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Non-Native Species Abundance Decreases the Co-Occurrence Between Native and Non-Native Species Through Time at Any Phylogenetic Distance

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ABSTRACT

Non-native species may cause cumulative impacts on native communities if their abundance continues to increase through time. This negative effect can reflect on the spatial distribution of native species, especially when native and non-native species are phylogenetically similar. Here, we assessed the spatial co-occurrence between native and non-native fish species using long-term abundance data from six locations in a Brazilian floodplain. We tested whether the co-occurrence of native and non-native species is influenced by non-native species abundance and time since first record, and whether the abundance effect is mediated by the phylogenetic relatedness between native and non-native species. We found that non-native abundance was more influential than the time since first record and co-occurrence between native and non-native species was lower when the non-native abundance was high, regardless of phylogenetic relatedness. The interannual variability in non-native species abundance may overshadow long-term trends in determining the temporal effects of non-native species.

1 | Introduction

Species introductions through human intervention have increased exponentially worldwide, being one of the greatest threats to biodiversity at local and regional scales (Bellard et al. 2016; Blackburn et al. 2014; Simberloff 2003). Introduced species often cause dramatic impacts on native populations, communities, and ecosystems (Catford et al. 2009; Haubrock et al. 2024; Simberloff et al. 2013; Toussaint et al. 2018), sometimes resulting in the extinction of native species and declines in biodiversity (Clavero et al. 2009). Most of these impacts are already fairly documented (Strayer 2012), yet challenges remain when studying the processes structuring invasion patterns (Strayer et al. 2019). Such challenges include monitoring non-native species over time, which can provide insights regarding their effects on native populations and communities. Several

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ecological and/or evolutionary processes modulate the dynamics of a non-native species over time (Haubrock, Pilotto, et al. 2023). For this reason, the time since the first record of non-native species should be explicitly considered when studying their impacts on native populations and communities to understand the effects of many non-native species adequately.

The invasion process can be divided into a series of stages (transport, introduction, establishment, and spread) in which filters must be overcome for a species or population to pass on to the next stage (Blackburn et al. 2011). In the spread stage, the population of the non-native species increases, usually showing a boom-bust population dynamic (Strayer et al. 2017), in which their abundance grows exponentially (i.e., "boom") and will eventually reach a long-term saturation, fluctuating through variation in growth rates (Haubrock et al. 2022). This pattern has been proposed as the "impact curve", where the cumulative abundance of non-native species exerts a cumulative impact on native communities (Haubrock et al. 2022; Soto et al. 2023). Therefore, one could expect that if non-native species abundance increases through time, its impact on native communities would also increase with the time since the introduction of the non-native species.

For instance, some studies evaluating the impact of non-native species through time reported that the spatial distribution of native species has changed after the introduction of non-native species (Bøhn et al. 2008; Pascual-Rico et al. 2020; Smith et al. 2019). This shift in spatial distribution may suggest competition between species because competing species usually share similar resources. However, if they have not co-evolved, they may not have mechanisms to partition space, time, or resources effectively to co-occur (Grassel et al. 2015; Reitalu et al. 2008; Schuette et al. 2013). By sharing similar resources, competing species usually show similar traits, which may be reflected in their phylogenetic relatedness ('phylogenetic signal'; Blomberg et al. 2003; Jucker et al. 2013). Several non-native species are closely related to native species (Xu et al. 2024) and have a certain degree of similarity with native species in the new environment (Vivó-Pons et al. 2023). Therefore, it may be expected that this pattern of similarity between native and non-native species can increase impacts on native communities.

In this case, similar native and non-native species may become spatially segregated if there is resource limitation in the environment (Procheş et al. 2008; Weber and Strauss 2016). This, in turn, would lead to a pattern of decreased co-occurrence between them to avoid direct interactions. Therefore, evaluating co-occurrence between native and non-native species in invaded communities through time may provide insights into the ecological and evolutionary processes that shape biological invasions. If non-native species adapt to the new environmental conditions faster than native species can develop mechanisms to reduce the harmful effects of introduction, long-term coexistence between them may not be possible (Priddis et al. 2009). As several communities constantly suffer from invasions, long-term data is key to disentangling the effects of natural variation in species abundance and co-occurrence patterns from those arising from interactions with non-native species (Lindenmayer et al. 2012).

In this study, we assessed the co-occurrence between native and non-native freshwater fish species through time using 30 years of abundance data from six lakes in a Brazilian floodplain. In this area, introductions of non-native fish species occurred over the years via different vectors (Angulo-Valencia et al. 2023; Ruaro et al. 2020). Thus, we tested whether the co-occurrence of native and non-native species changed as the invasion process progressed. We expected that the co-occurrence between species would decrease with the increase in the abundance of the non-native species and the time since the first record (Figure 1; left panel). In addition, we also tested whether the effect of non-native abundance was mediated by phylogenetic distance

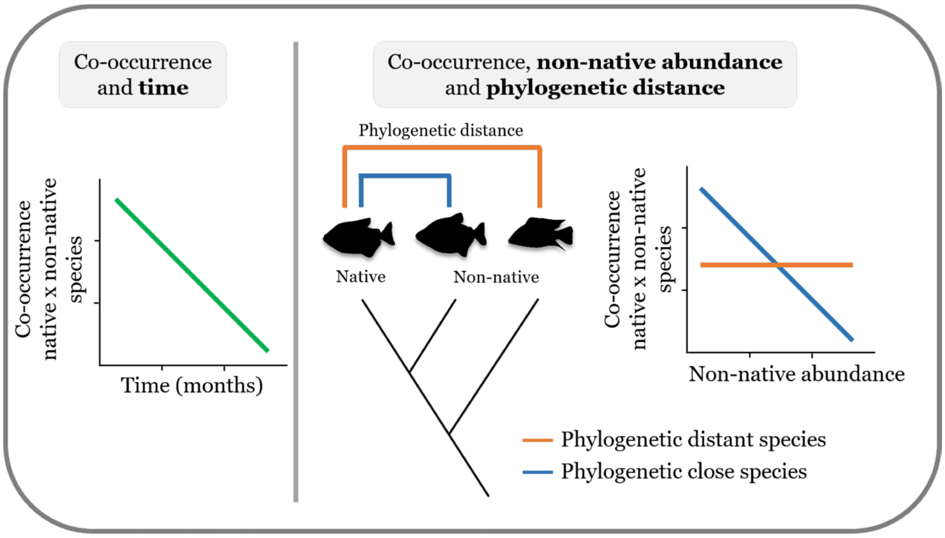

FIGURE 1 | Co-occurrence between native and non-native species is expected to be driven by time since first record (left panel), non-native abundance, and phylogenetic distance between the native and non-native species pairs (right panel). Co-occurrence between native and non-native species is expected to decrease with time since first record (green line, left panel). The effect of non-native abundance on co-occurrence is expected to be mediated by the phylogenetic distance between species pairs. We expect co-occurrence to decrease with non-native abundance for phylogenetically similar native and non-native species (blue lines), but not necessarily for phylogenetically distant species (orange lines).

(hereafter PD) between native and non-native species. We expected co-occurrence to decrease with non-native species abundance for phylogenetically similar species but not necessarily for phylogenetically distant species, which are assumed to compete less (Figure 1; right panel).

2 | Methods

2.1 | Study Area

This study was conducted in the Upper Paraná River floodplain, located in Southern Brazil (Figure 2). The main river of this floodplain is the Paraná River, the tenth largest river in the world in terms of water discharge and fourth in terms of drainage area ($5 \times 108\,\mathrm{m}^3$/year; $2.8 \times 10^6\,\mathrm{km}^2$, respectively; Agostinho and Zalewski 1996). This stretch of the floodplain is the last dam-free section of the Paraná River in Brazil, comprising 230 km between two large reservoirs: the Porto Primavera Dam upstream and the Itaipu Reservoir downstream (22°40′S to 22°52′S and 53°12′W to 53°38′W). In this section, there are a variety of habitats, including secondary channels, tributaries, and floodplain lakes permanently and indirectly connected to the river by groundwater or only during floods. Due to its high environmental heterogeneity provided by different habitats and seasonal floods, the biodiversity in the region is high (approximately 4500 large animal and plant species; around 200 are fish species; Ota et al. 2018), being considered a conservation priority with high socio-economic relevance (Agostinho et al. 2004).

Despite its relevance as a biodiversity refuge, the Upper Paraná River floodplain is one of the most threatened South American wetlands (Ruaro et al. 2020), suffering from several impoundments upstream and downstream. These impoundments have altered critical environmental conditions in the floodplain, such as reduced variability of the flood pulse (Agostinho et al. 2009), increased water transparency, reduced phosphorus concentrations, and transport of sediment and nutrients (Granzotti et al. 2018; Roberto et al. 2009; Stevaux et al. 2009). All of these impacts contribute to the invasion and establishment of non-native species. The Upper Paraná River ecoregion hosts the largest number of non-native fish species in the Neotropics (105 species; Gubiani et al. 2018). One of the most severe impacts occurred with the filling of the Itaipu Reservoir in 1982, which flooded a geographic barrier (i.e., waterfalls) located downstream of the floodplain and allowed the introduction of at least 33 fish species from the Lower Paraná River basin (Júlio Júnior et al. 2009; Skóra et al. 2015; Vitule et al. 2012). Additionally, human activities such as aquarium trade, stocking, aquaculture, and sports fishing also contributed to the introduction of non-native fish species in this floodplain (Angulo-Valencia et al. 2023; Ruaro et al. 2020).

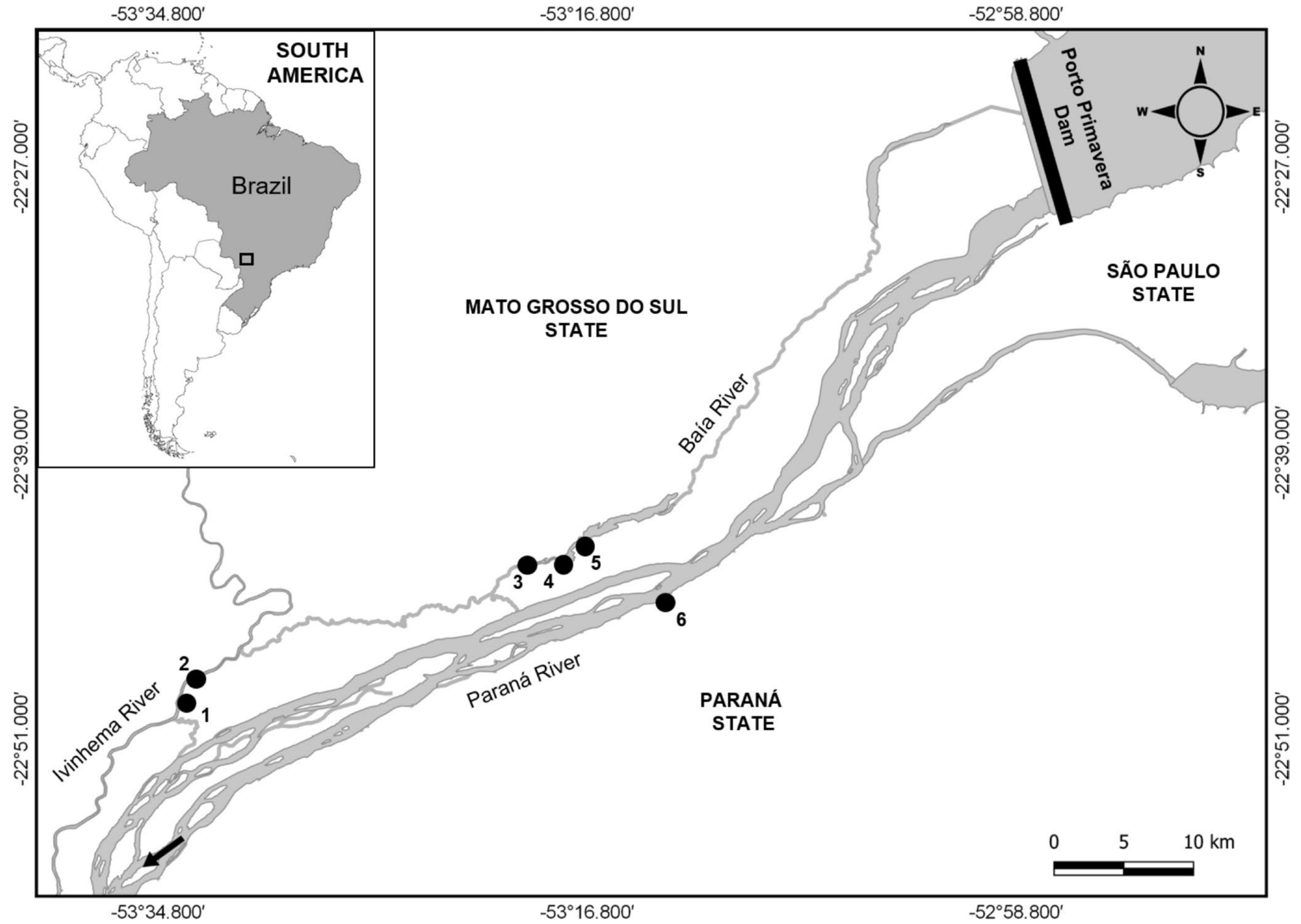

FIGURE 2 | Sampling sites in the Upper Paraná River floodplain. 1—Patos Lake; 2—Ivinhema River; 3—Guaraná Lake; 4—Baía River; 5—Fechada Lake; 6—Paraná River. The black arrow indicates the flow direction.

2.2 | Fish Sampling

We obtained fish community data from different projects conducted by the *Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura* (Nupélia) at the State University of Maringá, Southern Brazil. These projects encompassed 30 years, between 1987 and 2017, with a sampling periodicity almost continuous despite two short unsampled periods (1989–91 and 1995–99). Sampling was conducted quarterly in all surveys and was generally carried out in March, June, September, and December, except for 1988 (3 months sampled), 2003, and 2017 (2 months sampled). Therefore, sampling was conducted in 87 months throughout 30 years. Six sites were sampled in almost the entire time series (five sites in 1992, 1993, and 1994), including lotic (main channel of the river) and lentic environments (floodplain lakes; Figure 2). Finally, we considered in our study 510 different sampling events (considering each month × site; Table S1). To sample the fish community, a set of gillnets with different mesh sizes (24, 30, 40, 50, 60, 70, 80, 100, 120, 140, and 160 mm between opposite knots; 24 mm mesh used only from 2000 onward) were deployed in each sampling site for 24 h. Native and non-native species were sampled, euthanized, and identified to the species level during data collection. We updated species names post-data collection according to current taxonomic information (Ota et al. 2018). All sampling procedures were standardised across the sampling events. The abundance of species in each sample was expressed in catch per unit effort (CPUE—individuals/1000 m^2 of gillnets set during 24 h), which standardised the effort in catch from passive sampling. We registered occurrence information for 37 native and 28 non-native fish species from the Upper Paraná River floodplain (Table S2).

2.3 | Co-Occurrence

To estimate the co-occurrence between pairs of native and non-native species, we applied the metric developed by Griffith et al. (2016), available in the 'cooccur' package (version 1.3) from R software (version 4.1.2; R Core Team 2021). This metric applies the probabilistic model of species co-occurrence (Veech 2013) by measuring the number of sampling sites where two species co-occur. We consider co-occurrence as the occurrence of species simultaneously at a given site. Therefore, this metric provides the observed number of sites in which two species occur (OCo) and the expected number of sites in which the same two species occur (PCo). PCo is the product of the two species' probability of occurrence multiplied by the number of sampling sites. This probabilistic model is applied to all possible pairs of species. The model then returns one value of OCo and one value of PCo for each possible pair of species. Because we were interested in investigating whether a pair of species co-occurred more or less than expected by chance, we scaled the observed co-occurrence by the expected co-occurrence (OCo/PCo; hereafter excess co-occurrence). Therefore, values of excess co-occurrence lower than one indicate that species co-occur less than expected by chance, and values greater than one indicate that species co-occur more than expected by chance. We estimated the co-occurrence in each sampling month to obtain a time series of co-occurrence for each pair of native × non-native species. Estimating co-occurrence for each sampled month is required since species' spatial distributions and abundances change according to the hydrological cycle. Finally, we removed pairs of native × non-native species that never co-occurred in our time series, given that such species might have very different habitat requirements, which explains their lack of co-occurrence rather than competitive displacement. Most non-native species were introduced in the floodplain during our sampling times, and others were introduced a few years before our time series commenced (which would not be enough time for them to reach abundance levels that could exclude competitors before the beginning of our time series). Thus, we can assume that the lack of co-occurrence between species is not due to competitive displacement.

2.4 | Phylogenetic Distance

To obtain the phylogenetic distance (PD) between pairs of species, we used a set of phylogenies compiled from the bony fish phylogeny of Rabosky et al. (2018) using the function *fishtree_complete_phylogeny* from the 'fishtree' package (version 0.3.4; Chang et al. 2019). This procedure stochastically resolves polytomies in the phylogeny by placing missing species in the backbone of the tree. This is based on taxonomy and inferred divergence times, resulting in 100 phylogenetic hypotheses (Chang et al. 2019; Rabosky et al. 2018). We modified the cladal relationships between Characiformes, Siluriformes, and Gymnotiformes according to Hughes et al. (2018). Then, to calculate phylogenetic distances, we used the *cophenetic* function of the 'ape' package (version 5.6–2; Paradis and Schliep 2019). This calculates the cophenetic distances (i.e., based on tree branch lengths) between pairs of tips (i.e., species) in the phylogenies, with larger values indicating greater phylogenetic distance between species. This provided us with 100 phylogenetic distance matrices (one for each phylogenetic hypothesis), which were used in further analysis as the phylogenetic distance of each species pair. The PD matrices were strongly correlated to each other (pairwise r values ranging from 0.98 to 0.99), but we preferred to include the variation across them in the models to accurately account for phylogenetic uncertainties in our estimates (Rangel et al. 2015). PD values between pairs of native species ranged from 6.52 to 354.95, while PD between pairs of native and non-native species ranged from 44.01 to 362.02 (Figure S1). Several native × non-native species pairs displayed high PD (low phylogenetic relatedness; Figure S2), but most species pairs displayed intermediary values of PD (Figure S1B).

2.5 | Data Analysis

For each month and each possible pair of native × non-native species, we estimated the excess co-occurrence, the spatial occurrence of the native species, the abundance of the native and non-native species, and time since the first record of the non-native species. The spatial occurrence of each native species was calculated as the percentage of sites where the native species was present in each month. The abundance of each native and non-native species was estimated for each month as the mean CPUE across all sites where they were sampled. Time since the first record was considered as the time elapsed in months after the first registered occurrence of the species in the floodplain, ranging from 105 to 366 months (8–30 years). Species that occur sporadically in the time series (i.e., transient species, Snell Taylor et al. 2018) usually do not maintain viable local populations, so their co-occurrences are most likely a result of randomness (i.e., random encounters, stochastic fluctuations in abundance). To minimise this effect on co-occurrence time series, we removed pairs of species that occurred in less than 25% of the complete time series. Although there are no set criteria to define transient species in the literature (e.g., Magurran and Henderson 2003; Supp et al. 2015), this intermediate threshold was chosen considering the results of previous studies attesting to the robustness of ecological patterns to the use of different thresholds (Snell Taylor et al. 2018, 2020). Therefore, from 37 native and 28 non-native species that resulted in 1036 possible pairs of species, we only evaluated those that occurred in at least 21 months, and thus 623 pairs of species (Figure S3). The shortest co-occurrence time series had 21 months, and the longest had 86 months (considering the total of 87 months).

We first performed Linear Models to assess temporal trends in native and non-native species abundances, relating the abundance of each species to time. Secondly, we performed a Linear Mixed Effect Model (LME; Zuur et al. 2009a) to evaluate the drivers of the spatial occurrence of native species. We used the logit-transformed spatial occurrence of the native species as the response variable and time and the abundance of native and non-native species (both log-transformed) as fixed predictors. We included the abundance of native species in the model as a control, for spatial occurrence is correlated with local abundance. Time was estimated using Julian calendar time in months. We used the *lme* function in the 'nlme' package (version 3.1–160; Pinheiro et al. 2021) in R software version 4.1.2 (R Core Team 2021) to perform the models.

Finally, to test if the co-occurrence between native and non-native species was driven by non-native species abundance, time since first record, and phylogenetic distance, we performed a Linear Mixed Effect Model (LME) assuming a Gaussian error distribution, with the log-transformed excess co-occurrence being used as a response variable. We used the log-transformed native and non-native species abundance, time since first record of the non-native species, PD between each species pair, and the interaction between non-native abundance and PD as predictors (fixed effects). We used native and non-native species abundance as predictors because co-occurrence involves both species, and they should be treated equally in the model. Time since first record was estimated using Julian calendar time in months. In both models, all predictors were standardised by subtracting the mean and dividing by the standard deviation. Seasonality (dry or wet season) and identity of the species pair were used as random factors. These random factors were chosen for the following reasons. Firstly, seasonality (i.e., periods of low and high water levels in each year according to the hydrological cycle of the floodplain) may affect the co-occurrence between species, such that co-occurrence could be similar within seasons but different between seasons. Adding seasonality as a random factor implies that we assume the presence of its effect, but we are only interested in the long-term variation. Secondly, each pair of species displays a specific variation in co-occurrence over time due to the idiosyncrasies of each (e.g., non-native species were introduced at different times), but we are also not interested in this. We included the random factors in a nested structure (seasonality nested within each species pair, representing a time series). In addition, we added a correlation structure to minimise the effect of temporal autocorrelation in the model. To assess the best correlation structure (corAR1, corARMA(2, 0), or corARMA(1, 1)), we ranked competitive models according to the Akaike Information Criterion (AIC), following Zuur et al. (2009b). All models shared the same fixed and random predictors, differing only in the correlation structure used. The models were fitted using the lme function from the *nlme* package (version 3.1–160; Pinheiro et al. 2021) in R software (version 4.1.2; R Core Team 2021). Among the tested structures, the ARMA(2, 0) temporal autocorrelation structure was selected as the most suitable for the final model (Table S3). We then ran 100 models, each one with a different PD matrix originating from the 100 phylogenetic hypotheses, to incorporate the effect of phylogenetic uncertainty. Model results are presented as medians across the 100 models (Figure S4 and Figure S5). We also tested whether including native and non-native species identity, besides species pair and season as crossed random effects in the models, would be an important source of variation. To do so, we did not consider temporal autocorrelation and used the *lmer* function from the package lme4 (version 1.1–31; Bates et al. 2015). The results were not qualitatively different from the aforementioned models; therefore, we only provided their results in the Supporting Information (Table S4).

3 | Results

Native and non-native species varied in their long-term trends in abundance (Figure S6). Eighteen native species significantly decreased throughout the 30 years, 13 showed no significant long-term trend, and only eight significantly increased over time. On the other hand, 13 non-native species significantly increased in time, eight showed no significant long-term trend, and seven significantly decreased. The total abundance of native and non-native species showed similar variability over time, with increasing and decreasing trends (Figure 3). However, the total abundance of non-native species was higher in almost the entire time series. We found that the abundance of non-native species significantly decreased the spatial occurrence of native species, so that the number of sites where native species occurred was lower when the abundance of non-native species was high (Table 1). The spatial occurrence of native species also decreased over time. We used two heatmaps to illustrate the monthly variation in non-native species abundance and co-occurrence through time with each native species for the two most common non-native species in the floodplain (Figure S7).

We found a tendency of native and non-native species to co-occur significantly more than expected by chance when the abundance of native and non-native species is low, as observed from the significantly positive intercept (Table 2). However, the excess co-occurrence values decreased with increasing native and non-native abundances. Co-occurrence increased with time since the first record, but the effect was lower when compared to the native and non-native abundances (see standardised coefficients in Table 2; Figure S8).

Finally, we found a statistically significant interaction between non-native abundance and phylogenetic distance, such that, as the phylogenetic distance between species increases, the

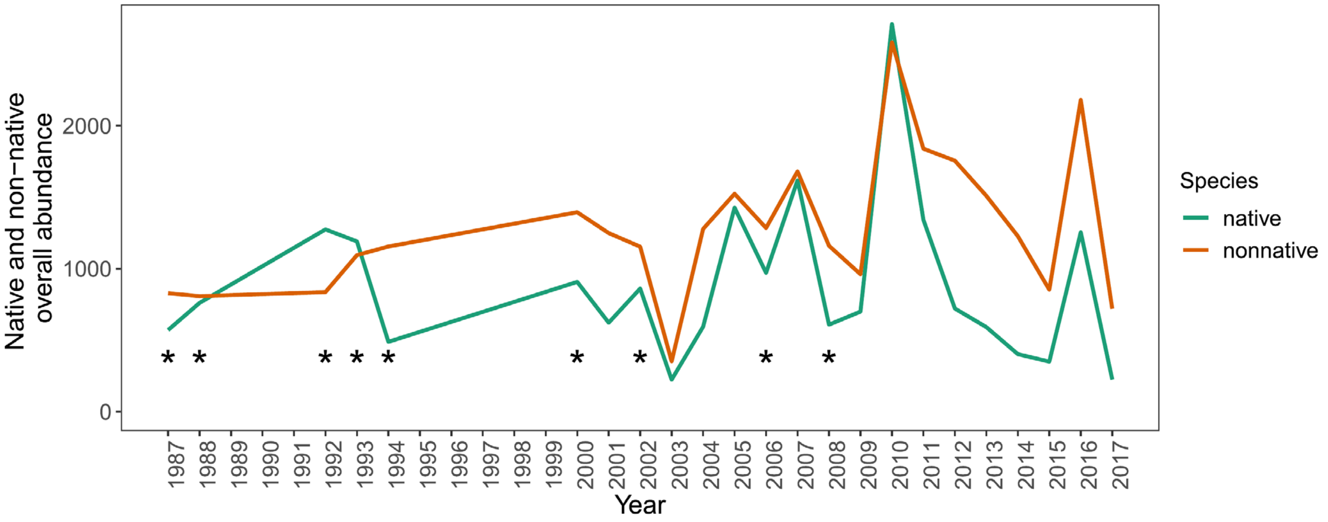

FIGURE 3 | Long-term trends in the total abundance (CPUE—individuals/1000 m^2 of gillnets set during 24 h) of native and non-native species. The abundance of each species was summed by year. The asterisks represent years with the first records of non-native species.

TABLE 1 | Results of Linear Mixed Model of the spatial occurrence of native species (percentage of occurrence per month, logit transformed) as a function of time and the abundance of non-native species. Explanatory variables were standardised prior to the analysis.

		Confidence intervals (95%)			
Parameter	**Estimate**	**Lower**	**Upper**	***t-value***	***p***
Intercept	0.08	0.05	0.11	4.87	< 0.001
Time	−0.09	−0.10	−0.08	−17.51	< 0.001
log Native abundance	0.94	0.92	0.95	152.83	< 0.001
log Non-native abundance	−0.03	−0.05	−0.02	−4.62	< 0.001
Marginal R^2/Conditional R^2	0.544/0.628				

TABLE 2 | Results of Linear Mixed Model between the log-transformed excess co-occurrence (the observed co-occurrence divided by the expected co-occurrence) and time since first record, log native abundance, log non-native abundance, and phylogenetic distance. Explanatory variables were standardised prior to the analysis. Values are medians across models resulting from 100 different phylogenetic hypotheses.

		Confidence intervals (95%)			
Parameter	**Estimate**	**Lower**	**Upper**	***t-value***	***p***
Intercept	0.21	0.20	0.22	35.28	< 0.001
Time since first record	0.01	0.01	0.02	5.10	< 0.001
log Native abundance	−0.13	−0.13	−0.12	−50.08	< 0.001
log Non-native abundance	−0.16	−0.17	−0.15	−50.92	< 0.001
Phylogenetic distance	−0.01	−0.02	−0.00	−2.27	0.030
log Non-native abundance * PD	−0.01	−0.02	−0.01	−4.05	< 0.001
Marginal R^2/Conditional R^2	0.224/0.344				

negative relationship between non-native abundance and excess co-occurrence becomes stronger (Figure 4). Therefore, the phylogenetic distance between species influenced the relationship between excess co-occurrence and non-native abundance, but the effect of non-native abundance on the excess co-occurrence was always negative, regardless of the phylogenetic relatedness between species.

4 | Discussion

Our study contributes to the growing literature about the temporal effects of biological invasions by investigating how co-occurrence between native and non-native freshwater fish species changes through time and which factors modulate these

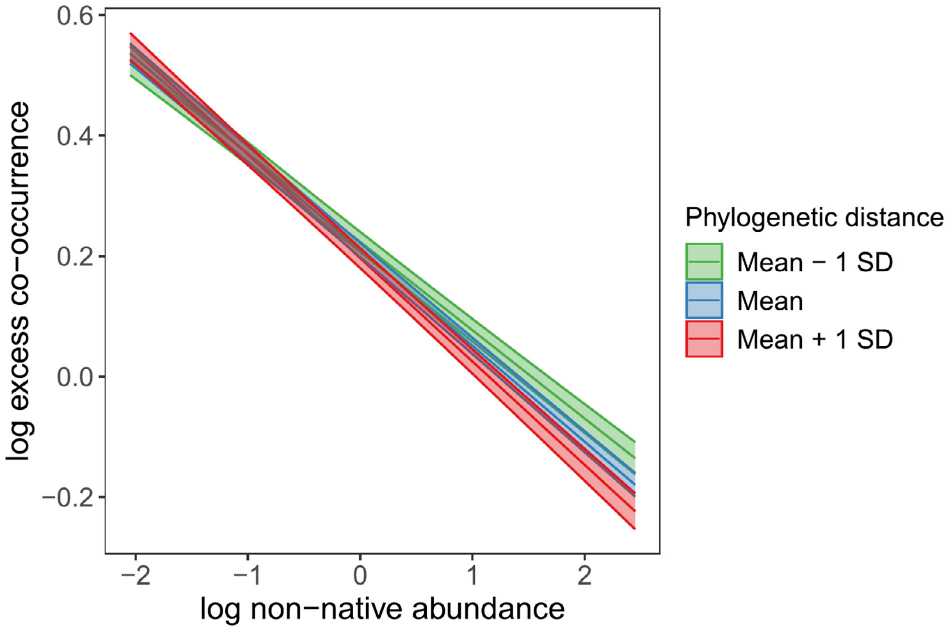

FIGURE 4 | Relationship between the log excess co-occurrence and non-native species abundance (CPUE—individuals/1000m^2 of gillnets exposed during 24h) and its interaction with the phylogenetic distance between native and non-native species. Different colours represent different levels of phylogenetic distance and how groups were defined: Green—low distance (mean—1 standard deviation); blue—intermediary distance (mean); red—high distance (mean + 1 standard deviation). Shaded lines represent 95% confidence intervals.

patterns. First, we found that the effect of time since first record was smaller than the effect of native and non-native abundances in driving species co-occurrence patterns. This suggests that population attributes that are variable through time are more important in determining how native and non-native species co-occur than solely how long a non-native species has been introduced. Second, native and non-native species were found to be co-occurring more than expected by chance when the abundance of native and non-native species was low. However, the co-occurrence between species decreased as the abundance of native and non-native species increased. It would be expected that higher abundances would result in higher encounter probabilities between species, but our results suggest that higher abundances might cause distributional shifts in native and non-native species. Finally, the phylogenetic distance between the pair of species mediated the effect of non-native abundance on the co-occurrence. We found a negative relationship between non-native species abundance and co-occurrence regardless of the phylogenetic distance between native and non-native species: as the phylogenetic distance between species increases, the negative relationship between non-native abundance and co-occurrence strengthens.

4.1 | Co-Occurrence Between Native and Non-Native Species Through Time

We found that the co-occurrence between native and non-native species increased with time. This was contrary to our expectations, which were based on the fact that the increased abundance of non-native species would affect the spatial distribution of native species, imposing a spatial shift to less optimal habitats. Consequently, native species would be spatially displaced, decreasing co-occurrence with non-native species in optimal sites. However, not all non-native species increased their population over time; some showed negative or insignificant trends (Figure S6B). As shown in Figure S7, the abundance of the two most common non-native species showed high intra-annual and interannual variation. This can also be expected for the other non-native species because irregular dynamics in abundance are common in non-native species populations (Strayer et al. 2019). This boom-bust dynamic of explosive growth and collapse of non-native species can be regularly cyclic or irregularly repeated (Haubrock et al. 2022; Soto et al. 2023; Strayer et al. 2017) and can explain the lack of significant long-term trends in the abundance of some species. If the population of a non-native species is often being down-regulated by biotic and/or abiotic factors, then it might not consistently reach a large enough size to affect native species. This dynamic indicates that a high intra- and inter-annual variation in non-native species abundance will likely be less important in influencing the co-occurrence between native and non-native species in a long-term scenario. Therefore, although we found a smaller effect of time since the first record on the co-occurrence compared to non-native abundance, temporal variability should still be considered when studying these patterns. Here, we did so by including the variability of abundance through seasons (i.e., dry and wet periods) and extreme events (i.e., such as large floods). This was extremely important to capture the real temporal effect.

4.2 | Non-Native Species Abundance Affects the Spatial Distribution of Native Species and the Co-Occurrence With Native Species

The models analysed in our study showed that higher non-native species abundance is significantly related to lower spatial occurrence of native species and lower co-occurrence between native and non-native species. The abundance of native species also influenced the co-occurrence between species; however, non-native species have been more abundant in the floodplain during the study period, so the probability of the non-native species affecting the co-occurrence is higher than that of native species. The boom period of non-native species (i.e., rapid abundance increase) may consequently result in spatial segregation between native and non-native species and limit the spatial occurrence of native species. If the high abundance of non-native species persists through time, this spatial segregation may lead to the displacement of native species from optimal habitats, altering their spatial distribution, decreasing their abundance, or even leading to their local exclusion (Bøhn et al. 2008; Ganassin et al. 2020; Pascual-Rico et al. 2020; Smith et al. 2019). This pattern can suggest negative interactions between native and non-native species, such as competition (Richter-Boix et al. 2013) and predation (Pelicice et al. 2015). Displacement of native species associated with the increase and spread of non-native populations has already been reported in invaded communities (Clavero et al. 2022; Jucker et al. 2013; Muñoz and Cavieres 2008; Pelicice et al. 2015). Our results add to this bulk of literature by showing that lower co-occurrence between native and non-native freshwater fish species is related to higher non-native species abundances. Therefore, even though both native and non-native species abundances influence the co-occurrence between them, the increase in abundance of non-native species will potentially be more harmful to the local community than the abundance increase of native species. Non-native species are currently contributing to biotic homogenisation worldwide (Petsch et al. 2022), and their number continues to rise globally (Mormul et al. 2022). Thus, our results are important to show that the population attributes of non-native species must be temporally monitored and that efforts must be directed to avoid non-native species' population growth (e.g., avoiding propagule pressure).

Several factors can improve the population growth of non-native species (Strayer et al. 2017). For example, non-native species can show pre-adaptations to the environmental conditions of the invaded area, for mainly non-native species conserve their climatic niche (Liu et al. 2020) and, therefore, may be able to recover from disturbances in the invaded area. All non-native species considered in this study are translocated species (e.g., non-native species that were introduced in geographically close basins or within the same country or large basin; see Table S2 for introduction vectors), so they all come from habitats with environmental conditions that are roughly similar to the invaded area. Considering this, our findings contribute to speculating on the impacts of translocated species in freshwater ecosystems (Rocha et al. 2023). It has been argued that species origin should not influence ecosystem management (Buckley and Catford 2016). However, we show that the variation in non-native species abundances from the same country or a basin in close proximity can affect the co-occurrence with native species. In addition, the proximity between the source and recipient ecosystems can increase the propagule pressure of the non-native species, which is positively associated with their establishment success (Cassey et al. 2018). Our results underscore that management policies should be reinforced to prevent transporting species in close proximity, even within the same country and between geographically adjacent regions.

4.3 | Role of Phylogenetic Distance in the Co-Occurrence Between Native and Non-Native Species

We expected that phylogenetically similar species would co-occur less when non-native species abundance was high and that the co-occurrence of phylogenetically distant species would be less affected by high non-native abundance. This is true for some cases, which have been mainly related to competitive processes (e.g., Gois et al. 2015; Pascual-Rico et al. 2020; Richter-Boix et al. 2013) and might guide science-based management decisions in order to minimise possible non-native species impacts on target native species in their spatial distributional range. However, we found that co-occurrence decreases with increasing non-native abundance at any level of phylogenetic distance between species. In our results, the intensity of this effect is higher for phylogenetically distant species, which co-occur less than phylogenetically similar species when non-native abundance is high. This result can be explained by either the limiting similarity principle (MacArthur and Levins 1967; Tilman 1982) or the environmental filtering hypothesis (Melbourne et al. 2007). The first hypothesis predicts that similar species will exclude one another due to strong niche overlap, limiting their co-occurrence. On the other hand, the environmental filtering hypothesis predicts that environmental variables will structure communities and filter similar species to inhabit certain environmental conditions, limiting the co-occurrence of phylogenetically distant species. In addition, the spatial segregation of phylogenetically distant species might also depend on habitat preferences because these species will likely occupy different habitat types. Therefore, our results suggest that the co-occurrence patterns between native and non-native species can result from the interplay between the limiting similarity principle and the environmental filtering hypothesis. However, as the non-native species studied here are translocated from geographically close basins, the effects of phylogenetic relatedness on co-occurrence may differ when considering communities with a wider range of phylogenetic distance between species, for example, with non-native species coming from different countries and continents. Investigating these scenarios may provide better targets for management actions in invaded communities.

5 | Conclusions

Our study demonstrates that evaluating the co-occurrence between native and non-native species through time offers a valuable approach to understanding the ecological processes underlying biological invasions by capturing the invasion process as it happens. We highlight the need for long-term studies to continuously evaluate the population dynamics of native and non-native species and communities through time (Haubrock, Carneiro, et al. 2023; Strayer et al. 2006). We also showed that evaluating patterns for several non-native species may provide a broader understanding of the community after invasions by including different levels of relatedness between species. Despite several studies focusing on specific trophic groups or trait similarities between native and non-native species (Ganassin et al. 2020; Grassel et al. 2015; Mathakutha et al. 2019), our results indicate that phylogenetically distant species may also suffer from negative impacts of biological invasions. Although our findings could be generalised to other freshwater groups besides floodplain fishes, analyses of non-native species abundance trends are still scarce due to data gaps across realms, taxa, and regions (Haubrock, Pilotto, et al. 2023). Therefore, we stress the need to investigate similar temporal patterns of biological invasions in other ecosystems and taxonomic groups, as time series community data become more available (e.g., Dornelas et al. 2018).

Author Contributions

Amanda Cantarute Rodrigues, Natália Carneiro Lacerda dos Santos, Luiz Carlos Gomes designed the study. Amanda Cantarute Rodrigues, Rafaela Vendrametto Granzotti, Natália Carneiro Lacerda dos Santos, Angelo Antonio Agostinho, and Luiz Carlos Gomes collected the data. Angelo Antonio Agostinho curated the data. Amanda Cantarute Rodrigues and Rafaela Vendrametto Granzotti performed the analysis. Amanda Cantarute Rodrigues, Natália Carneiro Lacerda dos Santos, and Rafaela Vendrametto Granzotti interpreted the results. Amanda Cantarute Rodrigues wrote the first draft, and all authors contributed substantially to revisions.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The derived data and R code that support the findings of this study are openly available in FigShare at https://doi.org/10.6084/m9.figshare.24967890. The raw data will be available in the same repository (embargoed until 28/02/2026).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.