function varIdent, with diversity nested by wetlands as the stratum. We considered quadratic terms for some ecosystem functions to evaluate potential nonlinear relationships.

We also modelled aquatic diversity against the number of functions above a threshold using generalized linear mixed effects model (GLMMs), assuming a Gaussian error distribution in the MASS package[48]. Because we wanted to know whether the relationships between species richness and functional diversity with ecosystem multifunctionality varied as a function of organismal group and among the four wetlands, we fitted the GLMM individually to each organismal group. We then extracted and plotted the linear coefficient (fitted values) of the relationship between biodiversity and each threshold level (1 to 99%; 99 thresholds) to each wetland system. This led us to examine changes in the shape of the fitted curve for each wetland at multiple thresholds.

*Effect of human pressure on biodiversity-multifunctionality relationships***.** We conducted linear mixed-effect models between human footprint (HFP) and biodiversity (species richness and functional diversity of single organismal groups and multidiversity). We found strong negative effects of HFP on biodiversity (Supplementary Figs. 5 and 6), allowing us to determine whether HFP altered the relationship between biodiversity and ecosystem multifunctionality. We then added interaction terms for HFP × species richness and HFP × functional diversity of each single organismal group and multidiversity to the mixed-effects models and measured the estimated coefficients of these interactions on ecosystem multifunctionality. Since biodiversity and HFP are both continuous variables, analyse their interactions could result in an interaction predictor that is collinear with the main effect[49]. Thus, we centered these variables by subtracting the sample mean from all input variable values. The mean of the centered variables is zero and the collinearity is reduced. We also scaled all the variables, dividing them by their standard deviations to interpret parameter estimates from models at a comparable scale. Since HFP is a continuous covariate, there are an infinite number of values we can use to analysis the effect of biodiversity on multifunctionality. For a better interpretation of the interactive effect, we selected three values (thresholds) of the scaled HFP: (i) a mean value (0), a value of standard deviation above the mean (1), and a value of standard deviation below the mean (–1). This is a common approach to analyse interaction between continuous predictors[50]. These three HFP values can be interpreted as three levels of HFP intensity, low intensity (below average), moderate intensity (on average) a high intensity (above average). The slopes of each relationship between HFP and species richness, functional diversity, and ecosystem multifunctionality are similar among wetlands, suggesting absence of any bias in our results (Supplementary Fig. 10).

*Pathways by which human pressure affects multifunctionality***.** To disentangle the direct and biodiversity-mediated pathways by which HFP affects multifunctionality, we ran structural equation modelling (SEM) using the R package lavaan[51]. Considering that all seven organismal groups worked in combination to determine multifunctionality (Fig. 2 and 3), we used their diversity to construct composite variables in our SEM. We combined the species richness and functional diversity of the seven organismal groups to construct a composite index for species richness and functional diversity, respectively. A composite index collapses the effects of multiple related variables into a single composite effect, thus representing a good way to analyse complex multivariate relationships in SEM[52]. We accounted for six ecosystem drivers: distance from equator, climate (mean annual temperature and precipitation), and aquatic characteristics (pH, conductivity, and water level) in the SEM. The SEM was fitted based on a meta-model (Supplementary Fig. 11). We calculated the standardized direct coefficients for each pathway within the model. We also estimated the indirect effect of HFP on multifunctionality mediated by diversity (species richness and functional diversity) of single organismal groups. To do so, we multiplied the coefficient of HFP on diversity (species richness and functional diversity) of a given organism group by the standardized loading of this organism group on composite. Finally, we multiplied the above result by the coefficient of composite on multifunctionality (Supplementary Table 11). We applied multigroup analysis in the SEM to evaluate whether (i) the effects of selected predictors (HFP, biodiversity, climate, space, and aquatic properties) on multifunctionality, as well as (ii) the effect of HFP on biodiversity varied across wetlands. We considered the four wetlands as the grouping variable (Amazon, Araguaia, Pantanal, and Paraná). We constructed a SEM model in which all parameters were free to differ between wetlands and a model in which all parameters were fixed (i.e., constrained to a single value determined by all wetlands). We compared the free model with the constrained model, where non-significant differences indicated no variation in pathway coefficients by wetlands, whereas significant difference indicated that pathway coefficients varied by wetlands. Because we found significant differences between the free and restricted/constrained model for both species richness and functional diversity, our next step was to understand which pathways differed. We only analysed the differences (multigroup) of the pathways including multifunctionality and biodiversity (species richness and functional diversity; Supplementary Table 10). Differences between other pathways within the model were not analysed. We evaluated the SEM fit using the comparative fit index (CFI; the model has a good fit when CFI ≥ 0.95) and the root MSE of approximation test (RMSEA; the model has a good fit when RMSEA ≤ 0.05). For our species richness model, the CFI was 0.997 and the RMSEA was 0.041, and for our functional diversity model the CFI was 0.998 and the RMSEA was 0.026, indicating a good model fit. All analyses were conducted in R version 3.4.4[53].

Data availability

The data that support the findings of this study are publicly available on Zenodo Digital Repository at https://doi.org/10.5281/zenodo.6406782

Code availability

The code that supports the findings and figures of this study is available on Zenodo Digital Repository at https://doi.org/10.5281/zenodo.6406786

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Author contributions

D.A.M., F.M.L-T., G.Q.R., and R.P.M developed the original ideas presented in the manuscript; FA.L-T. and L.F.M.V coordinated all the field operations; Human Footprint calculation was performed by T.S.S. Functional analysis was performed by D.A.M. Statistical modelling was performed by D.A.M. The first draft of the paper was written by D.A.M., and further drafts were written by D.A.M., G.Q.R., R.P.M., P.K., and B.J.C., and all of the authors contributed to the subsequent drafts.

Competing interests

The authors declare no competing interests.

Captions of main Figures 1-6.

Fig. 1| Intensity of the Human Footprint (HFP) across Brazil and the four Neotropical wetlands (Amazon, Araguaia, Pantanal, and Paraná). Activity data maps of the wetlands (built environments, crop land, pasture land, human population density, night-time lights, railways, roads, and navigable waterways) used in the HFP analysis in this study were extracted from ref[14]. The HFP data ranged from 0 to 50 according to the pressure of a suite of human activities. The HFP data on the four focal wetlands included low intensity (HFP < 1) and moderate/high intensity of human pressures (HFP < 18). Overall, Amazon and Araguaia had a relatively low/mean HFP intensity, while Pantanal and Paraná had mean/high HFP intensity. Colored rectangles represent each of the focused wetlands. The points within the rectangles highlight the sampling lakes in each wetland (n= 72 lakes).

Fig. 2| Relationship between the species richness of aquatic organisms and multifunctionality in Neotropical wetlands. The linear association between multifunctionality and the species richness of the seven selected taxonomic groups, and the composite metric of their joint richness (multidiversity; standardized between 0 and 1)[15] in four Neotropical wetlands; n = 72 lakes. Statistical analysis was performed using linear mixed-effect models. Dashed black and solid lines are predicted (fitted) values from LMMs for overall and local trends (for each wetland ecosystem), respectively. Shaded areas show 95% confidence interval for the overall trend. R^2 = marginal (i.e., variance of the fixed effects). **P* < 0.05, ***P* < 0.01, ****P* < 0.01. The richness of microcrustaceans, testate amoebae, and phytoplankton was log-transformed prior to the analysis. Full model results are provided in Supplementary Table 3. Multifunctionality is represented by the averaging index, which reflects changes in the average level of the 11 ecosystem functions. Very high averaging index levels (close to 1) mean that all functions reach their maximum level of performance simultaneously. By contrast, the lowest values (close to 0) mean all functions are at their minimum level of performance. Organisms' illustrations are from João Vitor Fonseca da Silva, Graduate Program in Compared Biology (PGB), State University of Maringá (http://www.pgb.uem.br/corpodiscente/doutorado).

Fig. 3| Relationship between the functional diversity of aquatic organisms and multifunctionality in Neotropical wetlands. The linear association between multifunctionality and the functional diversity of the seven selected taxonomic groups, and the composite metric of their joint functional diversity (multidiversity; standardized between 0 and 1)[15] in four Neotropical wetlands; n = 72 lakes. Statistical analysis was performed using linear mixed-effect models. Dashed black and solid lines are predicted (fitted) values from LMMs for overall and local trends (for each wetland ecosystem), respectively. Shaded areas show 95% confidence interval for the overall trend. R^2 = marginal (i.e., variance of the fixed effects). **P* < 0.05, ***P* < 0.01, ****P* < 0.01. The richness of microcrustaceans, testate amoebae, and phytoplankton was log-transformed prior to the analysis. Full model results are provided in Supplementary Table 3. Multifunctionality is represented by the averaging index, which reflects changes in the average level of the 11 ecosystem functions. Very high averaging index levels (close to 1) mean that all functions reach their maximum level of performance simultaneously. By contrast, the lowest values (close to 0) mean all functions are at their minimum level of performance. Organisms' illustrations are from João Vitor Fonseca da Silva, Graduate Program in Compared Biology (PGB), State University of Maringá (http://www.pgb.uem.br/corpodiscente/doutorado).

Fig. 4| Effect of Human Footprint (HFP) on the relationship between functional diversity and multifunctionality in Neotropical wetlands. a, Standardized coefficients (mean±s.e.m.) from LMMs for the isolated effect of species richness and the interactive HFP x species richness effect on multifunctionality. Model summary statistics is provided in Supplementary Table 7. **b**, ecosystem multifunctionality as a function of the species richness of single organismal groups and multidiversity on wetlands subject to low (solid blue line), medium (dashed black line), and high (solid red line) HFP intensity. The lines are predicted (fitted) values from LMMs models, in which the effect of species richness on multifunctionality is mediated at three levels of HFP, (i) medium: mean = 0; (ii) high: the standard deviation above the mean = +1; and (iii) low: the standard deviation below the mean = –1. Species richness and human footprint were mean-centered to remove the high collinearity[48]. All variables were scaled to interpret parameter estimates at a comparable scale. Multifunctionality is represented by the averaging index. Organisms' illustrations are from João Vitor Fonseca da Silva, Graduate Program in Compared Biology (PGB), State University of Maringá (http://www.pgb.uem.br/corpodiscente/doutorado).

Fig. 5| Effect of Human Footprint (HFP) on the relationship between functional diversity and multifunctionality in Neotropical wetlands. a, Standardized coefficients (mean±s.e.m.) from LMMs for the isolated effect of functional diversity and the interactive HFP x functional diversity effect on multifunctionality. Model summary statistics is provided in Supplementary Table 7. **b**, ecosystem multifunctionality as a function of the functional diversity of single organismal groups and multidiversity on wetlands subject to low (solid blue line), medium (dashed black line), and high (solid red line) HFP intensity. The lines are predicted (fitted) values from LMMs models, in which the effect of species richness on multifunctionality is mediated at three levels of HFP, (i) medium: mean = 0; (ii) high: the standard deviation above the mean = +1; and (iii) low: the standard deviation below the mean = –1. Functional diversity and human footprint were mean-centered to remove the high collinearity[48]. All variables were scaled to interpret parameter estimates at a comparable scale. Multifunctionality is represented by the averaging index. Organisms' illustrations are from João Vitor Fonseca da Silva, Graduate Program in Compared Biology (PGB), State University of Maringá (http://www.pgb.uem.br/corpodiscente/doutorado).

Fig. 6| The relationship between Human Footprint, climate, and water properties, and biodiversity, and ecosystem multifunctionality. **a,c** Structural equation modelling (SEM) allowed to disentangle the direct and indirect-biodiversity mediated effects of HFP on multifunctionality. Aquatic species richness, **a-b,** and functional diversity **c-d,** represented by a hexagon, were obtained through composite variables[48], including information about the diversity of seven taxonomic groups of aquatic organisms (see methods section). We accounted for multiple ecosystem drivers, including distance from the equator, climate (temperature and precipitation), and aquatic properties (pH, conductivity, and water level). We grouped the different categories of drivers (climate, space, and water properties) into the same box for graphic simplicity; nevertheless, it does not represent latent variables. Solid black and dashed gray arrows represent significant pathways ($P \leq 0.05$) and non-significant pathways ($P \geq 0.05$), respectively. The thickness of the significant pathways (arrows) represents the magnitude of the standardized regression coefficient. Numbers adjacent to arrows are the standardized effect size. R^2s for component models are given in the Supplementary Table 12. Significance levels are $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. For simplicity, we grouped the effects of ecosystem drivers (distance, HFP, climate and water properties) on the diversity of each of the seven taxonomic group in BOXES. Specifically, BOX A represents the effect of distance from the equator, BOX B the effect of HFP, BOX C the effect of climate, and BOX D the effect of water properties. Full model outputs and information about boxes A–D is provided in Supplementary Tables 8 and 9. **b,d,** represent the standardized indirect effects of the human footprint on multifunctionality mediated by species richness and the functional diversity of each organismal group used to compute the composite diversity (see Supplementary Table 11). Organisms' illustrations are from João Vitor Fonseca da Silva, Graduate Program in Compared Biology (PGB), State University of Maringá (http://www.pgb.uem.br/corpodiscente/doutorado).

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Captions of Extended Data Figures 1-4.

Extended Data Fig. 1| The relationship between the species richness of aquatic organisms and single ecosystem functions in neotropical wetlands. Significant links between the species richness of single taxonomic groups and multidiversity (joint richness of seven taxonomic groups of aquatic organisms) with 11 individual ecosystem functions. Statistical analysis was performed using linear mixed-effect models. The solid colored lines are predicted values of the LMMs and show the significant relationships between each taxonomic group and each individual ecosystem function. Non-significant relationships are not shown. Full model results are provided in Supplementary Table 5. All single ecosystem functions are scaled (z-score standard) for better graphical interpretation. Organisms' illustrations are from João Vitor Fonseca da Silva, Graduate Program in Compared Biology (PGB), State University of Maringá (http://www.pgb.uem.br/corpodiscente/doutorado).

Extended Data Fig. 2| The relationship between the functional diversity of aquatic organisms and single ecosystem functions in neotropical wetlands. Significant links between the functional diversity of single taxonomic groups and multidiversity (joint functional diversity of seven taxonomic groups of aquatic organisms) with 11 individual ecosystem functions. Statistical analysis was performed using linear mixed-effect models. The solid colored lines are predicted values of the LMMs and show the significant relationships between each taxonomic group and each individual ecosystem function. Non-significant relationships are not shown. Full model results are provided in Supplementary Table 6. All single ecosystem functions are scaled (z-score standard) for better graphical interpretation. Organisms' illustrations are from João Vitor Fonseca da Silva, Graduate Program in Compared Biology (PGB), State University of Maringá (http://www.pgb.uem.br/corpodiscente/doutorado).

Extended Data Fig. 3| Importance of species richness and ecosystem drivers for multifunctionality in neotropical wetlands. Standardized total effects (direct plus indirect effects) of seven ecosystem drivers and species richness to multifunctionality. The results were derived from the structural equation models (Fig. 5a). Species richness represents a composite variable that includes information about the species richness of seven groups of aquatic organisms. For the complete estimated model, see Supplementary Table 8.

Extended Data Fig. 4| Importance of functional diversity and ecosystem drivers for multifunctionality in neotropical wetlands. Standardized total effects (direct plus indirect effects) of seven ecosystem drivers and functional diversity to multifunctionality. The results were derived from the structural equation models (Fig. 5c). Functional diversity is a composite variable that includes information about the functional diversity of seven groups of aquatic organisms. For the complete estimated model, see Supplementary Table 9.