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Functional dissimilarity correlates to the co-occurrence patterns of native and non-native species

Amanda Cantarute Rodrigues[®] · Julien Cucherousset · Eduardo Ribeiro Cunha[®] · Natália Carneiro Lacerda dos Santos[®] · Luiz Carlos Gomes

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Abstract Many theories have been created to explain the mechanisms driving species coexistence. They are mainly based on biotic interactions and abiotic factors, which are being constantly affected by human activities. In invaded communities, novel ecological interactions among organisms are created and native and nonnative species have to coexist. This coexistence can be supported by different interactions (both positive and negative) and, in some cases, can be followed by negative impacts on the spatial distribution of native species. We aimed to assess the role of the functional differences and species status influencing co-occurrence patterns between native and non-native species at the Upper Paraná River floodplain, Southern Brazil. We estimated the co-occurrence between pairs of native and non-native species and their functional dissimilarity using morphological traits. We found a positive

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A. C. Rodrigues · L. C. Gomes Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais (PEA), Departamento de Biologia (DBI), Centro de Ciências Biológicas (CCB), Universidade Estadual de Maringá (UEM), Maringá, Paraná, Brazil

A. C. Rodrigues (⊠) · J. Cucherousset
Centre de Recherche sur la Biodiversité et
l'Environnement (CRBE), Université de Toulouse, CNRS,
IRD, Toulouse INP, Université Toulouse 3 – Paul Sabatier
(UT3), Toulouse, France
e-mail: amandacantarute@gmail.com

relationship between co-occurrence and functional dissimilarity between species: more similar native and non-native species tended to co-occur less. The cooccurrence was also related to species status: it was higher between pairs of native species than between pairs of native and non-native species. Niche differentiation may play an important role in driving the observed co-occurrence patterns at small spatial scales. However, this can lead to a limitation on the space use of species and modifications in the taxonomic and functional diversity of the native community. Although we recognize that species coexistence may be driven by several factors, we show here that the co-occurrence patterns of native and non-native species were affected by their functional dissimilarity.

Keywords Competition · Dam impacts · Fish community · Functional diversity · Invasion · Spatial segregation

E. R. Cunha

Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX, USA

N. C. L. dos Santos Departamento de Ecologia, Instituto de Biologia (IB), Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro, Brazil

L. C. Gomes Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia), Centro de Ciências Biológicas (CCB), Universidade Estadual de Maringá (UEM), Maringá, Paraná, Brazil

Introduction

Classically, species coexistence is predicted to be driven by their biological characteristics and mediated by the availability of resources in the environment (MacArthur and Levins 1967). Species coexistence could then occur by niche differentiation, when species are sufficiently different to reduce interspecific competition below intraspecific competition (Mac-Arthur and Levins 1967). When niche differentiation is insufficient, the fitness differences between species drive coexistence, with the species with higher competitive ability excluding other species (Chesson 2000). Based on these assumptions, it is therefore believed that competition is a strong driver of species coexistence, by shaping the observed patterns of species co-occurrence (Diamond 1975; Novella-Fernandez et al. 2021). More recently, other theories have been tested to explain the mechanisms driving species coexistence (Valladares et al. 2015) and it has been found that different mechanisms can act in different cases (Pereira et al. 2017). For example, some authors believe that ecological differentiation between species is not enough to significantly influence coexistence (Gravel et al. 2011). They suggest that the environmental variability would reflect in different responses of species to local environmental conditions, and that different population dynamics generated such as growth and mortality rates will promote species coexistence by influencing their neighbors differently. On the other hand, competition is still seen as a driver of coexistence, but only in communities considering multiway relationships between more than two competitors (e.g., intransitive competition; Soliveres and Allan 2018). However, these theories are mainly based on biotic interactions (both positive and negative) and abiotic factors. This means that recent human activities that are inducing environmental changes, modulating the spatial distribution of organisms, and the availability of resources may also affect the species coexistence patterns observed at local and global scales (Vitousek et al. 1997; Blois et al. 2013; O'Briain 2019).

One of the most challenging threats to native biodiversity is the introduction of species outside of their native range. The increased richness imposed by these introductions can affect the coexistence patterns previously stabilized between native species and creates novel ecological interactions among organisms (Mooney and Cleland 2001). During the introduction process, non-native and native species that do not share a coevolutionary history start to coexist. According to MacDougall et al. (2009), the introduction can be followed either by coexistence or exclusion of the native species. This is dependent on the strength of the niche or difference in fitness, but both coexistence and exclusion can occur (Godoy and Levine 2014). For example, the coexistence between native and non-native species can be supported by facilitative interactions, where the non-native species facilitate native species by several mechanisms (Rodriguez et al. 2006). In addition, several consequences on the native community after an introduction have been documented (Mooney and Cleland 2001). Regarding the effects on the spatial distribution of native species on its natural range, non-native species can impose niche displacement of native species (Richter-Boix et al. 2013), modify their abundance and original spatial distribution (Parker et al. 1999; Sowersby et al. 2015; Ganassin et al. 2020), and completely eliminate them through competitive exclusion (Bøhn et al. 2008; Whitney and Gabler 2008; Priddis et al. 2009). These effects have been widely found between native and non-native species that are functionally similar or phylogenetically related (Gois et al. 2015; Smith et al. 2019; Pascual-Rico et al. 2020), suggesting that the coexistence between similar and/ or related species may not be achieved. Therefore, the lack of co-evolution history between native and non-native species can help to elucidate the transient dynamics of species displacement during or after species invasion (Sax et al. 2007). For this reason, biological invasions represent a unique opportunity to investigate how ecological and evolutionary processes may shape local patterns of diversity within communities (Verhoeven et al. 2011; Valladares et al. 2015).

In freshwater ecosystems, the introduction of non-native species can be a result of different sources, such as translocations, stocking, escape from aquaculture and the construction of impoundments (Júlio Júnior et al. 2009; Ortega et al. 2015). Here, we use a unique model ecosystem, which experienced a massive introduction of > 30 nonnative fish species after the permanent flooding of a geological barrier when building the reservoir of the Itaipu power plant in a Neotropical river (Júlio Júnior et al. 2009; Vitule et al. 2012; Skóra et al. 2015). Non-native species that historically occurred

downstream the geological barrier have colonized areas located upstream following dam construction (Júlio Júnior et al. 2009), with both native and non-native species originating from the same basin but from two distinct ecoregions (i.e., large areas "encompassing one or more freshwater systems with a distinct assemblage of natural freshwater communities and species"; Abell et al. 2008). In addition, the small geographical distance between both communities resulted in a similar evolutionary history where many congeners coexist in both ecoregions and developed under very similar environmental conditions (Skóra et al. 2015). This event has been studied by Vitule et al. (2012), where they found that there was an increase in the similarity between both regions after the elimination of the barrier, suggesting a homogenization of the two assemblages. Skóra et al. (2015) subsequently intended to explain what determined the establishment success of species. They found contrasting results, where the functional similarity between native and non-native species both explained the success and the failure of those species that could not be established in the new area. Recently, a study evaluating global freshwater fish invasions suggested that the probability of occurrence of nonnative species is related to the phylogenetic proximity with the recipient community (Xu et al. 2024), which can also be attributed to the successful establishment of the translocated species in our study.

In this study, we aim to understand the drivers of co-occurrence between the native community and the non-native species that invaded the region after the flooding of the geographical barrier. Our first objective was to test the relationship between functional dissimilarity and co-occurrence for pairs of native and non-native species. We used functional dissimilarity between pairs of species because it is important to consider pairwise niche differences if we want to evaluate long-term coexistence (Levine et al. 2017). Thus, as niche differentiation tends to stabilize coexistence between species (Valladares et al. 2015), we hypothesized that functionally similar native and non-native species are less likely to co-occur than expected by chance. Our second objective was to test if coexistence was affected by species status (native and non-native). Our hypothesis was that pairs of native species co-occur more than pairs of native and non-native species, since co-evolved native species should show compatible niche segregation leading to a stable coexistence between them (Reitalu et al. 2008; Schuette et al. 2013; Grassel et al. 2015).

Methods

Study area

This study was conducted in the Upper Paraná River floodplain, located in the Upper Paraná hydrographic ecoregion (sensu Abell et al. 2008) in Southern Brazil. Historically, the Upper Paraná ecoregion was separated from the lower part of the Paraná River basin (the Lower Paraná ecoregion) by a natural and effective barrier, the Sete Ouedas Falls (average water flow of 13,000 m³). In 1982, the construction of the Itaipu Reservoir at the Lower Paraná ecoregion, with a flooded area of 1350 km² and 150 km downstream the Sete Quedas, completely flooded the falls, connecting both upper and lower parts of the river, which allowed the colonization and spread of several species endemic to the Lower Paraná ecoregion into the upper part of the river (Fig. 1). The floodplain is not part of the reservoir (the dam is located 230 km downstream), but was affected by the introduction of several fish species. Around 33 new introduced species dispersed and were registered after the connection between the two regions, representing 14 families and six orders, and many of them became relatively abundant after the introduction and distributed throughout the floodplain (Júlio Júnior et al. 2009; Casimiro et al. 2017; Angulo-Valencia et al. 2023). This was the largest freshwater invasion event to occur in South America in terms of numbers of taxa (Skóra et al. 2015), causing a homogenization of the two ecoregions (Vitule et al. 2012).

Fish sampling

Fish distribution data were obtained from a longterm ecological research program developed at the Upper Paraná River floodplain (Angulo-Valencia et al. 2022). Fishes were sampled during the dry season of the years 2000 and 2001 (May and August of each year) and 2010 and 2011 (June and September of each year), for a total of eight sampling campaigns. In each sampling campaign, 20 sites were surveyed, including the main channel of the river, connected



Fig. 1 Paraná River before (A, B, C and D) and after (E, F, G, and H) the flooding of the Sete Quedas Falls. The floodplain studied is located 80 km upstream the falls. Before the construction of the Itaipu Dam, the falls represented an effective geographical barrier separating both upper and lower por-

tions of the Paraná River (**C** and **D**). In **G** and **H**, the connection between the two portions are displayed, which allowed the massive introduction event in the upper portion of the River, including the studied floodplain

and isolated floodplain lakes, covering an area of approximately 250 km^2 to capture a larger spatial distribution of species. A total of 160 samples were collected during this period. To sample fish, sets of gillnets with different mesh sizes (24, 30, 40, 50, 60, 70, 80, 100, 120, 140 and, 160 mm between opposite knots) were deployed in each sampling site for 24 h and all sampled individuals were collected and identified to the species level (Angulo-Valencia et al. 2022).

Native and non-native species were classified following Júlio Júnior et al. (2009), who considered their original distribution (i.e., before the establishment of the Itaipu reservoir).

Co-occurrence

For each possible combination of species (native x native and native x non-native pairs of species),

we quantified a species co-occurrence metric using the 'cooccur' R package (Griffith et al. 2016). This method uses a probabilistic model that finds the observed likelihood of two species co-occur (OCo), and also calculates the expected likelihood of the same pair of species co-occur at a random chance (PCo). We consider co-occurrence as species occurring at the same time at a given site. We used as input data the occurrences of each species in all sites and years. The model then returns us one value of OCo and one value of PCo for each possible pair of species. We believe this approach can provide us a realistic pattern of the co-occurrence between species, since it considers both spatial and temporal variability. Therefore, if we find high co-occurrence between species, we can assume they are more probably to coexist. We acknowledge that occurrence of species can be driven by several factors, but analyzing pairwise co-occurrences provide us information of one species related to another, which allow us to make inferences about both species. Because we were interested in investigating if a pair of species cooccurred more or less than expected by chance, we scaled the observed by the expected co-occurrence using the quotient of OCo and PCo. Therefore, values of scaled co-occurrence lower than one indicate that species co-occur less than expected by chance, values equal one indicate that species co-occur the same as expected by chance, and values higher than one indicate that species co-occur more than expected by chance. We removed pairs of species that showed observed co-occurrence values equal zero in further analyses since our objective was to evaluate pairs of species with lower and/or higher co-occurrence, and not absence of co-occurrence, assuming that species that never co-occurred most likely explore completely different resources. Finally, we did not consider nonnative species from other introduction sources, ensuring that all non-native species would have the same time-period after overcoming the geographical barrier (Blackburn et al. 2011) and consequently the same time-period that they likely started to co-occur with native species. Although we recognize that other nonnative species introduced by other sources may also affect species coexistence patterns, we chose to not consider them to avoid the effect of time on the cooccurrence between new and old pairs of native and non-native species. Among the 2703 pairs of species, 996 pairs of species never co-occurred. Therefore, the scaled co-occurrence was estimated for 1707 pairs of species, of which 871 are pairs of native species and 836 are pairs of native and non-native species. Following Thuiller et al. (2010), we use the term coexistence to infer when both species are frequently interacting on a small spatial scale.

Functional diversity

Trait-based approaches are highly recommended to estimate dissimilarity between native and non-native species (Thuiller et al. 2010). To estimate functional dissimilarity, we first obtained the functional traits of the studied species from FISHMORPH (Brosse et al. 2021) that include 10 morphological traits (nine unitless ratios and body size; Online Resource 1), commonly used in assessments of morphological diversity of freshwater fishes. Five species from the Upper Paraná River floodplain were not available in this database (*Hypostomus strigaticeps, Hoplias* sp.2, *Hoplias* sp.3, *Trachelyopterus* sp. and *Potamotrygon amandae*) and, for these species, we measured the functional traits using pictures following Brosse et al. (2021).

Functional dissimilarity between species was calculated using the functional traits of each species (F matrix) and by calculating the Gower's distance (Gower 1966) on the F matrix to obtain the functional dissimilarity matrix. Gower's distance was used because it is the most suitable metric for datasets with a few missing trait values (Marie et al. 2015). We estimated the best functional space following Marie et al. (2015), which presented eight dimensions (mean standardised distance = 0.000475). The functional dissimilarity between species was measured as the standardised distance between each pair of species in the functional space. Therefore, lower values indicate that species are closer in the functional space (more functionally similar) and higher values indicate that species are more distant in the functional space (more functionally dissimilar).

Data analysis

We performed a Linear Mixed Model (LMM; Zuur et al. 2009) using the scaled co-occurrence as response variable to test the relationship between functional dissimilarity and co-occurrence for native and non-native pairs of species. As predictor



Native species

Native species

Non-native species

Fig. 2 Scaled co-occurrence values between a native species and b native and non-native species. Grey squares represent pairs of species that did not co-occur. Right bar plots represent species occurrence. Different colours in species names indicate different taxonomic orders. Green: Characiformes; orange: Gymnotiformes; dark blue: Cichliformes; pink: Siluriformes; red: Myliobatiformes; light blue: Pleuronectiformes

variables, we used the functional distance as fixed term and the identity of native species as random factor with a random intercept. We tested if there was a positive and significant relationship between scaled co-occurrence and functional distance (positive β estimate and p < 0.05). For LMM analysis, we used the *lmer* function in 'lme4' package (Bates et al. 2015), the 'lmerTest' package (Kuznetsova et al. 2017) to obtain model significance and the *r.squaredGLMM* function from the 'MuMIn' package (Barton 2020) to obtain model performance.

To test if coexistence patterns differ with species status, we compared scaled co-occurrence values between pairs of native species (native \times native) and pairs of native and non-native species (native \times nonnative) using a Linear Mixed Model (LMM) with the scaled co-occurrence as response variable. As predictor variables, we used the group as fixed term and the identity of native species as random factor with a random intercept. For LMM analysis, we used the same functions mentioned above for the first hypothesis. We log-transformed the scaled co-occurrence data to test both hypotheses. All analyses were performed in R software version 4.1.2 (R Core Team 2021).

Results

A total of 53 native and 25 non-native fish species were registered in the Upper Paraná River floodplain, belonging to six orders (Characiformes, Gymnotiformes, Myliobatiformes, Cichliformes, Pleuronectiformes and Siluriformes), 22 families and 53 genera (Online Resource 2). Native species were present in all 160 samples and non-native species were absent in two samples. Among the 10 most common species (occurring in more than 50% of the samples), six were native and four were non-native (Online Resource 3—Fig. 1).

There was a large variation in the scaled co-occurrence among the 871 pairs of native species (Fig. 2a): 25.83% of pairs of species co-occurred less than expected by chance (values lower than one; yellow squares in Fig. 2) and 70.15% of pairs of species cooccurred more than expected by chance. For 836 pairs of native and non-native species, 25.48% of pairs of species also co-occurred less than expected by chance and 71.29% of pairs of species co-occurred more than expected by chance, but with a lower degree when compared to native pairs of species (fewer dark squares in Fig. 2b than in Fig. 2a).

The functional distance between pairs of native and non-native species in the functional space ranged from 0.048 (more similar species) to 0.742 (less similar species) (Online Resource 3, Fig. 2). For native and non-native pairs of species, there was a positive and significant relationship between the scaled co-occurrence and the functional distance between species (Linear Mixed Model; r² conditional: 0.12, p < 0.0001; Fig. 3), indicating that the more similar the native species were to non-native species, the less they co-occurred. We also found a significant difference in the co-occurrence between pairs of native species and pairs of native and non-native species (Linear Mixed Model; r^2 conditional: 0.18, p < 0.001), indicating that native and non-native species cooccur less when compared to the co-occurrence only between native species (Fig. 4).

Discussion

Studying how non-native species coexist with native species represents an opportunity to better understand the ecological mechanisms that shape community assembly and species coexistence (Gallien and Carboni 2017). Using a unique case that allowed the introduction and establishment of multiple non-native species in a Neotropical river, we provide novel insights into the co-occurrence patterns of native and non-native species. In support of our hypothesis, we found that more functionally similar pairs of species (i.e., native and non-native) co-occurred less, indicating that the co-occurrence patterns of native and nonnative fish species in the Upper Paraná River floodplain were affected by their functional dissimilarity. We also found support for our second hypothesis, as the co-occurrence of pairs of native and non-native species was lower when compared to the co-occurrence between pairs of native species, indicating that species status may affect species coexistence.



Fig. 3 Significant relationship between functional dissimilarity and co-occurrence (scaled values, log-transformed) between native and non-native pairs of species (native \times non-native group)



Fig. 4 Co-occurrence (scaled values) for pairs of only native species (black points; native \times native group) and for pairs of native and non-native species (gold points; native \times non-native group)

Therefore, our results suggest that niche differentiation (i.e., differences between species) may play an important role in driving the observed co-occurrence patterns, making functionally dissimilar native and non-native species more spatially aggregated, and similar native and non-native species more spatially segregated. If temporally persistent, the spatial segregation may lead to the suppression of native species because the access to optimal sites would be limited by the presence of the similar non-native species (Wisz et al. 2012; Novella-Fernandez et al. 2021).

During introduction, non-native species usually face multiple ecological filters (Gallien and Carboni 2017). One of them is the environmental barrier, where local environmental conditions filter species based on their ecological niches and physiological adaptations (e.g., environmental filtering theory; Gallien and Carboni 2017). This filter may allow nonnative species with pre-adaptations to the new environment to co-occur at a regional scale with native species. We believe that non-native species originating from the Lower region should be adapted to the main environmental conditions of the Upper region, as both regions had a small geographical distance and similar hydrological conditions (Abell et al. 2008; Angulo-Valencia et al. 2023). Indeed, Skóra et al. (2015) studying the same introduction event, affirm that the success of some non-native species in the Upper region may be attributed to the functional similarity between the native community, and the phylogenetic relatedness of some species (i.e., same family and genus) may also have contributed to their establishment (Xu et al. 2024). Besides environmental conditions, the distribution of non-native species in another habitat can also be affected by biotic filters (Diez et al. 2008; Gallien and Carboni 2017), because non-native species will likely interact with native species. This new coexistence between native and non-native species can be supported by different interactions. Positive interactions in the form of facilitation, where native species would be supported by non-native species, can occur through habitat modification, increased availability of a food source, competitive release and predatory release (Rodriguez et al. 2006; Valverde et al. 2020). On the other hand, negative interactions such as predation (Pelicice et al. 2015) and competition might also occur, with the latter believed to be strong at local spatial scales where the environment and resources are homogenous (Davies et al. 2005; 2011; Mouillot et al. 2007; Park et al. 2020). In our study system, co-occurrence of species was evaluated at fine spatial scales (sampling sites), and we found an effect of the functional diversity on species spatial distribution patterns. This effect depended on the level of similarity between species: the more similar a pair of species is, the less they co-occur. Therefore, despite native and nonnative species showing increased functional similarity (which allowed non-native species to inhabit and spread throughout the floodplain), their co-occurrence was mediated by the spatial segregation at fine scales.

Finding this spatial segregation between functionally similar native and non-native species may suggest competition between them (Richter-Boix et al. 2013; Smith et al. 2019; Pascual-Rico et al. 2020), but this idea is mainly based on pairwise interactions. Nowadays it is also important to consider that the network of species will also shape coexistence, since different competitive mechanisms may arise when considering indirect effects of other species in complex communities with a high number of species (Levine et al. 2017). Some empirical evidence shows that for fish, it is more likely to find hierarchical competition (i.e., there is one dominant competitor excluding all others; Henriksson et al. 2016) rather than intransitive competition (i.e., there is no single best competitor; Soliveres and Allan 2018). However, environmental conditions are expected to drive intransitive interactions (Soliveres and Allan 2018), and factor as heterogeneity should enhance the degree of intransitivity in competition (Allesina and Levine 2011; Schreiber and Killingback 2013). Therefore, we could expect that in floodplain systems the intransitive competitions should be higher. Besides, competition may also be considered as a continuous variable, ranging from transitive to intransitive along environmental gradients and through time (Soliveres and Allan 2018). This shows us that the mechanism behind species coexisting may be continuously changing, that is why searching for patterns beyond temporal and spatial scales is of extreme importance.

According to this, the environmental variability can also impose a variation on the interactions between native and non-native species, reflecting on their coexistence (Valladares et al. 2015). Shifts in resource use can alleviate or worsen interactions between native and non-native species, which can be caused by fluctuations in water level and food availability (Reinas et al. 2022). In floodplains, the seasonal changes of chemical and physical characteristics, community composition and resource availability caused by the flood pulse have important consequences for the coexistence of native and nonnative species (Thomaz 2022). For instance, shifts in the trophic niche during flooding period (e.g., Abujanra et al. 2009; Quirino et al. 2015, 2017) may reduce niche overlap between species and decrease competition, enhancing the possibility of coexistence over longer periods. Besides, different growth responses and recovery patterns following environmental changes may also alter species dominance and reflect their interactions with other species (Gravel et al. 2011). Therefore, environmental changes can modulate coexistence between native and non-native species by influencing species interactions, which will directly influence invasion success and ecological impacts.

We found that pairs of native species showed increased co-occurrence when compared to co-occurring native and non-native species. In general, native species can benefit more for co-occurring between themselves since they have co-evolved and likely have stabilized interactions, which can be beneficial to stabilize coexistence (Linnell and Strand 2000). For instance, in a hierarchical competition situation or in a predator-prey interaction, a subordinate species can display different strategies to avoid direct contact with dominant competitors and predators (i.e., niche partitioning; Schuette et al. 2013), which would result in long-term coexistence. However, native and nonnative species may not display mechanisms to avoid competition (Pascual-Rico et al. 2020). In this case, the co-occurrence between similar native and nonnative species might increase competition and result in a habitat niche shift for the native species (Rodrigues et al. 2018; Moquet et al. 2021; Pascual-Rico et al. 2020) and/or; in some cases, competitive exclusion (Hardin 1960; Bøhn et al. 2008). Besides that, an interesting factor to be further investigated is the co-occurrence only between non-native species. It is known that non-native species can facilitate the establishment of others (i.e., "invasion meltdown"; Simberloff and Von Holle 1999; Ricciardi 2001), and this may have benefited the establishment of this high amount of species all at once. Accordingly, it is also necessary to further investigate if these introductions facilitated the introduction of other non-native species in the floodplain in the following years, since the Upper Paraná ecoregion is known to host the largest number of non-native fish species in the Neotropics (105 species; Gubiani et al. 2018).

In conclusion, integrating information on the functional diversity to understand the spatial distribution of organisms has potential to improve our understanding of co-occurrence patterns between native and non-native species in wild communities. Although we recognize that species coexistence may be driven by several factors, we show here that native and non-native species are co-occurring according to their functional similarity. In a context where biological invasions keep increasing, the introduction of species, if followed by changes in the spatial distribution of native species, may result in modifications in the taxonomic and functional diversity of the native community. Therefore, evaluating how the co-occurrence between species changes in a temporal scale is a next step to follow the spatial distribution of native species and identify possible impacts. Besides, environmental factors are also important drivers of the coexistence between species, and it is necessary to consider environmental changes when evaluating invaded communities, since interactions among organisms may change due to environmental variability. As anthropogenic processes are increasing biological invasions and, consequently, the coexistence between native and non-native species, evaluating the potential impacts of such invasions in native communities and ecosystem functioning is needed.

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Author contributions The study conception and design were performed by Amanda Cantarute Rodrigues, Eduardo Ribeiro Cunha, Natália Carneiro Lacerda dos Santos and Luiz Carlos Gomes. The analysis was conducted by Amanda Cantarute Rodrigues, Julien Cucherousset and Eduardo Ribeiro Cunha. The first draft of the paper was written by Amanda Cantarute Rodrigues and Julien Cucherousset and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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