



**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2017

Warming and top predator loss drive ecosystem multifunctionality

Antiqueira, Pablo Augusto P ; Petchey, Owen L ; Romero, Gustavo Quevedo

Abstract: Global change affects ecosystem functioning both directly by modifications in physicochemical processes, and indirectly, via changes in biotic metabolism and interactions. Unclear, however, is how multiple anthropogenic drivers affect different components of community structure and the performance of multiple ecosystem functions (ecosystem multifunctionality). We manipulated small natural freshwater ecosystems to investigate how warming and top predator loss affect seven ecosystem functions representing two major dimensions of ecosystem functioning, productivity and metabolism. We investigated their direct and indirect effects on community diversity and standing stock of multitrophic macro and microorganisms. Warming directly increased multifunctional ecosystem productivity and metabolism. In contrast, top predator loss indirectly affected multifunctional ecosystem productivity via changes in the diversity of detritivorous macroinvertebrates, but did not affect ecosystem metabolism. In addition to demonstrating how multiple anthropogenic drivers have different impacts, via different pathways, on ecosystem multifunctionality components, our work should further spur advances in predicting responses of ecosystems to multiple simultaneous environmental changes.

DOI: <https://doi.org/10.1111/ele.12873>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-145891>

Journal Article

Published Version

Originally published at:

Antiqueira, Pablo Augusto P; Petchey, Owen L; Romero, Gustavo Quevedo (2017). Warming and top predator loss drive ecosystem multifunctionality. *Ecology Letters*, 21(1):72-82.

DOI: <https://doi.org/10.1111/ele.12873>

LETTER

Warming and top predator loss drive ecosystem multifunctionality

Pablo Augusto P. Antiqueira,¹
Owen L. Petchey^{2,3} and
Gustavo Quevedo Romero^{4,5*}

Abstract

Global change affects ecosystem functioning both directly by modifications in physicochemical processes, and indirectly, via changes in biotic metabolism and interactions. Unclear, however, is how multiple anthropogenic drivers affect different components of community structure and the performance of multiple ecosystem functions (ecosystem multifunctionality). We manipulated small natural freshwater ecosystems to investigate how warming and top predator loss affect seven ecosystem functions representing two major dimensions of ecosystem functioning, productivity and metabolism. We investigated their direct and indirect effects on community diversity and standing stock of multitrophic macro and microorganisms. Warming directly increased multifunctional ecosystem productivity and metabolism. In contrast, top predator loss indirectly affected multifunctional ecosystem productivity via changes in the diversity of detritivorous macroinvertebrates, but did not affect ecosystem metabolism. In addition to demonstrating how multiple anthropogenic drivers have different impacts, via different pathways, on ecosystem multifunctionality components, our work should further spur advances in predicting responses of ecosystems to multiple simultaneous environmental changes.

Keywords

Biodiversity, climate change, ecosystem functioning, predator loss, tank-bromeliad.

Ecology Letters (2018) 21: 72–82

INTRODUCTION

Environmental changes could cause distinct and substantial effects on ecosystem functioning and ecosystem multifunctionality (i.e. the simultaneous performance of multiple ecosystem functions) by changing diversity and biomass of ecological communities (Soliveres *et al.* 2016). Climate change (e.g. warming) is among the main current environmental changes, threatening biodiversity and ecosystem functioning worldwide (Walther 2010). The direct impact of higher temperatures can strongly influence different ecosystem functions related to productivity (Yvon-Durocher *et al.* 2015) or metabolism (Yvon-Durocher *et al.* 2010, 2011b). Also, warming can change community diversity (Gruner *et al.* 2017) and biomass (Dossena *et al.* 2012), which can impact single ecosystem functions (Dossena *et al.* 2012; Yvon-Durocher *et al.* 2015) and multifunctionality (Perkins *et al.* 2015). Many studies have reported that organisms from higher trophic levels (i.e. top predators) are more sensitive to environmental and climate change than lower trophic levels and subsequent changes to their abundance/diversity can cause strong indirect effects on ecosystem functioning (Petchey *et al.* 1999; Estes *et al.* 2011).

Current research investigating anthropogenic impacts on the ecosystem functioning has focused mostly on diversity within single groups or trophic levels (i.e. horizontal diversity) (Walther 2010), usually of plants, and single ecosystem

functions (Hooper *et al.* 2005). From such research, it is difficult to predict the impact of species loss in multitrophic communities and from higher trophic levels. Nevertheless, predators play a critical role in maintaining the structure and stability of communities, and their loss may have a variety of cascading indirect effects on ecosystems (Schmitz *et al.* 2010; Estes *et al.* 2011; Terborgh 2015). For instance, changes in predator diversity can affect ecosystem functioning both directly (via nutrients provided by faeces and carcasses) or indirectly by altering the diversity and biomass of other organisms, which themselves directly affect the ecosystem (Lefcheck *et al.* 2015; Soliveres *et al.* 2016). Moreover, the functional effect of different groups can interact within and between trophic levels (Soliveres *et al.* 2016). So far, we know relatively little about how different biological groups, across multiple trophic levels, interact with each other to affect ecosystem multifunctionality in the presence of anthropogenic drivers.

Combined climate change (warming) and top predator diversity loss occurs in natural systems, but we lack empirical evidence about how their combination might affect ecosystem functioning and multifunctionality. To address this gap, we conducted a manipulative field experiment evaluating the effects of these drivers on multifunctionality using tank-bromeliads as freshwater model system (Fig. 1a and b). Natural microecosystems (e.g. tank-bromeliads) are excellent models to investigate these effects – their small size enables high

¹Programa de Pós-Graduação em Ecologia, Instituto de Biologia (IB), Universidade Estadual de Campinas (UNICAMP), Campinas, Brazil

²Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

³URPP Global Change and Biodiversity, University of Zurich, Zurich, Switzerland

⁴Departamento de Biologia Animal, Instituto de Biologia (IB), Universidade Estadual de Campinas (UNICAMP), Campinas, Brazil

⁵Brazilian Research Network on Climate Change (Rede Clima),

*Correspondence: E-mail: ggromero@unicamp.br

replicability, realism, natural environmental variance and high multitrophic diversity (Srivastava *et al.* 2004; Romero & Srivastava 2010). Furthermore, microecosystems enable elucidation of causal ecological mechanisms, like predator contribution to nutrient cycling (Ngai & Srivastava 2006), cross-ecosystem effects (Romero & Srivastava 2010), habitat size influence on biodiversity and ecosystem functioning (Srivastava *et al.* 2008) and climate influence on multitrophic structure and function (Romero *et al.* 2016; Marino *et al.* 2017).

We predicted that top predator diversity loss and temperature increase affect multifunctionality directly and indirectly through changes in multitrophic community biomass and diversity (Fig. 1c). Warming can affect ecosystem functioning directly by increasing biochemical reaction rates (Brown *et al.* 2004), and indirectly by altering important trophic relationships and community structure (Petchey *et al.* 1999; Walther 2010; Vucic-Pestic *et al.* 2011). There are two pathways of warming to affect community standing stock. First, warming can decrease the community standing stock biomass due to underlying metabolic constraints operating on individual organisms and limiting their resource and nutrient acquisition. This metabolic demand is expected to increase in larger organisms (Brown *et al.* 2004; Daufresne *et al.* 2009; Yvon-Durocher *et al.* 2011a). Second, in the presence of plentiful resources, warming can increase the standing stock biomass due to an increase in the energetic requirement of the organisms in higher temperatures, thus resulting in an increase in resource consumption (Dossena *et al.* 2012; Hannesdóttir *et al.* 2013). These warming induced alterations in community standing stock can substantially impact ecosystem functioning (Dossena *et al.* 2012). Furthermore, since some species are more sensitive to warming than others, increase in temperature can reduce species richness (Gruner *et al.* 2017) and alter species composition (Perkins *et al.* 2010; Antikueira 2017), which may impact single ecosystem functions and multifunctionality (Perkins *et al.* 2010, 2015).

Likewise, top predator loss can negatively affect multifunctionality directly by decreasing nutrient provisioning to the ecosystem (e.g. via faeces and prey carcasses), or indirectly by increasing the diversity and biomass of organisms, via reduced prey consumption, which directly affects multifunctionality (Fig. 1c). However, the strength of these drivers may vary according to multifunctionality components, since some ecosystem functions may be more sensitive to climate change and biodiversity loss than others (Yvon-Durocher *et al.* 2011b). Furthermore, interaction strengths and predator consumption rates can be affected by warming (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011) and, thus, these drivers can interact, thus exacerbating or mitigating their impacts on multifunctionality. For example, warming can increase or decrease prey consumption rate by predators, which in turn, can modify their indirect effects in the ecosystem. We show that multiple anthropogenic changes increase the multifunctional ecosystem productivity both direct and indirectly, via a positive impact on the diversity of the detritivore macrofauna, but caused mix effects on multifunctional ecosystem metabolism. Our study brings new evidence of how multiple anthropogenic stressors affect different dimensions of ecosystem functioning mediated by multitrophic micro- and macroorganisms.

METHODS

Experimental design

The experiment involved warming according to the climate change scenario in Brazil for the next 100 years, and top predator diversity loss, and observation of multiple aquatic ecosystem functions (e.g. productivity, decomposition, and nutrient cycling) of tank-bromeliad phytotelmata. Experimental units were 45 experimental *Neoregelia johannis* (Carrière) L.B. Smith bromeliads purchased from a commercial greenhouse, then washed and treated them with 5% sodium hypochlorite and antibiotics to remove macroinvertebrates and unnatural bacteria. The plants were again washed, measured and taken to the field for experimentation. Further details of the study system and organisms are provided in the Appendix S1.

On the first day of the experiment, we filled the experimental tanks (bromeliads) with a 50:50 mix of rain and bromeliad water, the latter being the source of microorganisms. Bromeliad water was homogenised from 15 naturally growing *Neoregelia johannis* bromeliads of similar size to those experimental ones. The same 15 bromeliads were the source of the diverse macroinvertebrate communities that were added to the 45 experimental bromeliads. To collect the macroinvertebrates, we carefully washed each bromeliad to remove detritus (which was dried and weighted), and sorted the most common functional groups found [e.g. collectors, shredders, scrappers, filter-feeders and small predators (mesopredators)]. To standardise the detritus amounts in the experimental plants, we added to each approximately 5 g (the average dry biomass of detritus found in naturally growing plants) of fallen leaves of *Eugenia uniflora* L. (Myrtaceae). This assembly protocol minimised initial differences in abundances of the main invertebrate groups and detritus amounts among the experimental bromeliads. Evaporate was replaced with equal amount of rainwater every 2 days. Shelters constructed with wire and transparent plastic sheet prevented rain from falling into the bromeliads.

To simulate warming we used a heating system consisting of heaters and temperature sensors with a temperature control system and digital monitor (Fig. 1a). The warming treatment was composed of three temperature levels: (1) control (ambient temperature), (2) average projected for 2040 (2 °C above ambient), and (3) 2100 (4 °C above ambient) (IPCC 2014; PBMC 2015). The reference temperature (e.g. from control bromeliads) is transmitted to the first temperature controller that transfers the temperature value to a second controller that regulated the heaters from the second plant to increase the temperature by 2 °C (estimate to 2040). Additionally, a third controller heater was connected to the second, and increased the heater temperature by 2 °C in relation to the second controller, and by 4 °C (prediction for 2100) compared to the ambient temperature (Fig. 1a). Water temperature in each experimental bromeliad was recorded every hour (Fig. S1). The biological system replicated the natural variation in temperature day and night, thus simulating the real daily variation. The increased temperature treatment thus covered scenarios of lower (+2 °C) and higher (+4 °C) levels of

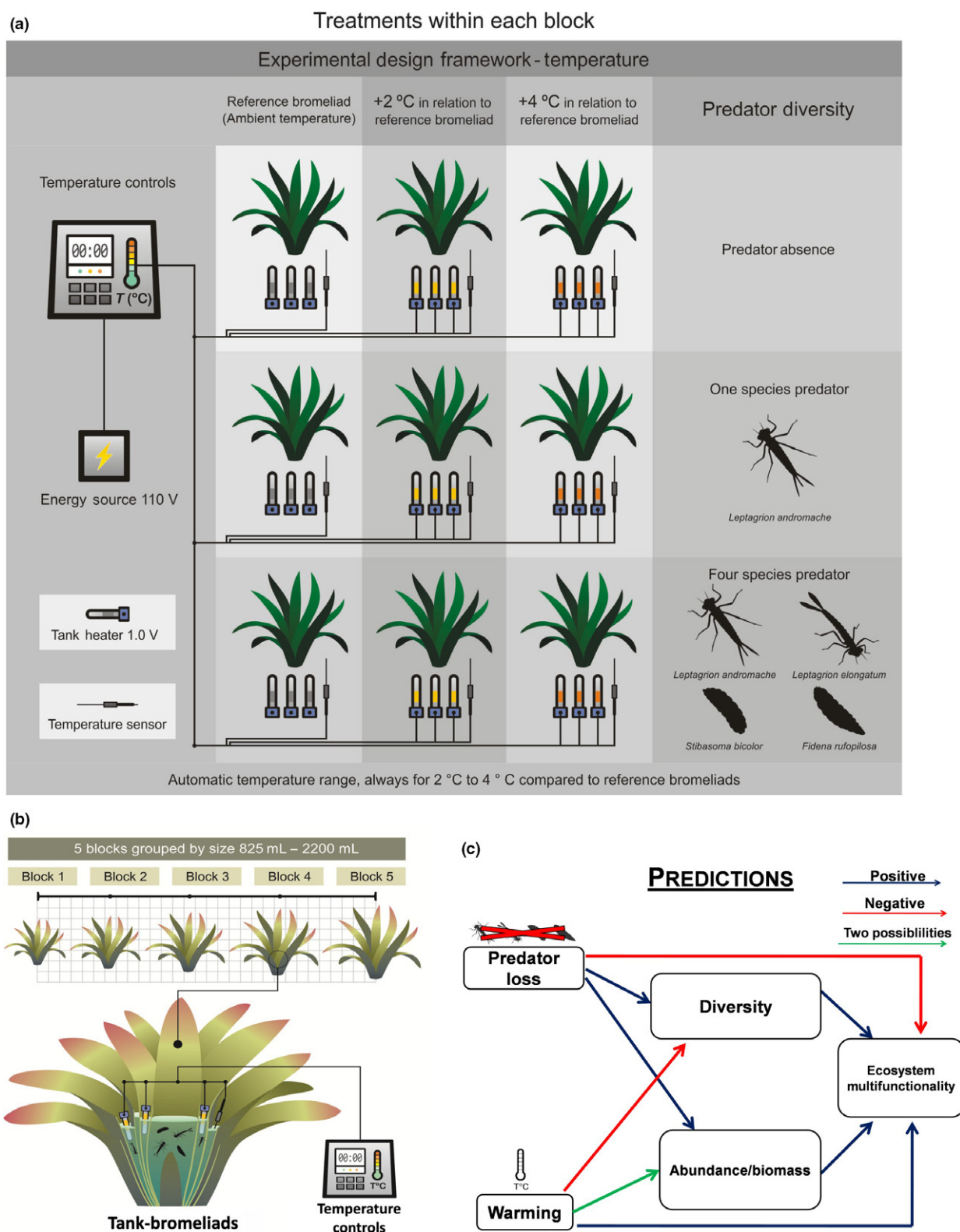


Figure 1 Conceptual framework, experimental design, and temperature manipulation system. (a) Diagram of the field experiment design: nine treatment combinations per block (five blocks). Warming was composed of three temperature levels: (1) control (ambient temperature), (2) average projected for 2040 (ambient +2 °C) and (3) 2100 (ambient +4 °C). Predator diversity treatments had three levels combined orthogonally with warming treatments: (1) predator absent (control), (2) low predator diversity (one predator species) and (3) high predator diversity (four predator species). (b) Illustration of the distribution of the treatments set up as a gradient of bromeliad size (bromeliad water-holding capacity); (c) Main predictions of the direct and indirect positive and negative effects of warming and predator diversity on ecosystem multifunctionality. Blue arrows denote positive effects, red arrows denote negative effects and green arrows denote both possibilities (see text).

global warming (Fig. S1). The method we used is original and potentially more realistic than manually heated systems that use underwater heaters, increasing the temperature at regular time intervals. Our heating system was based on the field site temperature, and we used automatic temperature controllers connected to the Total Control[®] software (Rio de Janeiro, Brazil). This ensured a constant elevation above ambient of 2 °C and 4 °C in the warming treatments (Fig. S1). The software was connected to all controllers and allowed digital access to each plant, measuring the temperature variation throughout the experiment (Fig. 1a and b).

We manipulated three levels of the predator diversity: (1) no predators, (2) low diversity (one species): the most common aquatic top predator in our study system, *Leptagrion andromache* (Hagen in Selys, 1876) (Zygoptera); and (3) high diversity (four species): two damselfly larvae: *Leptagrion andromache* (Zygoptera) and *Leptagrion elongatum* (Selys, 1876) (Zygoptera), and two horsefly larvae: *Stibasoma bicolor* Bigot, 1892 (Tabanidae) and *Fidena (Laphriomyia) rufopilosa* (Ricardo) (Tabanidae). We followed a substitutive design whereby, across a diversity manipulation, total density (or mass) of organisms is held constant (at *T* grams per ml) while species richness (*S*) changes. This requires that the number or mass of individuals scales with *T/S*. In our experiment, we kept constant the number of individual predators (i.e. all the bromeliads had the same number of top predators) across the predator richness manipulation, thus requiring reduced abundance of each predator in higher diversity treatment. This ensures that differences in predator effects reflect real differences in diversity and not their relative abundance (Griffin *et al.* 2008). After 30 days of the experiment, we added the same number of individuals again to account for predator deaths. In the higher diversity treatment, horsefly larvae individuals from different species were added at different times (at the beginning and after 30 days) due to natural variation in their availability. To control the size variation in the bromeliads and spatial environmental variation, we made five blocks each with nine treatments (warming vs. predator diversity combination) randomly distributed within. Tank-bromeliad total volume was stratified across blocks (range 825–2200 mL, Fig. 1b). The study was carried out from April to July, when insect abundance is typically at its highest. The average air temperature close to the bromeliads during the experiment was 20.5 °C.

Macrofauna and microorganisms

To investigate macroinvertebrate responses we dissected and washed each leaf of each bromeliads at the end of the experiment (after 75 days). This method ensures that all macroinvertebrates are sampled. We collected all detritus and water in white trays and fractionated them with two soil sieves (125 and 800 µL) to aid invertebrates sampling. We recorded the size, biomass, abundance and species/morphospecies of all aquatic invertebrates visible to the naked eye (> 0.5 mm) (Romero & Srivastava 2010). We sampled a total of 19 004 individuals of 84 morphospecies.

We calculated response variables related to diversity and biomass of macroinvertebrate community. Macrofauna diversity was analysed through (1) richness (number of species)

and (2) the effective species diversity (hereafter called diversity) of detritivore and colonised predators. The effective species diversity was estimated by the exponent of Shannon entropy (Jost 2006), which takes into account the richness and relative abundance of species and has been used in studies investigating the relationship between biodiversity and ecosystem multifunctionality (e.g. Thompson & Gonzalez 2016). Additionally, we estimated total biomass (standing stock) of detritivores and of predators.

Bacterial community composition in water and detritus was assessed at the end of the experiment via Denaturing Gradient Gel Electrophoresis (DGGE) (Muyzer *et al.* 1993; Thompson 2014). The denaturing gradient (urea and formamide) of the gel used for separation of the DNA fragments was 30–65%. We analysed the images of the gels using the Bionumerics software (version 6.6; Applied Maths, Kortrijk, Belgium), after conversion and normalisation of the profiles, and using the bands present in all samples. We used a binary matrix generated based on the presence/absence of bands in each sample to obtain the bacterial operational taxonomic units (OTUs), using 3% as taxonomic distance cutoff (or 97% 16S rRNA sequence similarity). Although DGGE usually samples the most abundant microorganisms, it has been proven to be a valuable tool to quantify relative differences in diversity among microbial communities (Thompson 2014). Bacterial density was estimated using real-time PCR (see Appendix S2 for details).

Ecosystem multifunctionality

We sampled seven ecosystem processes: (1) *in vivo* chlorophyll-*a* as a measurement of algal primary productivity, (2) ammonium as the inorganic nitrogen release through ammonification (macronutrient cycling), (3) turbidity, (4) chromophoric dissolved organic matter (CDOM) related to organic matter processing; (5) decomposition, by detritus biomass loss, (vi) dissolved O₂, related to aquatic metabolism and (vii) ¹⁵N, related to nitrogen flux from detritus to bromeliads (see Appendix S3 for details). We investigated the distribution of each process and carried out a principal component analysis (PCA) with the variables previously standardised and centred. The first two PC axes represented the majority of variation present in the original seven variables (axis 1 56% and axis 2 18%) and were used as two independent dimensions of ecosystem functioning. Interpretation of these two axes was by assessing their strength of correlation with each original ecosystem process (Fig. S2). This procedure resulted in the following two ecosystem multifunctionality components, related to and summarising different and important ecosystem properties.

PC1 axis – ecosystem productivity

The first PC axis is positively correlated with ammonium ($r = 0.94$), chlorophyll *a* ($r = 0.96$), CDOM ($r = 0.90$), turbidity ($r = 0.92$) and ¹⁵N from bromeliad leaves ($r = 0.58$). Ammonium is a waste product of animal metabolism and an important component of nitrogen cycling in aquatic environments. Chlorophyll *a* (algae density) is a measurement of primary productivity; algae use ammonium as a resource for growth and provide resource for the aquatic community. CDOM and turbidity are waste products from decomposition,

mainly by detritivore activity and excretion, releasing nutrients into the water through the process. Finally, ^{15}N from bromeliad leaves is a measurement of nitrogen flux from detritus to bromeliad tissue, hence a product of nitrogen cycling in bromeliads (Ngai & Srivastava 2006). We term this multifunctionality component *multifunctional ecosystem productivity*.

PC2 – ecosystem metabolism

The second PC axis is positively correlated with detritus biomass loss ($r = 0.80$) and dissolved O_2 ($r = 0.71$). These ecosystem functions are part of the aquatic metabolism (Lampert & Sommer 2007), mainly from the decomposition process, which is the key process in bromeliad ecosystem. Aquatic detritus decomposition depends on detritus (e.g. biomass) and water (e.g. oxygen) features (Lampert & Sommer 2007). Dissolved O_2 is an essential element of the ecosystem respiration, influencing the flux of matter and energy in the system (Silva-Junior et al. 2014). Thus, we term this multifunctionality compartment *multifunctional ecosystem metabolism*.

Average ecosystem multifunctionality index

To investigate how the ecosystem responded to environmental changes and predator diversity in a single index, we used the standard averaging approach, a common method to evaluate ecosystem multifunctionality (Maestre et al. 2012). This index was calculated by the average of the z-scores of each of the seven variables measured.

Statistical analyses

To evaluate the effects of climate change (warming) and top predator diversity loss on ecosystem functioning we fitted piecewise structural equation models (Lefcheck 2016) to each separate ecosystem process and each of the two multifunctionality components (productivity and metabolism). Structural equation models are a suitable tool to evaluate direct and indirect effects in ecological systems (Grace et al. 2010). Specifically, we used piecewiseSEM to investigate whether the warming, top predator diversity loss and their interaction affect ecosystem functioning directly or indirectly by influencing the diversity and biomass/density of bacteria and macroorganisms from different functional groups. The models were created using linear mixed effect models (lme – Pinheiro & Bates 2000) considering block as a random effect. We checked the multicollinearity in each component model by calculating the variance inflation factor (VIF) for each predictor. $\text{VIF} > 3$ indicates possible collinearity, and was not present in our data. Warming was evaluated using the temperature average of each experimental bromeliad (obtained every hour throughout the experimental period) as a continuous independent variable. Since the overall impact of high top predator diversity treatment (4 spp.) did not differ from low species diversity treatment (1 spp.) ($P > 0.05$, Fig. S3), we considered these treatments as top predator presence/absence in the piecewiseSEM analyses.

We evaluated three different models for each EF and multifunctionality component. The three models differed how biotic and abiotic drivers could affect ecosystem properties. (1) directly or indirectly via species richness (i.e. species richness

mediated indirect effects), (2) directly or indirectly via community standing stocks (productivity mediated indirect effects) using consumer biomass (macroorganisms) or density (bacteria) as variables, and (3) directly and indirectly via species diversity (i.e. effective number of macroinvertebrate species of detritivore and colonising predators). In addition, since pH is a physico-chemical water parameter that can strongly impact community and ecosystem structure, we also used pH (measured by a digital portable pH-meter, CyberScan 600) in the models.

We reduced the number of variables using Akaike Information Criteria corrected for small sample size (AICc), implemented in the *piecewiseSEM* R package (Lefcheck 2016; R Core Team 2016). This resulted in simpler and more robust models to test direct and indirect effects of warming and trophic changes on ecosystem functioning, mediated by community diversity and biomass. We compared the full model (including all variables related to diversity or productivity, pH and interactions between experimental drivers) with reduced, nested models in piecewiseSEM according to their AICc values ($\text{AIC}_{\text{stepn}} - \text{AIC}_{\text{finalmodel}}$) (Table 1). We considered $\Delta\text{AICc} > 2$ units to distinguish models. The full and reduced final models here differed in at least $\Delta\text{AICc} = 102.60$ units (see Table 1 and Table S1–S3). We present the standardised coefficient for each path from each model and estimated the indirect effects through coefficient multiplication. The significance of paths coefficients in the final models was obtained by bootstrapping (1000 randomisations) in the *lavaan* R package (Rosseel 2012). However, contrary to *piecewiseSEM*, *lavaan* does not fit random effects (e.g. block). We compared these results with the significance obtained by maximum likelihood from *piecewiseSEM* (see Tables S4–6) and found qualitatively identical results. Model fits were evaluated using Shipley's test of d-separation through Fisher's C statistic (Table 1).

RESULTS

Diversity (richness and effective species diversity) was the most sensitive component of community structure to the experimental treatments, and predator diversity loss had stronger effects than warming (Figs 2–4). Top predator absence increased detritivore diversity by 14% compared to the treatments including one and four predator species. Treatments with one predator species had similar effects to those including four predator species (Fig. S3). On the other hand, the treatment with one predator species substantially decreased detritivore richness compared to the treatments with high predator diversity (decreasing by 17%) and absence of top predators (decreasing by 12%) (Fig. S3B). Richness of detritivores was the only community component to respond differently to each predator treatment (1 spp. and 4 spp.) (Fig. S3), but had no distinct impact on ecosystem functioning both when we analysed predator treatments as a continuous (Fig. S4) or as presence/absence variable (Fig. 2). Furthermore, the community standing stock of macro- and microorganisms was not affected by any treatment (Fig. 3, Fig. S3C).

The best predictor in species richness models (i.e. selected by AIC) was the colonised predator richness for multifunctional ecosystem productivity (Table 1, Fig. 2a) and average

Table 1 Model selection by corrected Akaike information criterion (AICc) performed to reduce community components related to species richness, standing stock and species diversity of bacteria, detritivores and colonised predators

Model selection steps	Variables removed from the full model	AICc	Δ AICc	Fisher's C	P
Richness models					
MEP – full model	–	410.72	363.42	5.72	0.679
1	DR	155.63	108.33	16.69	0.551
2	DR+pH	92.68	45.38	24.28	0.083
3	DR+pH+Temp:Pred	84.47	37.17	27.8	0.114
Final	DR+pH+Temp:Pred+BR	47.30	0	17.3	0.367
MEM – full model	–	410.72	368.02	5.72	0.679
1	pH	164.84	122.14	21.9	0.081
2	pH+Temp:Pred	154.80	112.10	24.80	0.073
3	pH+Temp:Pred+BR	76.87	34.17	14.56	0.692
Final	pH+Temp:Pred+BR+PR	42.70	0	12.70	0.694
Average – full model	–	410.72	359.81	5.72	0.679
1	pH	164.69	113.78	21.75	0.084
2	pH+Temp:Pred	155.89	104.98	25.89	0.056
3	pH+Temp:Pred+BR	83.77	32.86	21.46	0.257
Final	pH+Temp:Pred+BR+DR	50.91	0	20.91	0.182
Standing stock models					
MEP – full model	–	410.59	362.64	5.59	0.693
1	pH	157.25	109.3	14.31	0.427
2	pH+ Temp:Pred	149.03	101.08	19.03	0.267
3	pH+ Temp:Pred+BD	82.71	34.76	20.40	0.311
Final	pH+ Temp:Pred+BD+DR	47.95	0	17.95	0.327
MEM – full model	–	410.59	327.33	5.59	0.693
1	pH	160.54	112.31	17.60	0.226
2	pH+Temp:Pred	149.46	101.23	19.46	0.246
3	pH+ Temp:Pred+BD	83.26	35.03	20.95	0.282
Final	pH+ Temp:Pred+BD+PB	48.23	0	18.23	0.311
Average – full model	–	410.59	327.32	5.59	0.693
1	Temp:Pred	357.62	274.35	7.62	0.666
2	Temp:Pred+BD	139.41	56.14	9.41	0.895
Final	Temp:Pred+BD+DB	83.27	0	20.96	0.281
Diversity models					
MEP – full model	–	147.78	107.68	4.84	0.565
1	Temp:Pred	135.34	95.24	5.34	0.720
2	Temp:Pred+PD	69.29	29.19	6.98	0.859
Final	Temp:Pred+PD+pH	40.10	0	10.10	0.607
MEM – full model	–	147.78	102.60	4.84	0.565
1	Temp:Pred	139.38	94.20	9.38	0.312
2	Temp:Pred+pH	75.22	30.04	12.91	0.375
Final	Temp:Pred+pH+PD	45.18	0	15.18	0.232
Average – full model	–	147.78	104.50	4.84	0.565
1	Temp:Pred	137.05	93.77	7.05	0.531
2	Temp:Pred+pH	74.49	31.21	12.18	0.431
Final	Temp:Pred+pH+PD	43.28	0	13.28	0.349

We included all steps of the model selection and the set of variables removed from the full model in each step. To evaluate model fit, we used Fisher's C statistic and its associated *P*-value for each model (*P* > 0.05 indicate adequate model fit). Experimental treatments: Temp=warming effect, Pred=top predator loss effect. Species richness model: DR=detritivore richness, PR=predator richness, BR=bacteria richness; full richness model: $Y \sim \text{Temp} * \text{Pred} + \text{BR} + \text{DR} + \text{PR} + \text{pH}$, with *Y*=ecosystem multifunctionality response variable. MEP= Multifunctional Ecosystem Productivity, MEM= Multifunctional Ecosystem Metabolism, and Average= Average Ecosystem Multifunctionality. Community productivity models: BD=bacterial density, DB=detritivore biomass, PB=predator biomass; full standing stock model: $Y \sim \text{Temp} * \text{Pred} + \text{BD} + \text{DB} + \text{PB} + \text{pH}$. Species diversity models: DD=detritivore diversity and PD=predator diversity; full species diversity model: $Y \sim \text{Temp} * \text{Pred} + \text{DD} + \text{PD} + \text{pH}$.

multifunctionality (Fig. S5), and detritivore richness for multifunctional ecosystem metabolism (Table 1, Fig. 2b). In contrast, for community standing stock, the best predictor was detritivore biomass for multifunctional ecosystem productivity (Table 1, Fig. 3a) and metabolism (Table 1, Fig. 3b), and the colonised predator biomass for average multifunctionality (Table S2, Fig. S5). For the species diversity model, the best predictor in all multifunctionality components was detritivore diversity (Table 1, Fig. 4; Table S3 Fig. S4).

Structural equation modelling revealed direct effects of warming on multifunctional components of ecosystem productivity (multifunctional productivity axis), metabolism (multifunctional metabolism axis) and average ecosystem multifunctionality (Figs 2–4, Fig. S5). Furthermore, there were indirect effects of top predator loss on multifunctional ecosystem productivity mediated by an increase in species diversity (Fig. 4a). Top predator loss also increased detritivore richness, which however, had no effect on ecosystem

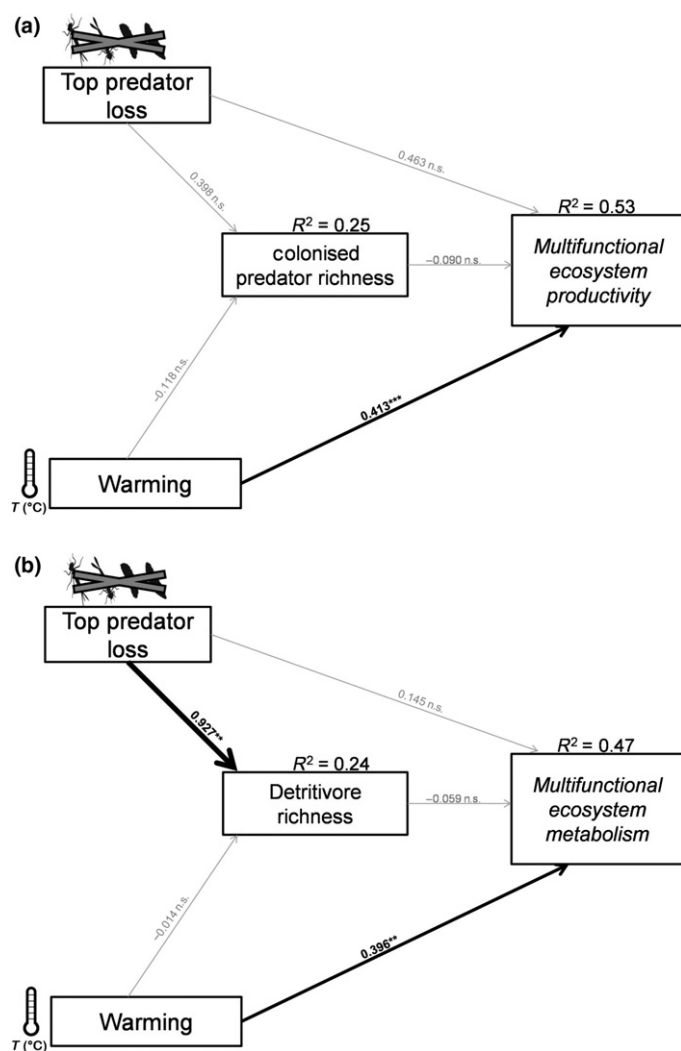


Figure 2 Structural equation models of warming and top predator loss effects on species richness of detritivores and coloniser predators, and on: (a) multifunctional ecosystem productivity, (b) multifunctional ecosystem metabolism. Solid black arrows represent significant positive paths ($P \leq 0.05$ piecewise SEM). Arrows for non-significant paths ($P \geq 0.05$) are in light gray. The thickness of the significant paths represents the magnitude of the standardised regression coefficient or effect sizes, given on the arrows. R^2 s for component models are given on the boxes of endogenous variables.

multifunctionality (Fig. 2). In contrast, the community standing stocks were not affected by any experimental driver (Fig. 3).

The average multifunctionality responded similarly to multifunctional ecosystem productivity (Fig. S5). Indeed, multifunctional ecosystem productivity and average multifunctionality were strongly correlated ($R^2=0.86$, Fig. S12). The variance explained (R^2) for multifunctional ecosystem productivity (Figs 2–4) and average multifunctionality models (Fig. S5) were much higher than for multifunctional ecosystem metabolism, and for any other function in isolation (Figs. S7–S13). Also, top predator loss indirectly increased multifunctional ecosystem productivity ($r = 0.250$) and average ecosystem multifunctionality ($r = 0.200$) by increasing the diversity of detritivores,

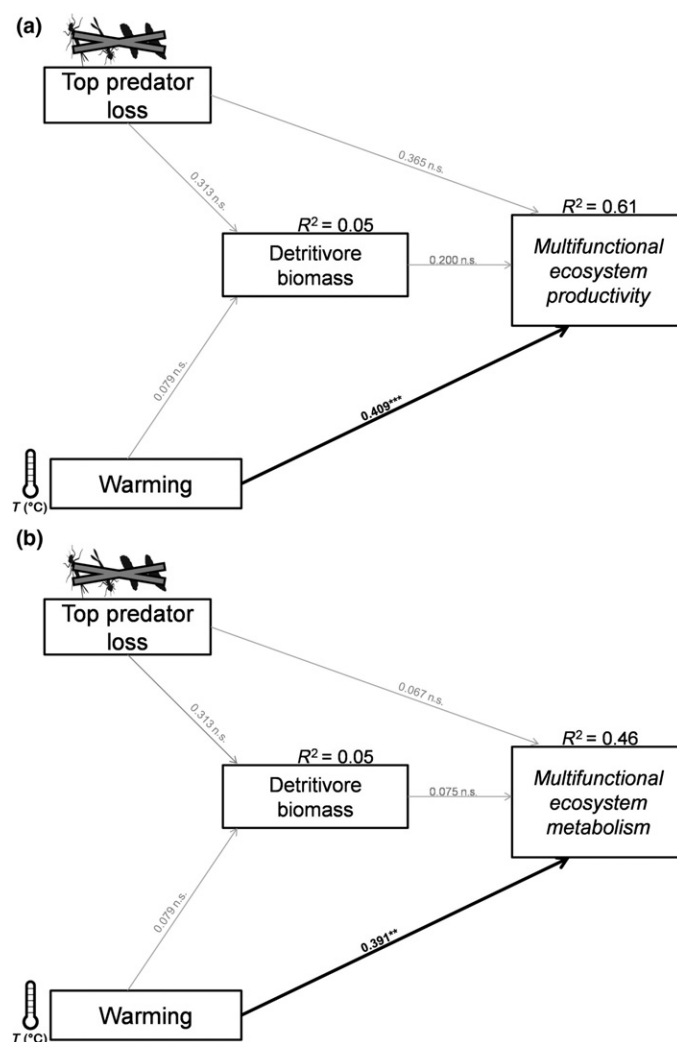


Figure 3 Structural equation models of warming and top predator loss effects on community standing stock biomass of detritivores and on: (a) multifunctional ecosystem productivity, (b) multifunctional ecosystem metabolism. Solid black arrows represent significant positive paths ($P \leq 0.05$ piecewise SEM). Arrows for non-significant paths ($P \geq 0.05$) are in light gray. The thickness of the significant paths represents the magnitude of the standardised regression coefficient or effect sizes, given on the arrows. R^2 s for component models are given on the boxes of endogenous variables.

which has itself a positive effect on multifunctional ecosystem productivity (Fig. 4a). Nevertheless, top predator loss did not affect multifunctional ecosystem metabolism. We did not observe an interaction effect between the experimental treatments for any ecosystem function or multifunctionality components. Additionally, pH had a positive direct effect on average ecosystem multifunctionality (Fig. S5B), but did not affect multifunctional ecosystem productivity and metabolism (Table 1).

DISCUSSION

Our findings support the prediction that climate warming can directly affect ecosystem functioning, increasing detritus biomass loss, dissolved nutrients (ammonium), organic matter

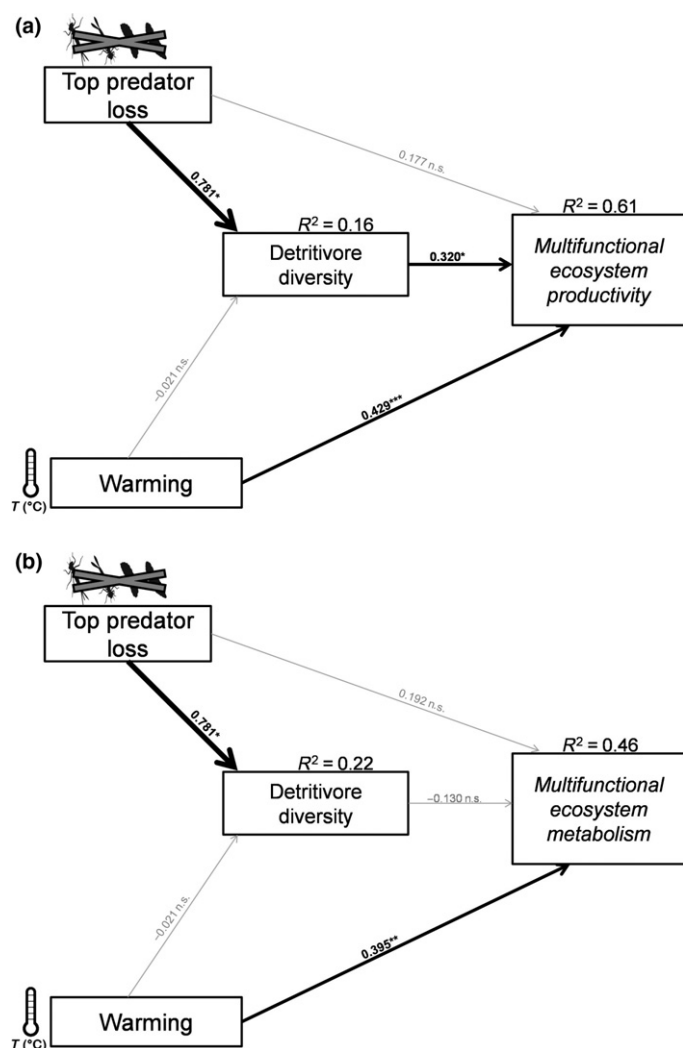


Figure 4 Structural equation models of warming and top predator loss effects on species diversity (obtained by equivalent numbers) of detritivores on: (a) multifunctional ecosystem productivity, (b) multifunctional ecosystem metabolism. Solid black arrows represent significant positive paths ($P \leq 0.05$ piecewise SEM). Arrows for non-significant paths ($P \geq 0.05$) are in light gray. The thickness of the significant paths represents the magnitude of the standardised regression coefficient or effect sizes, given on the arrows. R^2 s for component models are given on the boxes of endogenous variables.

production (turbidity and CDOM), and primary productivity (algae density) (see Supporting Information). Consequently, warming directly increased ecosystem multifunctionality, likely due to increased rates of biochemical reactions and metabolic demands of individuals at higher temperatures (Brown *et al.* 2004). The positive impact of warming on organic matter production could be caused by the direct effect of temperature on leaching (Chergui & Pattee 1990), or indirectly by enhancing litter processing by detritivores and decomposers (Ferreira & Chauvet 2011). We did not observe any changes in the standing stock or diversity of macroorganisms or bacteria in warming scenarios, suggesting that these indirect effects of temperature on ecosystem functioning are weak in our system. Thus, we demonstrated that predicted warming can strengthen

metabolism, and physicochemical and nutrient dynamics in freshwater systems. To our knowledge this is the first study to report empirically in a tropical ecosystem, that warming can affect different multifunctionality ecosystem components (here productivity and metabolism) in concert via direct and indirect pathways.

Top predator loss caused strong indirect effects on multifunctional ecosystem productivity component and average ecosystem multifunctionality via increasing in the diversity of detritivorous macroinvertebrates (diversity mediated indirect effects). Hence, ecosystem productivity increased with increasing diversity (but not richness or biomass) of detritivores. While some studies have reported changes in single ecosystem function and multifunctionality caused by multitrophic richness and biomass (Soliveres *et al.* 2016), others do not show this pattern (Perkins *et al.* 2010). We reported that species contribution to ecosystem functioning depended on their relative abundances (i.e. via effective number of species), suggesting that diversity parameters are a better predictor of ecosystem functioning than other community parameters, such as standing stock. The absence of richness effects on ecosystem functioning may suggest a functional redundancy in our system (Hooper *et al.* 2005), with compensation among species' abundances. Thus, predation seems to affect biodiversity (Terborgh 2015), but also ecosystem functioning via community diversity component that considers the relative abundance of species. Our results suggested that predator loss effects were as strong as warming on different components of ecosystem multifunctionality. These results are supported by previous evidence (Hooper *et al.* 2012; Tilman *et al.* 2014) that biodiversity loss is as important as the direct effects of global change stressors. We highlight that top predator conservation can play important roles in the maintenance of the system, and their loss can exacerbate the impacts of climate change on ecosystem multifunctionality.

Warming, top predator loss, and other environmental changes are often each investigated in isolation, even though they often occur simultaneously (Estes *et al.* 2011). If environmental changes have interactive effects (i.e. synergistic or antagonistic) then predicting their combined effects from their individual effects will be difficult. We did not observe interactions between warming and predator loss on ecosystem functioning. This result contradicts previous reports of synergistic or antagonistic effects of multiple anthropogenic stressors (e.g. predator loss, climate change) on biodiversity or ecosystem function (Greig *et al.* 2012; Perkins *et al.* 2015). Thus, interactive effects between multiple drivers may not be a ubiquitous phenomenon and can vary with ecosystem type and structure (Côté *et al.* 2016). Our study highlights the importance of understanding how different stressors act on different components of biodiversity and ecosystem, and of considering both isolated and interactive effects of different anthropogenic drivers.

Although top predator loss indirectly affected ecosystem productivity via changes in a component of community structure (diversity), it did not affect multifunctional ecosystem metabolism component. These results suggest that some components of the ecosystem seem to be less sensitive to changes in community structure than others. Many functions that

make up ecosystem productivity (in our study the productivity term also includes nutrient cycling) are strongly affected by biotic activity. For example, it is well known that primary productivity, organic matter production and nutrient cycling are strongly impacted by multiple autotrophic and heterotrophic species, which themselves depend on food web structure (Ngai & Srivastava 2006; Estes *et al.* 2011; Greig *et al.* 2012). On the other hand, ecosystem metabolism, despite being related to ecosystem productivity via ecosystem respiration (Yvon-Durocher *et al.* 2011b), was resistant to alterations in community structure. Ecosystem respiration and metabolism can be modified by many variables (Mahecha *et al.* 2010), including community abundance and biomass (Allen *et al.* 2005). But in our system, ecosystem metabolism was not directly related to the ecosystem productivity and was solely dependent on abiotic conditions, especially temperature, consistent with the metabolic theory of ecology (Brown *et al.* 2004). Thus, it is possible that ecosystem metabolism is more sensitive to changes in abiotic conditions (e.g. temperature, Yvon-Durocher *et al.* 2012), and in some biotic components (e.g. biomass, which did not change in our study), but less sensitive to diversity (Dossena *et al.* 2012).

We observed that ecosystem multifunctionality, but not all individual functions, responded to the experimental divers. This indicates greater sensitivity of ecosystem multifunctionality to the manipulated drivers than any single ecosystem functions. This was also evidenced by the variance (R^2) explained for multifunctionality models (except metabolism) which was higher than those explained for any of the functions in isolation. If individual ecosystem functions can have a particular response to an environmental driver (Jing *et al.* 2015; Perkins *et al.* 2015), multiple environmental drivers may cause stronger impacts to multiple ecosystem functions simultaneously. Likewise, once different species play different functions in an ecosystem, many species are needed to perform multiple functions simultaneously (Hector & Bagchi 2007; but see Gamfeldt & Roger 2017). Also, small changes in their diversity can have stronger effects on ecosystem multifunctionality than any of the functions in isolation. This emphasises, and we highlight, the importance to consider multifunctionality, and not only ecosystem functions in isolation, when investigating the impact of environmental changes and biodiversity loss.

To investigate ecosystem multifunctionality, we observed several ecosystem processes/functions and summarise them using PCA, in order to find and then analyse combinations of correlated processes. Similarly, PCA approaches have frequently been used to evaluate and summarise habitat, environment, and trait variables [e.g. using PCA scores as a measure of environmental heterogeneity (e.g. Yando *et al.* 2016) and when estimating functional trait diversity (Trisos *et al.* 2014)]. While some previous studies have calculated multifunctionality as the average of several observed functions and provided valuable insights (e.g. Maestre *et al.* 2012), we argue that analysing multifunctionality is fundamentally a multivariate problem. Thus, an appropriate multivariate method is an important tool (but not exclusive) for analyses of ecosystem multifunctionality. Approaches such as using PCA to reveal dominant axes of multifunctionality, synergies and tradeoffs among functions, and to allow analyses of these

axes will certainly add to insights gained from other approaches.

Ecosystems worldwide are facing biodiversity loss due to anthropic environmental changes (Naeem *et al.* 2012). However, some elements of the communities could be more sensitive to these changes than others. We observed that community abundance and biomass seem to be more resistant or resilient to experimental drivers than community diversity. It is possible that there was variation among species' responses to environmental changes that maintained the overall community biomass, despite the changes in community diversity (Antiqueira 2017). For example, it is likely that changes in species diversity and composition due to predator loss (Antiqueira 2017) can be compensated by other species that maintain the community biomass similar among the predator loss treatments. Indeed, many studies have reported the sensitivity of diversity components to environmental stressors and their consequences to ecosystem functioning (Hooper *et al.* 2012; Naeem *et al.* 2012; Tilman *et al.* 2014). Thus, for conservation studies, community diversity parameters could be a better indicator of environmental impacts on ecosystems than standing stock.

Despite long-standing interest in the importance of environmental changes (e.g., climate change) and predator diversity loss, up to now we did not know how they combine to affect multiple community and ecosystem multifunctionality properties. Our findings shed new light on the impact of climate change and predator diversity loss on freshwater ecosystem functioning. We empirically demonstrated that multiple anthropogenic drivers can have different impact to ecosystem multifunctionality components. While an abiotic stressor (warming) increased ecosystem productivity and metabolism, a biotic change (predator loss) impacted only ecosystem productivity indirectly via detritivore diversity. The continuous increase in ecosystem productivity in response to anthropogenic factors could be an alarming indicator. The increase in organic matter and nutrient dissolved in the water, as well as algal density, can generate eutrophication in freshwater systems (Ansari *et al.* 2010). Thus, predator loss and warming could trigger long-term eutrophication, which could be ameliorated by maintaining top predatory species. The complex responses of the ecosystems and biodiversity to climate change and predator diversity loss highlight the critical role of maintaining the environment with balanced abiotic conditions and biodiversity components.

ACKNOWLEDGEMENTS

The authors thank A.L. Mendonça, J. T. Macedo, B.M. de Oliveira, P.M. de Omena, G.H. Migliorini for fieldwork help and invertebrate surveys; V.P. Santos and V.M. Oliveira for bacterial analyses. The Predictive Ecology Group at the University of Zurich and LimBio group for valuable comments in first results version. S.A. Vieira, H.M.P.M. Sarmento, S.F. Reis, M.M. Pires, M.F.K. Becker, P.M. Omena and T. Gonçalves-Souza for valuable comments in first manuscript version. The authors also acknowledge three anonymous referees for providing valuable suggestions that significantly improved the quality of the manuscript. This study was

funded by a São Paulo Research Foundation (FAPESP) grant coordinated by G. Q. Romero. P.A.P. Antikeira received a PhD scholarship from the FAPESP (Proc. N°2014/04603-4). G.Q. Romero was also supported by BPE-FAPESP (Proc. N°2016/01209-9) and CNPq-Brazil research grants. This paper is a contribution of the Brazilian Network on Global Climate Change Research funded by CNPq (grant #550022/2014-7) and FINEP (grant #01.13.0353.00).

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

AUTHOR CONTRIBUTIONS

P.A.P.A and G.Q.R designed the experiments. P.A.P.A. performed the experiments. P.A.P.A, O.L.P and G.Q.R analysed the data. P.A.P.A, O.L.P and G.Q.R wrote the paper.

DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.m3p21>.

REFERENCES

- Allen, A.P., Gillooly, J.F. & Brown, J.H. (2005). Linking the global carbon cycle to individual metabolism. *Funct. Ecol.*, 19, 202–213.
- Ansari, A.A., Gill, S.S. & Khan, F.A. (2010). Eutrophication: threat to aquatic ecosystems. In: *Eutrophication: Causes, Consequences and Control* (eds Ansari, A.A., Gill, S.S., Lanza, G.R. & Rast, W.). Springer, Netherlands, pp. 143–170.
- Antikeira, P.A.P. (2017). Effects of climate change on community structure and ecosystem functioning using tank-bromeliads as a model system. PhD Thesis. University of Campinas, Brazil.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.
- Chergui, H. & Pattee, E. (1990). The processing of leaves of trees and aquatic macrophytes in the network of the River Rhone. *Intern. Revue Hydrobiol. Hydrogr.*, 75, 281–302.
- Côté, I.M., Darling, E.S. & Brown, C.J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B*, 283, 20152592.
- Daufresne, M., Lengfellner, K. & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proc. Natl Acad. Sci. USA*, 106, 12788–12793.
- Dossena, M., Yvon-Durocher, G., Grey, J., Montoya, J.M., Perkins, D.M., Trimmer, M. *et al.* (2012). Warming alters community size structure and ecosystem functioning. *Proc. Biol. Sci. Roy. Soc. B*, 279, 3011e3019.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011). Trophic downgrading of planet Earth. *Science*, 333, 301–306.
- Ferreira, V. & Chauvet, E. (2011). Synergistic effects of water temperature and dissolved nutrients on litter decomposition and associated fungi. *Glob. Chang. Biol.*, 17, 551–564.
- Gamfeldt, L. & Roger, F. (2017). Revisiting the biodiversity–ecosystem multifunctionality relationship. *Nat. Ecol. Evol.*, 1, s41559–017.
- Grace, J.B., Anderson, T.M., Olff, H. & Scheiner, S.M. (2010). On the specification of structural equation models for ecological systems. *Ecol. Monograph*, 80, 67–87.
- Greig, H.S., Kratina, P., Thompson, P.L., Palen, W.J., Richardson, J.S. & Shurin, J.B. (2012). Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. *Glob. Chang. Biol.*, 18, 504–514.
- Griffin, J.N., De La Haye, K.L., Hawkins, S.J., Thompson, R.C. & Jenkins, S.R. (2008). Predator diversity and ecosystem functioning: density modifies the effect of resource partitioning. *Ecology*, 89, 298–305.
- Gruner, D.S., Bracken, M.E., Berger, S.A., Eriksson, B.K., Gamfeldt, L., Matthiessen, B. *et al.* (2017). Effects of experimental warming on biodiversity depend on ecosystem type and local species composition. *Oikos*, 126, 8–17.
- Hannesdóttir, E.R., Gíslason, G.M., Ólafsson, J.S., Ólafsson, Ó.P. & O’Gorman, E.J. (2013). Increased stream productivity with warming supports higher trophic levels. *Adv. Ecol. Res.*, 48, 285–342.
- Hector, A. & Bagchi, R. (2007). Biodiversity and ecosystem multifunctionality. *Nature*, 448, 188.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P. & Lavorel, S. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.
- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E., Hungate, B.A., Matulich, K.L. *et al.* (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486, 105–108.
- IPCC (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds Core Writing Team, Pachauri, R.K., Meyer, L.A.). IPCC, Geneva, Switzerland, pp. 151.
- Jing, X., Sanders, N.J., Shi, Y., Chu, H., Classen, A.T., Zhao, K. *et al.* (2015). The links between ecosystem multifunctionality and above-and belowground biodiversity are mediated by climate. *Nat. Commun.*, 6, 8159.
- Jost, L. (2006). Entropy and diversity. *Oikos*, 113, 363–375.
- Lampert, W. & Sommer, U. (2007). *Limnology: The Ecology of Lakes and Streams*, 2nd edn.. Oxford University Press, New York.
- Lefcheck, J.S. (2016). piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.*, 7, 573–579.
- Lefcheck, J.S., Byrnes, J.E., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N. *et al.* (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nat. Commun.*, 6, 6936.
- Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M. *et al.* (2012). Plant species richness and ecosystem multifunctionality in global drylands. *Science*, 335, 214–218.
- Mahecha, M.D., Reichstein, M., Carvalhais, N., Lasslop, G., Lange, H., Seneviratne, S.I. *et al.* (2010). Global convergence in the temperature sensitivity of respiration at ecosystem level. *Science*, 329, 838–840.
- Marino, N.A., Srivastava, D.S., MacDonald, A.A.M., Leal, J.S., Campos, A. & Farjalla, V.F. (2017). Rainfall and hydrological stability alter the impact of top predators on food web structure and function. *Glob. Chang. Biol.*, 23, 673–685.
- Muyzer, G., De Waal, E.C. & Uitterlinden, A.G. (1993). Profiling of complex microbial populations by denaturing gradient gel electrophoresis analysis of polymerase chain reaction-amplified genes coding for 16S rRNA. *Appl. Environ. Microbiol.*, 59, 695–700.
- Naeem, S., Duffy, J.E. & Zavaleta, E. (2012). The functions of biological diversity in an age of extinction. *Science*, 336, 1401–1406.
- Ngai, J.T. & Srivastava, D.S. (2006). Predators accelerate nutrient cycling in a bromeliad ecosystem. *Science*, 314, 963–963.
- PBMC (2015). Executive summary: impact, vulnerability and adaptation to climate change. In: *Primeiro Relatório de Avaliação Nacional Sobre Mudanças Climáticas (RAN1) of the Painel Brasileiro de Mudanças Climáticas (PBMC)* (eds Assad, E.D. & Magalhães, A.R.). COPPE, Rio de Janeiro, RJ, Brazil, pp. 31.
- Perkins, D.M., McKie, B.G., Malmqvist, B., Gilmour, S., Reiss, J. & Woodward, G. (2010). Environmental warming and biodiversity–ecosystem functioning in freshwater microcosms: partitioning the effects of species identity, richness and metabolism. *Adv. Ecol. Res.*, 43, 177e209.

- Perkins, D.M., Bailey, R.A., Dossena, M., Gamfeldt, L., Reiss, J., Trimmer, M. *et al.* (2015). Higher biodiversity is required to sustain multiple ecosystem processes across temperature regimes. *Glob. Chang. Biol.*, 21, 396–406.
- Petchey, O.L., McPhearson, P.T., Casey, T.M. & Morin, P.J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, 402, 69–72.
- Pinheiro, J.C. & Bates, D.M. (2000). *Mixed-effects Models in S and S-Plus*. Springer, New York.
- R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org/>. Last accessed August 15, 2017.
- Rall, B.C., Vucic-Pestic, O., Ehnes, R.B., Emmerson, M. & Brose, U. (2010). Temperature, predator–prey interaction strength and population stability. *Glob. Chang. Biol.*, 16, 2145–2157.
- Romero, G.Q. & Srivastava, D.S. (2010). Food-web composition affects cross-ecosystem interactions and subsidies. *J. Anim. Ecol.*, 79, 1122–1131.
- Romero, G.Q., Piccoli, G.C., de Omena, P.M. & Gonçalves-Souza, T. (2016). Food web structure shaped by habitat size and climate across a latitudinal gradient. *Ecology*, 97, 2705–2715.
- Rosseel, Y. (2012). lavaan: an R Package for structural equation modeling. *J. Stat. Softw.*, 48, 1–36.
- Schmitz, O.J., Hawlena, D. & Trussell, G.C. (2010). Predator control of ecosystem nutrient dynamics. *Ecol. Lett.*, 13, 1199–1209.
- Silva-Junior, E.F., Moulton, T.P., Boëchat, I.G. & Gücker, B. (2014). Leaf decomposition and ecosystem metabolism as functional indicators of land use impacts on tropical streams. *Ecol. Ind.*, 36, 195–204.
- Soliveres, S., Van Der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C. *et al.* (2016). Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature*, 536, 456–459.
- Srivastava, D.S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S.P., Miller, T.E. *et al.* (2004). Are natural microcosms useful model systems for ecology? *Trends Ecol. Evol.*, 19, 379–384.
- Srivastava, D.S., Trzcinski, M.K., Richardson, B.A. & Gilbert, B. (2008). Why are predators more sensitive to habitat size than their prey? Insights from bromeliad insect food webs. *Am. Nat.*, 172, 761–771.
- Terborgh, J.W. (2015). Toward a trophic theory of species diversity. *Proc. Natl Acad. Sci. USA*, 112, 11415–11422.
- Thompson, C.L. (2014). Analysis of Community Dynamics in Environmental Samples Using Denaturing Gradient Gel Electrophoresis. In: *Environmental Microbiology: Methods and Protocols* (eds Paulsen, I.T. & Holmes, A.J.). Humana Press, New York, pp.(45–55).
- Thompson, P.L. & Gonzalez, A. (2016). Ecosystem multifunctionality in metacommunities. *Ecology*, 97, 2867–2879.
- Tilman, D., Isbell, F. & Cowles, J.M. (2014). Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Evol.*, 45, 471–493.
- Trisos, C.H., Petchey, O.L. & Tobias, J.A. (2014). Unraveling the interplay of community assembly processes acting on multiple niche axes across spatial scales. *Am. Nat.*, 184, 593–608.
- Vucic-Pestic, O., Ehnes, R.B., Rall, B.C. & Brose, U. (2011). Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Glob. Chang. Biol.*, 17, 1301–1310.
- Walther, G.R. (2010). Community and ecosystem responses to recent climate change. *Phil. Trans. R. Soc. B*, 365, 2019–2024.
- Wei, T. (2013). corrplot: Visualization of a correlation matrix. R package version, 73.
- Yando, E.S., Osland, M.J., Willis, J.M., Day, R.H., Krauss, K.W. & Hester, M.W. (2016). Salt marsh-mangrove ecotones: using structural gradients to investigate the effects of woody plant encroachment on plant–soil interactions and ecosystem carbon pools. *J. Ecol.*, 104, 1020–1031.
- Yvon-Durocher, G., Jones, J.I., Trimmer, M., Woodward, G. & Montoya, J.M. (2010). Warming alters the metabolic balance of ecosystems. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 365, 2117e2126.
- Yvon-Durocher, G., Montoya, J.M., Trimmer, M. & Woodward, G. (2011a). Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. *Glob. Change Biol.*, 17, 1681e1694.
- Yvon-Durocher, G., Montoya, J.M., Woodward, G., Jones, I.J. & Trimmer, M. (2011b). Warming increases the proportion of primary production emitted as methane from freshwater mesocosms. *Glob. Change Biol.*, 17, 1225e1234.
- Yvon-Durocher, G., Caffrey, J.M., Cescatti, A., Dossena, M., del Giorgio, P., Gasol, J.M. *et al.* (2012). Reconciling the temperature dependence of respiration across timescales and ecosystem types. *Nature*, 487, 472e476.
- Yvon-Durocher, G., Allen, A.P., Cellamare, M., Dossena, M., Gaston, K.J., Leita, M. *et al.* (2015). Five years of experimental warming increases the biodiversity and productivity of phytoplankton. *PLoS Biol.*, 13, e1002324.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Editor, Franck Courchamp

Manuscript received 20 April 2017

First decision made 17 May 2017

Second decision made 26 July 2017

Third decision made 21 September 2017

Manuscript accepted 4 October 2017