

RESEARCH ARTICLE

Functional diversity loss and taxonomic delays of European freshwater fish and North American breeding birds

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Handling Editor: Raul Costa-Pereira**Abstract**

1. Biodiversity is temporally dynamic, reflecting historical environmental conditions and influencing ecosystem stability. Colonisation and extinction dynamics frequently exhibit asynchronous patterns, resulting in net imbalances and thus to long-lasting richness trends. If these trends are not functionally random, functional net imbalances between colonisations and extinctions (fNICE) are likely to emerge.
2. Using community time series data of European freshwater fish and North American breeding birds, we investigated how fNICE differs from its taxonomic equivalent (tNICE), to provide a comprehensive picture of biodiversity dynamics.
3. Our findings reveal that taxonomic and functional delays are a prevalent feature, challenging the assumption of an immediate response to environmental changes. Taxonomic delays manifest as extinction debts and colonisation credits, while functional delays indicate a shift in the balance between functional gains and losses over time. Moreover, we found that taxonomic and functional imbalances are not always directly correlated, although some specific patterns were found consistently for fish and birds.
4. Early colonisations outpaced functional gains, indicating that although new species arrived earlier than the extinction of other species, the acquisition of new functional traits lagged. Although this may temporarily stabilise communities, as functional redundancy can mitigate loss of function via local extinctions, excessive redundancy can compromise biodiversity's capacity to respond to environmental variations, thereby undermining long-term resilience.
5. In conclusion, understanding the intricate temporal dynamics of biodiversity responses is paramount for effective conservation practices. While short-term observations may suggest an equilibrium between diversity and the environmental conditions, our results underscore the importance of considering long-term dynamics and the interplay between species traits and changing environments. The metrics tNICE and fNICE are valuable tools for quantifying these temporal dynamics and unravelling their consequences for ecosystem stability. Incorporating

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these insights into conservation strategies can aid in proactively preserving biodiversity and safeguarding the integrity of ecosystems.

KEYWORDS

diversity dynamics, functional disequilibrium, functional turnover, taxonomic delays

1 | INTRODUCTION

Community biodiversity does not always respond in the immediate aftermath of environmental shifts (Hanski & Ovaskainen, 2002; Kuussaari et al., 2009; Vellend et al., 2006), thus suggesting that communities are often not in equilibrium with their current environment but rather with past conditions (e.g. Guo et al., 2020; Rowan et al., 2016; Sandel et al., 2020). The signature of past environmental conditions or events on extant diversity has been documented across extended temporal scales. Insular diversity and endemism of angiosperms have been profoundly shaped by the abiotic conditions experienced during the Last Glacial Maximum, subsequently impacting their contemporary diversity (Weigelt et al., 2016). The extant diversity of other taxa, such as fish, showed also delayed responses to historical factors (e.g. Oberdorff et al., 1997; Tedesco et al., 2005), which is in turn also reflected in their functional structure (e.g. Côte et al., 2019; Ordonez & Svenning, 2015, 2016). More recently, delays in diversity responses have been investigated in relation to human-induced disturbances (Figueiredo et al., 2019; Kuussaari et al., 2009). For instance, recently urbanised areas (i.e. shift in habitat type) are likely to exhibit delays in extinctions (i.e. extinction debts). On the other hand, delays in colonisations (i.e. colonisation credits) are more likely under habitat loss (e.g. loss of grassland; Haddou et al., 2022). Similarly, over the last decade in the European Alps, cold-adapted plants are experiencing extinction debts while warm-dwelling species exhibit colonisation credits (Rumpf et al., 2019). Overall, the responses to environmental changes are not systematically immediate, and we need to account for these delays when defining and implementing biodiversity conservation strategies.

Several methods have been proposed to quantify lags in diversity responses, although they rely on explicitly considering the environmental changes experienced such as habitat fragmentation (Tilman et al., 1994) or climate change (e.g. Devictor et al., 2012). Recently, a new approach was developed using only community time series to infer the net imbalance between colonisations and extinctions (hereafter, NICE; Kuczynski et al., 2023). Based on this metric, considering cumulative colonisations and extinctions over time and interpreted against the backdrop of a neutral model, European freshwater fish and American breeding birds exhibited delays in extinctions (Kuczynski et al., 2023). The NICE metric, in its taxonomic version, has two major advantages. First, it decomposes changes into losses and gains, providing a more nuanced picture than net change or turnover over time. Second, it quantifies the imbalance without reference to a specific environmental driver, which is critical as the data are not always available and/or the underlying processes

are not always identified. Although the NICE metric is intuitive, easy to use and only requires community occurrence time series, it disregards species functional traits and thus the potential delays in functional responses.

Changes in species identity over time (i.e. taxonomic temporal turnover) can have dramatic consequences in regard to the occupied niches by the coexisting species (i.e. functional temporal turnover). In particular, generalist species tend to successfully spread over space, replacing specialist species (Clavel et al., 2011), which are commonly declining (e.g. Fisher et al., 2003; Julliard et al., 2004; Munday, 2004; Rooney et al., 2004) resulting in a higher functional redundancy within communities (i.e. functional homogenisation; Fisher & Owens, 2004). High functional similarity between species might enhance community stability and resilience in face of disturbance (i.e. insurance hypothesis; Biggs et al., 2020). However, a strong imbalance in favour of generalist species might lead to a low diversity of responses to changes and a decrease in the buffering ability of the community in face of disturbances (Hooper et al., 2005; Loreau & de Mazancourt, 2008; Olden, 2006).

Incorporating traits (i.e. “any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organisation”, Violle et al., 2007) in the assessments of delays in diversity responses presents significant challenges. First, relevant traits should be selected, when possible, considering potential future meta-studies to allow comparing across taxa as well as across studies. For example, traits can be grouped into three categories based on the main assembly process they respond to, namely dispersal, biotic interactions and environmental filtering (Bauer et al., 2021). On the other hand, using as many traits as possible allows one to capture as much of the functional niche occupied by the community as possible and is therefore a common practice in functional ecology studies. Following the selection of relevant traits, appropriate functional diversity metrics must be selected. A commonly used metric is the functional volume occupied by co-occurring species within a given ecological community (Mason & Moullot, 2013), usually standardised relative to the functional volume of the regional species pool, which allows for comparisons across space, taxa, studies and over time.

The complementary use of the NICE metric and the functional volume can allow us to investigate the consequences of taxonomic delays in diversity changes, as previously highlighted (Kuczynski et al., 2023). Previous frameworks, such as the one proposed by Chao et al. (2021), have attempted to account for various facets of diversity (i.e. taxonomic, functional and phylogenetic). However,

they often assess changes over time assuming perfect parsimony and thus by investigating only the net change in diversity. A more nuanced approach involves decomposing global change into distinct components of losses and gains. This allows for the identification of the relative role of loser and winner species within ecosystems (e.g. Fulton, 2011; Hoveka et al., 2022; Rosset & Oertli, 2011). Thus, combining NICE and the functional volume into one metric will give insights on the balance between lost and gained components of the functional volume. In order to do so, we developed an analogous metric to the taxonomic NICE (hereafter tNICE), the functional Net Imbalance between colonisations and extinctions (hereafter fNICE), integrating functional volume and allowing inference about whether gain and loss in functional volume are balanced, assuming that communities are historically at the equilibrium with their environment and have no unfilled niche (Figure 1a,b).

We have assessed fNICE to the same datasets as in Kuczynski et al. (2023), namely European freshwater fish and American breeding birds time series (Figure 1c). In particular, investigating

the relationship between tNICE and fNICE can help understanding community temporal dynamics in relation to the niche complementarity of coexisting species. The link between the two metrics depends on whether the species underlying tNICE patterns are functionally unique or redundant (Figure 2). When species driving tNICE patterns are functionally unique, we expect to see significant changes in fNICE as these species contribute significantly to the functional richness of the community through niche complementarity. In particular, if these species are going extinct or are colonising the community, both tNICE and fNICE will be negative and positive, respectively, with fNICE exhibiting more pronounced trends (i.e. $|fNICE| > |tNICE|$). However, should these unique species show opposite trends to the overall tNICE patterns (e.g. undergoing extinction while tNICE indicates early colonisations), fNICE and tNICE will exhibit disparate, or even opposite, patterns. Finally, when species are functionally redundant, they will attenuate the patterns from tNICE to fNICE (i.e. $|fNICE| < |tNICE|$) as the taxonomic changes will only weakly be mirrored by the functional ones.

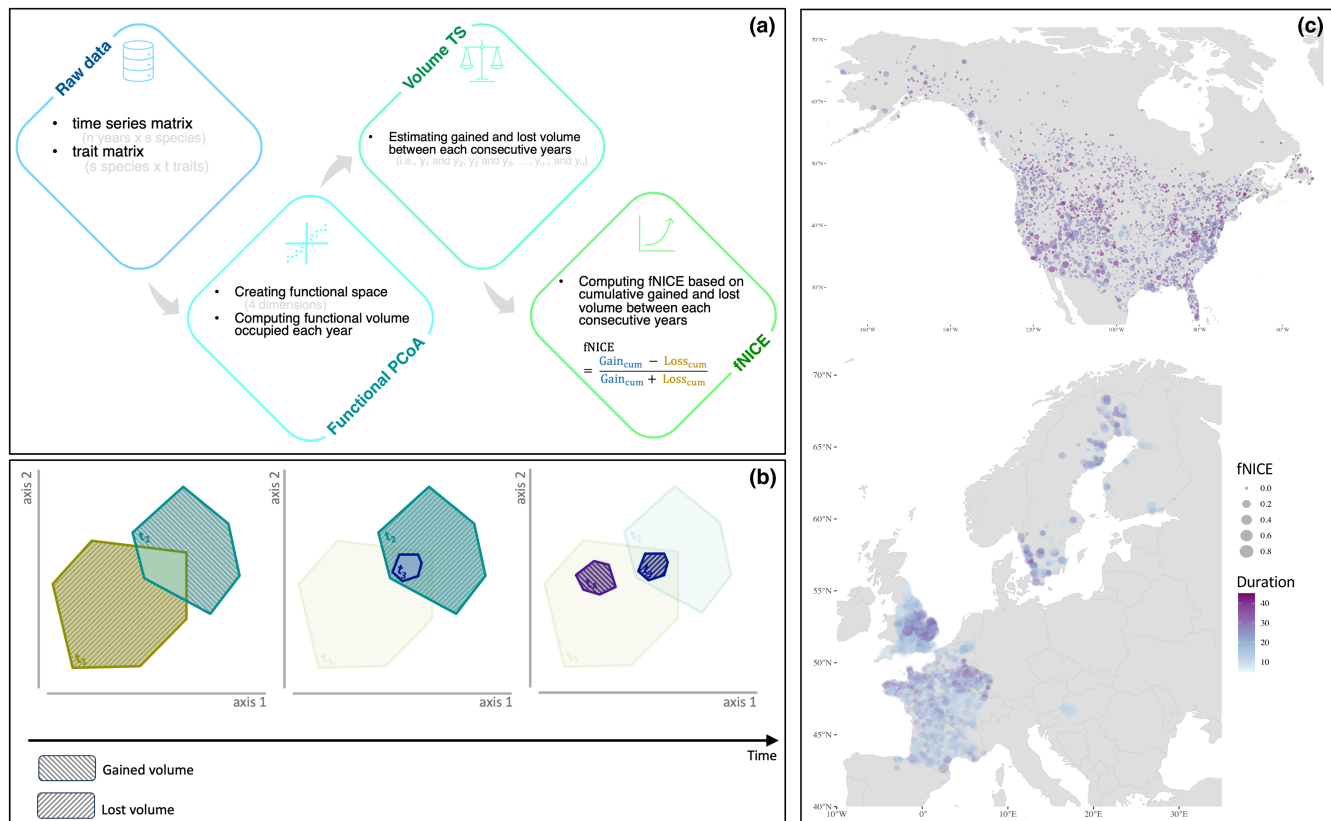


FIGURE 1 Panel (a) is the analytical framework used to compute the functional Net Imbalance between colonisations and extinctions (fNICE) for a given time series. First, the data used are a community matrix where rows are years and columns species abundances or occurrences. All the samples have to be taken at the same location. From the data, a principal coordinates analysis (PCoA) is run based on all species present at least once during the time series and the adequate number of axes is kept (here only two are shown for graphical purpose). Then, each year's functional volume is computed. From each pair of consecutive years, the lost and gained are computed as the unique part of the volume occupied by the first and the consecutive year, respectively. Finally, one gets a time series of lost and gained volumes from which cumulative losses and gains can be computed to calculate fNICE. Panel (b) presents the calculation of fNICE in terms of cumulative volume lost and gained over time. Specifically, the lost volume refers to the volume of the first year that does not intersect with the volume occupied during the second year, while the gained volume refers to the volume from the second year that does not intersect with the first year. Panel (c) shows the distribution of data for North American breeding birds and European freshwater fish. The size indicates the absolute value of fNICE observed for each time series, while the colour represents the length of the time series in years.

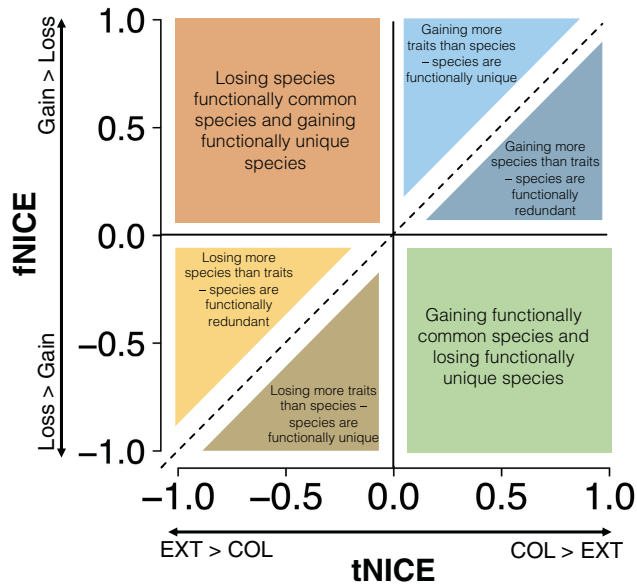


FIGURE 2 Theoretical figure of the relationship between taxonomic NICE (tNICE, x-axis) and functional NICE (fNICE, y-axis).

2 | MATERIALS AND METHODS

2.1 | Community time series

To infer the temporal dynamics of tNICE and fNICE, we used the same community time series as in Kuczynski et al. (2023). In particular, we used two highly curated databases. First, the RivFishTIME database, which covers freshwater fish abundance time series (Comte et al., 2021). We focused our analyses on 3036 European time series with at least 10 years of available data. The final dataset included time series starting in 1951 and ending in 2019, with an average of 12 sampled years ($SD=6.6$ years). Second, we used the North American Breeding Bird Survey database, which represents 4317 time series with at least 10 years sampled, comprising time series starting in 1966 and ending in 2021 (29 sampled years on average ± 12.5 years; Ziolkowski Jr. et al., 2021). To compare our results to a neutral baseline, a model based on the theory of island biogeography was used to generate artificial data similar to the studied datasets (see Methods—Simulated data in Kuczynski et al., 2023 for more details). The dynamics of this model are implemented in the R package *island* (Ontiveros et al., 2019). Assuming that all species are equivalent (i.e. same colonisation and extinction rates), and independent, we have simulated the temporal dynamics of a community, given its initial richness, the number of species in the pool and the colonisation and extinction rates. In the simulated data, colonisation and extinction rates were set as equal. In particular, these rates have been determined using empirical data, namely the average number of colonisation events over the empirical time series divided by time series duration. We simulated 4999 time series of presence-absence data using the *function_PA* (Ontiveros et al., 2019). For each simulated time series, species were randomly drawn from a species pool, based on the total number of species observed for a given time

series. We randomly sampled time series length and initial species richness from the observed distribution of these values in the empirical databases. Unlike Kuczynski et al. (2023), we did not use the null model that fully removed temporal autocorrelation as random species dynamics (i.e. no autocorrelation) were less ecologically relevant to quantify diversity changes at the community level.

2.2 | Traits data

To assess functional diversity, we used 21 ecology related traits and 7 morphological traits for fish (Comte & Olden, 2017; Froese & Pauly, 2017) and 18 ecology related traits and 10 morphological ones for birds (Tobias et al., 2022; Wilman et al., 2014; Tables S1 and S2). Although the ecological traits for fish were mostly related to habitat use whereas the ones for birds were mostly related to their trophic habits, thus informing about different aspects of the niche, we kept all of these traits, to capture as much information as possible regarding their niche. Overall, traits were weakly correlated to each other for both taxa (correlation coefficients ranged from 0 to 1, median_{fish}=0.05 and median_{birds}=0.17). For fish, strong correlations were observed for two traits (neritic and sublittoral) exhibiting very low interspecific variability, while for birds strongly correlated traits were all related to trophic habits. Trait completeness for a given trait for fish species ranged from 15% to 100%, with an average of 80% completeness. For birds, traits were fully documented for all species. For simulated data, we randomly attributed traits to species while keeping the trait combinations as observed in the empirical data.

2.3 | Taxonomic net imbalance between colonisations and extinctions

To quantify tNICE, we used the same methodology as described in Kuczynski et al. (2023). To summarise, for each species for each time series, colonisations and extinctions were estimated using optimal linear estimation models (Clements et al., 2013). Then, across species, the cumulative numbers of colonisations (COL) and extinctions (EXT) were computed and tNICE was calculated as followed: $COL - EXT / COL + EXT$. The metric tNICE ranges from -1 to 1 , with negative values meaning that extinctions happen earlier than colonisations, and positive values indicating that colonisations are happening earlier than extinctions.

2.4 | Functional net imbalance between colonisations and extinctions

To compute fNICE, the first step was to compute the functional volume for each time step. To do so, we estimated the functional volume occupied by co-occurring species at each time step in a 4-dimensional space, allowing a good representation of the variance in the functional data (Maire et al., 2015; Table S3, Figure S2). We

used the Gower's distance that allow missing values in the trait data and mixed types of traits (i.e. categorical, binary and numerical). Each time series was characterised by a slightly different space as the space was defined based on all species sampled during a given time series (i.e. local species pool). Then for each time step, we quantified the lost and gained volume and computed fNICE as $(\text{Gain} - \text{Loss}) / (\text{Gain} + \text{Loss})$ (Figure 1b). We ran this for three sets of traits, for each taxa: all, ecological and morphological traits (Tables S1 and S2). The results for each subset are only presented in the Appendix as they are similar to the global analyses (Figures S2, S4 and S5, Tables S4–S7).

2.5 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Ecological community	Local plot	3036 (fish) + 4317 (birds)

2.6 | Statistical analysis

To assess the consistency between both metrics, tNICE and fNICE, we conducted a Spearman correlation test. Additionally, we ran linear mixed-effects models to estimate global trends in tNICE and fNICE. Year was used as the explanatory variable and site was used as a random effect. We also computed local trends using linear models, with year as the predictor variable in order to extract the resulting slope. A positive slope indicates that colonisations are occurring earlier while a negative slope means that extinctions are happening earlier than they did previously. Furthermore, we explored the impact of time series duration on the observed trends to quantify potential biases from short time series. To achieve this, we applied generalised additive model with location, scale and shape (GAM LSS) models, which can handle heteroscedasticity in the data (Stasinopoulos & Rigby, 2008). Finally, since species richness and tNICE trends were weakly correlated ($\text{cor}_{\text{fish}} = -0.1$, $p = 0.003$; $\text{cor}_{\text{birds}} = -0.2$, $p < 10^{-3}$, Figure S1), we tested whether trends in functional volume and in fNICE were also correlated using a Pearson correlation test. A strong correlation between changes in the functional volume and in fNICE would suggest that changes in functional volume alone can indicate the disequilibrium between gained and lost volume over time. Conversely, if both metrics are independent, this would suggest that fNICE provides additional complementary information about functional diversity dynamics. All analyses have been run with R (R Core Team, 2023) and the main script is available on Zenodo and Github.

3 | RESULTS

fNICE spanned the complete range for both taxa and showed a mean value near to zero, indicating an absence of global functional

diversity imbalance. tNICE and fNICE were found to be weakly but significantly correlated for both taxa ($\text{cor}_{\text{Fish}} = 0.05$, $p = 0.03$ and $\text{cor}_{\text{Birds}} = -0.05$, $p = 0.001$) when all traits were considered (Table S4). By contrast, simulated data did not exhibit such a link, suggesting that species going locally extinct and colonising communities did not exhibit a random combination of functional traits. For birds, this pattern was also found when only considering ecological traits ($\text{cor} = -0.06$, $p < 0.001$; Table S4). Overall, the most common pattern was a positive value of tNICE associated with a lower value of fNICE (either positive or negative; Figure 3, Figure S3), suggesting that colonisations happened earlier than extinctions while new species did not necessarily add new traits to the community they are colonising. In particular, positive tNICE were associated with negative fNICE values (for fish: $n_{\text{all}} = 610$, $n_{\text{eco}} = 630$ and $n_{\text{morpho}} = 518$

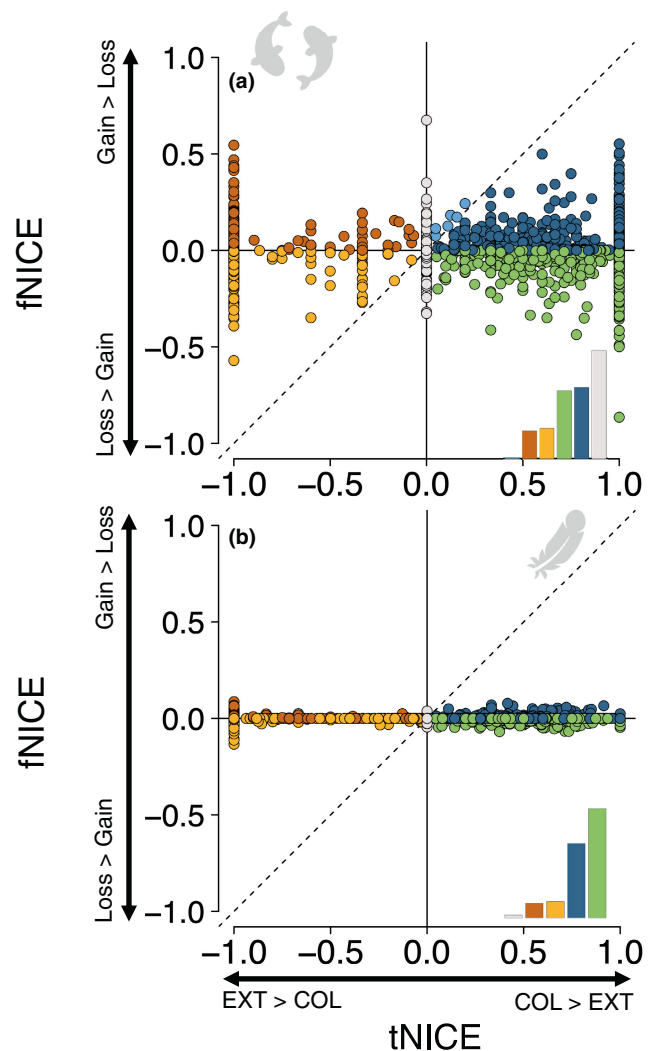


FIGURE 3 Relationship between tNICE (x-axis) and fNICE (y-axis). Each point represents the final value of tNICE and fNICE for a given time series (i.e. each community is represented only once). Bar plots represent the proportion of sites related to each of six scenarios presented in Figure 2 and highlighted here by the different colours (light grey points are communities for which tNICE=0). The upper panel (a) represents fish data, while the lower one (b) represents bird data.

out of 1777 communities; for birds: $n_{\text{all}}=2167$, $n_{\text{eco}}=2177$ and $n_{\text{morpho}}=1894$ out of 4261 communities; Table S5), suggesting that communities have lost key functional trait combinations, which were not replaced by functionally equivalent species but by species with already present traits. On the other hand, communities with both positive tNICE and fNICE values but with fNICE lower than tNICE (for fish: $n_{\text{all}}=640$, $n_{\text{eco}}=610$ and $n_{\text{morpho}}=516$ out of 1777 communities; for birds: $n_{\text{all}}=1479$, $n_{\text{eco}}=1469$ and $n_{\text{morpho}}=1752$ out of 4261 communities; Table S5) experienced earlier colonisations than extinctions, while functional gains did not happen as early as colonisations (i.e. gained species are mostly functionally redundant). Less commonly, negative tNICE values were associated with higher fNICE values (either negative or positive; Figure 3, Figure S3). Both tNICE and fNICE being negative, with less negative fNICE values (for fish: $n_{\text{all}}=272$, $n_{\text{eco}}=270$ and $n_{\text{morpho}}=212$ out of 1777 communities; for birds: $n_{\text{all}}=326$, $n_{\text{eco}}=303$ and $n_{\text{morpho}}=313$ out of 4261 communities; Table S5), suggest that extinctions happened earlier than colonisations and that the species that went extinct tend to have common functional traits (i.e. functionally redundant with coexisting species). On the other hand, negative tNICE and positive fNICE (for fish: $n_{\text{all}}=249$, $n_{\text{eco}}=249$ and $n_{\text{morpho}}=252$ out of 1777 communities; for birds: $n_{\text{all}}=289$, $n_{\text{eco}}=312$ and $n_{\text{morpho}}=301$ out of 4261 communities; Table S5) showed early extinctions associated with gain in functional richness, suggesting that mostly functionally common species were lost while the few gained species were highly functionally original (i.e. high increase in functional richness).

3.1 | Temporal trends in fNICE

Overall, although fNICE were initially positive, they have decreased over time (Table S6, Figure S5), suggesting losses in functional richness have increased relative to gains over time. This was consistently true for birds but for fish only when all traits were considered together. Furthermore, while species richness and tNICE trends were weakly correlated ($\text{cor}_{\text{fish}}=-0.1$, $p=0.003$; $\text{cor}_{\text{birds}}=-0.2$, $p<10^{-3}$; Figure S1), fNICE trends were not correlated with changes in functional volume for fish ($\text{cor}=-0.02$, $p=0.4$) but, albeit significantly, only weakly for birds ($\text{cor}=-0.03$, $p=0.04$). Decrease over time was observed also for simulated data but only for all traits for fish and for morphological traits based fNICE for birds (Table S6, Figure S5). Trends were not affected by the time series length (Table S7, Figure S6).

4 | DISCUSSION

Despite an increase in functional diversity and no global imbalance in functional gains and losses, we found local functional imbalance as well as taxonomic imbalance, especially for dispersal-limited taxa such as river fish. In particular, taxonomic delays in favour of colonisations (i.e. extinction debts) are associated with the loss of unique functional traits within communities. Overall, trends in functional equilibrium suggest that debts in functional diversity are being paid

yet communities are eventually experiencing losses in their functional diversity.

4.1 | Functional imbalance between gains and losses

On a global scale, we found no significant imbalance between the gains and losses in functional richness. The scale dependency of functional imbalance mirrors findings on taxonomic diversity and its associated delays. Specifically, estimates of species richness changes exhibit variations in magnitude and direction (i.e. increase or decrease) across different spatial scales, with no consistent trends across study systems (Chase et al., 2019). This variability across scales can be attributed to the non-linear scale dependency of colonisations and extinctions themselves (Jarzyna & Jetz, 2018), mirrored by their relative equilibrium. These variations across spatial scales can result from landscape context (Ernault & Alard, 2011; Guardiola et al., 2018; Koyanagi et al., 2017) but also higher extinction rates at smaller scales (Cousins & Vanhoenacker, 2011).

Our observations revealed an averaging effect, where equally strong but opposing patterns counteract the signals of pronounced patterns. Notably, fNICE values spanned both extremes of their possible range for both taxa. This suggests communities may experience imbalances that either favour gains or losses in functional volume, depending on specific contextual factors and contingencies. In cases of an imbalance skewed towards functional gains, this does not necessarily imply an absence of trait loss. Rather, it suggests that gains may outweigh losses or that the loss of traits has yet to happen. Conversely, an imbalance in favour of functional losses suggests a local loss of certain functional traits, although it does not preclude the possibility of some traits being gained. The contrast between local and global patterns emphasises the need to account for spatial scale when exploring community dynamics, highlighting the scale dependency of the underlying mechanisms for both studied taxa. Moreover, we found more variability in fNICE values for fish than for birds, for both observed and simulated values. This could result from the selected traits, which are likely to reflect different niche dimensions for each taxon. For fish, the selected traits reflected habitat use and movement abilities and in a lesser extent trophic habits, whereas for birds, traits were related to trophic habits and movement abilities but not explicitly to habitat use. Thus, this difference might result from habitats being more impacted in the last decades than resources which would result in a high lability in the functional structure in fish and to a lesser extent in birds.

4.2 | Relationship between taxonomic and functional imbalances

Patterns of taxonomic and functional imbalances, due to some degree of correlation, exhibited specific associations in our studied

systems. Taxonomic and functional diversity are not always linked (e.g. Jarzyna & Stagge, 2023), and they may display both convergence and divergence depending on the scale, taxa and system (e.g. Kovalenko et al., 2019). In our study, we observed that taxonomic imbalance skewed towards earlier colonisations (indicated by positive values of tNICE) was mostly associated with lower fNICE values (i.e. $tNICE > fNICE$). This suggests that newly colonising species ("winners") do not necessarily introduce novel traits, often displaying functional redundancy with the local coexisting species. Conversely, species facing extinction ("losers") tend to exhibit unique combinations of traits. Two main patterns emerged in both avian and aquatic ecosystems. First, early colonisations outpaced functional gains (i.e. $tNICE > fNICE > 0$), indicating that although new species arrived earlier than the extinction of other species, the acquisition of new functional traits lagged. Second, communities experienced the loss of pivotal functional species, which were not replaced by functionally equivalent counterparts but rather by species with traits already present (i.e. $tNICE > 0$ and $fNICE < 0$). In both cases, a global functional diversity loss ensued (e.g. Abadie et al., 2011; Devictor et al., 2008). In particular, based on the simulated data, no discernible correlation between fNICE and tNICE was observed, implying that the traits lost during species extinctions in empirical data were not random (e.g. Coulon et al., 2004). However, unlike prior studies, this increase in functional redundancy did not manifest in a specific subset of traits, for both taxonomic groups.

The augmentation of redundancy can be beneficial, up to a certain threshold, as it enhances community stability (Biggs et al., 2020). In this context, even if one species faces extinction, another can compensate in terms of ecosystem functions due to similar functional traits (Lawton et al., 1993; Walker, 1992). For instance, the loss of function of South American plant communities would not occur until after the neutral extinction of about 75% of the species because of a strong functional redundancy between co-occurring species (Fonseca & Ganade, 2001). Nonetheless, an increasing functional redundancy, given a system's carrying capacity (i.e. low niche complementarity), could eventually reduce the diversity of responses to environmental fluctuations and the long-term ability to face disturbances (Levine & HilleRisLambers, 2009; Turnbull et al., 2013) as response diversity is a critical attribute of ecosystems, safeguarding against collapse by increasing resilience (Mori et al., 2013). Functional diversity loss can be attributed to several mechanisms. First, specialist species, inherently having narrow ecological niches, tend to thrive in stable environments, whereas ecological generalists adapt to environmental unpredictability (Abadie et al., 2011; Futuyama & Moreno, 1988). Consequently, environmental shifts towards increased environmental variability can sort species out based on their degree of specialisation (e.g. Devictor et al., 2008), resulting in increased functional redundancy. Moreover, high environmental stress, a common consequence of ongoing global changes (Allen et al., 2018), favours species equipped with specific adaptive traits capable of withstanding strong environmental

harshness (Diamond, 1975; Keddy, 1992). As environmental stress intensifies, the availability and/or diversity of resources (e.g. food, shelter) decreases, leading to increased inter-species competition for these limited resources (Chesson, 2000). Consequently, only species with the necessary traits to thrive in such conditions are expected to survive; environmental filtering being a major assembly rule (Mayfield et al., 2009; Webb et al., 2002). In this context, species with analogous adaptive traits, such as drought resistance mechanisms or the capacity to survive in environments with highly unpredictable temperature variations, may proliferate in affected communities. Finally, the introduction and potential spread of non-native species can strongly impact the functional distinctiveness of native communities (e.g. Angulo-Valencia et al., 2022; Tordoni et al., 2019; Toussaint et al., 2018). Non-native species are often generalists or robust competitors (e.g. Aslan, 2019; Nurkse et al., 2016), possessing traits or adaptations enabling them to thrive and reproduce across a broad spectrum of environmental conditions (e.g. Havel et al., 2015; Olsson et al., 2009). This competitive edge can result in larger populations and accelerated growth rates for non-native species (e.g. Grotkopp & Rejmánek, 2007), which many increase their dominance within local communities (e.g. David et al., 2017; Morales et al., 2013; Torchin et al., 2003).

Overall, redundancy can enhance stability at first by preserving ecosystem functions even when species are lost. However, if redundancy increases excessively due to factors like environmental stress and the spread of non-native species, it might reduce the diversity of responses to environmental changes and long-term resilience. Here, we showed that taxonomic delays were associated with functional ones, resulting in a loss of functional diversity, which ultimately reduces the ability of ecosystems to cope with disturbances and challenges their survival.

4.3 | Trends in functional imbalance

Ecological communities are dynamic entities in which the balance between gains and losses in both taxonomic and functional diversity is fluctuating (e.g. Loranger et al., 2016; Purschke et al., 2013). Over time, these dynamics might lead to losses in functional volume catching up with gains from new species (e.g. Baker et al., 2021). While it may seem that the current functional state mirrors an equilibrium between coexisting species' ecological niches and the present environmental conditions, here we showed that communities are actually experiencing a dynamic functional disequilibrium.

Functional dynamics go beyond a simple count of species and delve into the complex interactions between functional traits and delays in taxonomic diversity changes. Our study reveals that this change in the functional diversity balance does not merely hinge on the length of time series data; it is not an artefact of temporal scale nor sampled time window (e.g. Dove et al., 2023). Moreover, current functional diversity indices might not fully

capture the delays in functional dynamics. The delayed change in functional structure is likely due to delays in species changes, as some species might be able to survive and even thrive in suboptimal conditions, combined with the fact that these species tend to have specific functional traits (e.g. Naaf & Wulf, 2011; Prisco et al., 2016; Rader et al., 2014). These non-random losses are likely the result of increasing environmental filtering and interspecific competition. As the environment undergoes pervasive changes (i.e. increasing environmental harshness), the competition for limited resources intensifies, leading to the selection of the best competitors with specific adaptive traits, who then become the 'winners' (e.g. Filgueiras et al., 2021).

The loss of functional diversity, which appears to get stronger over time, may eventually cause local ecosystem collapse. For instance, in modelled communities, high diversity prevents non-native predator colonisation; however, a gradual loss of native species causes the system to collapse (Downing et al., 2012). These modelled results might expand on real-world communities, such as in Lake Victoria, where the Nile perch introduction led to a strong delay in the extinction of most cichlid species (Verschuren et al., 2002). This highlights that the complexity and diversity of communities can prevent extinctions and secondary extinctions (i.e. species going extinct as a result of a first set of extinctions) and thus collapse (Dunne & Williams, 2009).

4.4 | Delays and conservation perspectives

Identifying delays in taxonomic and functional diversity changes provides a time window for intervention before it is too late. In particular, areas with important temporal lags in their response to global change can simply be mapped, efficiently highlighting potential high-priority areas (e.g. Semper-Pascual et al., 2018; Soga & Koike, 2013). Early warning signals of approaching tipping points of loss of diversity might also help prevent potential ecosystem collapse (Essl et al., 2015). However, delays in taxonomic and functional responses suggest that historical reference states, which are used in conservation ecology as a baseline to estimate the goal to reach in terms of naturalness and pristineness, may no longer exist (Bürgi et al., 2017). While historical perspectives have been crucial in developing critical hypotheses to explain past and current patterns of biodiversity, they may be less relevant. The observed delays may prompt us to think ahead and shift our framework regarding the baseline used for conservation ecology. Specifically, one could use a contemporary reference state that is similar in terms of abiotic conditions to the studied sites but exhibits a high standardised native species richness (McNellie et al., 2020; Sinclair et al., 2002; Symstad & Jonas, 2014).

Finally, lags in functional and taxonomic diversity may be indicators of secondary extinctions. These result from the time lag required for indirect interactions to occur (Brown et al., 2001; Yodzis, 1988). The time lag between a species extinction and subsequent extinctions depends on several factors, including the trophic

positions of the different species (Borrvall & Ebenman, 2006), the trophic uniqueness of the species involved (Petchey et al., 2008), as well as trophic redundancy in the community (Emer et al., 2018; Sanders et al., 2018, p. 20; Valiente-Banuet et al., 2015), the species richness of the community (Borrvall & Ebenman, 2006), and connectivity at the metacommunity scale (Leibold et al., 2004). These different mechanisms provide several leverage points for conservation. For example, higher richness can be achieved with a larger suitable habitat patch (Macarthur & Levins, 1967), while the creation of habitat corridors enhances dispersal rates and thus potential recolonisations and rescue effect (e.g. Newmark et al., 2017) and thus increases the adaptive capacity of the system (Vaughan & Gotelli, 2021). In addition, conservation actions at the species level, such as focusing on large-bodied frugivore seed dispersers (Brodie et al., 2014) or top predators (Borrvall & Ebenman, 2006; Pimm & Gilpin, 2014) might prevent cascading extinctions resulting in severe diversity loss.

5 | CONCLUSIONS

If we are to understand diversity dynamics, our analytical frameworks need to incorporate functional disequilibrium and underlying functional turnover. While short-term patterns might suggest equilibrium, our findings emphasise the importance of considering long-term dynamics, as what we observe within short time spans may not accurately represent true ecological equilibrium within communities. Identifying phylogenetic disequilibrium would complement functional and taxonomic patterns, by considering the lost and gained branches of the phylogenetic tree giving some evolutionary insights on the diversity dynamics. Conservation efforts are vital, making essential the need to account for these temporal delays and the intricate interplay between species' traits and their changing environment. Incorporating these dynamics will help ensuring a more comprehensive and accurate approach to preserving ecological integrity. The proper detection and quantification of these unpaid debts might support opportunities for proactive biodiversity conservation through critical habitat restoration and targeted actions (Kuussaari et al., 2009).

AUTHOR CONTRIBUTIONS

The study was designed by HH and LK. LK was responsible for data acquisition, analysis, interpretation and article writing. HH reviewed the different versions of the manuscript. AMBU collected trait data for birds. All authors reviewed and approved the final version and unanimously agreed on its submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All used data are from publicly available sources, which are cited in the manuscript. The R script is available on GitHub: <https://github.com/Lucie-KCZ/FunctionalDelays> and Zenodo: <https://doi.org/10.5281/zenodo.11201077>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Traits for European fish.

Table S2. Traits for birds.

Table S3. Averaged eigen values of the PCoA.

Table S4. Correlation between fNICE and tNICE, based on raw and SES of fNICE.

Table S5. Contingency table of the values of tNICE and fNICE for observed time series/Corresponding to the colours on Figure 2.

Table S6. Temporal trends in fNICE observed and simulated data.

Table S7. Results of the GAMLSS for the effect of TS length on fNICE.

Figure S1. Relationship between trends in species richness and trends in tNICE.

Figure S2. Temporal trends in the functional volume of communities for fish (A) and birds (B).

Figure S3. Relationship between observed and simulated tNICE and fNICE.

Figure S4. Relationship between tNICE and fNICE.

Figure S5. Trends in fNICE over time.

Figure S6. Time series influence on trends estimates of fNICE.

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