






PERSPECTIVE 

Spatial Insurance of Distinct Ecological Functions

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ABSTRACT

Biodiversity can buffer ecosystem functioning against disturbances by allowing species to compensate for the functions lost through the extirpation of other species, a key process known as ecological insurance. Functional ecology has extended this idea by emphasising trait redundancy amongst species that help buffer core ecosystem functions. However, some functions might be supported only by species with distinct combinations of trait values, which are less likely to be redundant within local communities. Here, we present a new and widely applicable framework to quantify the spatial insurance of locally functionally distinct species amongst communities. Our framework characterises how communities can disproportionately insure (functional sources) or depend on (functional sinks) neighbour communities, a dual relationship that is not captured by traditional metrics of functional beta diversity. We illustrate the application of our framework at broad spatial scales for plants and birds, highlighting biogeographic patterns of functional sources and sinks. This trait-based spatial perspective reveals functional vulnerability, as illustrated by bird communities where functional sources were disproportionately impacted by human activities. It also provides a new approach to identify regions that differ in potential resilience to environmental change and to inform conservation strategies grounded in spatial trait distributions, supporting the preservation of functional distinctiveness beyond a focus on local biodiversity metrics.

1 | Introduction

A central hypothesis in ecology is that biodiversity stabilises ecosystem functioning by enabling species to compensate for one another when environmental conditions change (Loreau et al. 2021). This hypothesis, coined as ecological insurance (Yachi and Loreau 1999), posits that species respond asynchronously to disturbances in a changing environment within communities. As some species decline, others thrive, maintaining

the resilience of key biological and ecosystem processes over time (Dee et al. 2019). A critical component of this hypothesis is spatial dynamics. Local ecological stability to changes in the environment depends not only on the species present within a community, but also on the proximity of neighbouring communities that host potential colonists capable of replacing locally declining species (Loreau et al. 2003; Wang and Loreau 2016). Temporal and spatial insurance mechanisms act synergistically, ensuring the stability of ecosystem functioning under

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environmental change (Loreau et al. 2021). Originally, ecological insurance considered taxonomic diversity only, and ecosystem functioning primarily in terms of aggregate, additive properties, such as primary productivity, nutrient cycling or biomass accumulation (Yachi and Loreau 1999). In this context, stability arises when fluctuations in the performance or abundance of some species are offset by others, buffering variation in these summed properties over time (Yachi and Loreau 1999; Loreau et al. 2003).

However, ecological communities are multifunctional (Gross et al. 2017) and species can contribute in different ways to ecosystem processes. A functional trait perspective addresses this key issue (Diaz and Cabido 2001; Garnier et al. 2016; de Bello et al. 2025) by recognising that the diversity of functional traits is more informative than taxonomic diversity itself (Cadotte et al. 2011; Gross et al. 2017; de Bello et al. 2021). Indeed, functional traits of organisms capture different dimensions of their phenotypes (Violle et al. 2007; Laughlin 2014; Mouillot et al. 2021; Díaz 2025), and thus represent different ways to respond to environmental changes (through ‘response’ traits) and to contribute to ecosystem functioning (through ‘effect’ traits) (Lavorel and Garnier 2002). In this functional trait perspective, temporal functional insurance occurs when species with similar traits, that is, likely to fulfil similar functions (e.g., Sosiak and Barden 2021), replace one another over time within a given community, allowing key functions to persist at the ecosystem level (Mori et al. 2013; de Bello et al. 2021; Mahaut et al. 2025). In this context, it is no longer a question of linking ecosystem stability to biodiversity, but rather to use the stability of community trait composition as a surrogate of ecosystem functioning stability (McLean et al. 2019). Spatial functional insurance extends this logic across space: a functional loss in one community can be compensated if functionally similar species are present in nearby communities and capable of colonising. So, the level of spatial insurance depends on both local functional redundancy, which captures the presence of species with similar trait values, and the spatial distribution (and dispersal) of these species across the landscape.

For example, in tropical forests, tree regeneration relies on the presence of animals with specific traits related to seed dispersal, such as diet (e.g., frugivory) or mobility (Dennis and Westcott 2006). A given plant community may require seed dispersers with particular trait values to maintain regeneration processes. If these species disappear locally, their ecological role can only be maintained if functionally similar dispersers are present in nearby communities and can potentially recolonise or compensate (Osuri et al. 2016). A large body of work has focused on the temporal dimension of functional insurance (de Bello et al. 2021; Ross et al. 2023), but, surprisingly, the extent to which the spatial insurance of ecosystem functions is influenced by the functional redundancy between spatially adjacent communities has been overlooked so far (but see, Gaüzère, Blonder, et al. (2023), for trophic interactions). What is important here is not just the local stability of ecological functions against temporal fluctuations, but also the ability of neighbouring communities within a region to insure (i.e., rescue) ecological functions through dispersal towards a focal community, especially in cases of local species extirpations due to human pressures (Waldock et al. 2024) or habitat degradation (Haddad et al. 2015).

This question is even more critical for rare phenotypes and/or distinct functional traits (Mouillot et al. 2013; Grenié et al. 2017; Violle et al. 2017; Dee et al. 2019; Loiseau et al. 2020) because their decline is less likely to be compensated by other species through dispersal from neighbouring communities. Functionally distinct species represent a small fraction of species characterised by distinct trait combinations and limited redundancy (Violle et al. 2017). For example, the green humphead parrotfish (*Bolbometopon muricatum*) displays very distinct functional trait values, such as large body size and powerful beak-like jaws, while being a keystone species in coral reef ecosystems (Bellwood et al. 2003); or the Celebes crested macaque (*Macaca nigra*), which feeds on more than one hundred species of fruits (O'Brien and Kinnaird 1997) is crucial to the seed dispersal of tropical trees (Figure 1). These species are unlikely to be dominant in abundance so they may be more at risk than



FIGURE 1 | The coral reef fish *Bolbometopon muricatum* (Green humphead parrotfish) and the Indonesian tropical forest macaque *Macaca nigra* (Celebes crested macaque) are non-dominant species with distinct ecological traits that provide essential but unique functions to the ecosystems where they occur. Photo credits: *Bolbometopon muricatum*, Rick Stuart Smith and *Macaca nigra*, David Slater.

others (e.g., Murgier et al. 2021) although they significantly contribute to aggregated ecosystem properties such as biomass production (Dee et al. 2019; Delalandre et al. 2022; Pigot et al. 2025) or ecosystem resilience (McLean et al. 2019). In this context, the spatial insurance of distinct functional traits is critical for maintaining and stabilising ecosystem functions, but it remains largely unexplored. It might critically support ecosystem functioning over a regional scale in a context of global erosion due to climate change and human impacts. Here, we provide a new and integrative framework for measuring the spatial insurance of distinct functional traits, offering an extension to classical ecological insurance theory. We show how this framework can be applied from the regional to the global scale. We then discuss the implications, challenges, and perspectives of protecting functionally distinct species at multiple spatial scales under functional source-sink dynamics.

2 | Conceptual Framework

The metacommunity perspective (Leibold et al. 2004) offers a simple yet powerful approach to define and measure the spatial insurance of functional traits. In our framework, the functional trait space, that is, a multidimensional space derived from species' functional trait values, where distances between species reflect their overall functional dissimilarity (Mouillot et al. 2021), is defined at the regional scale while functional insurance is assessed within local communities (Figure 2). A focal community can both receive functional insurance from neighbouring communities (hereafter 'inward' insurance), and provide insurance to others (hereafter 'outward' insurance). *Inward insurance* represents the proportion of the focal community that is insured by neighbouring communities, that is, how much of its functional trait space is covered by overlapping neighbourhood

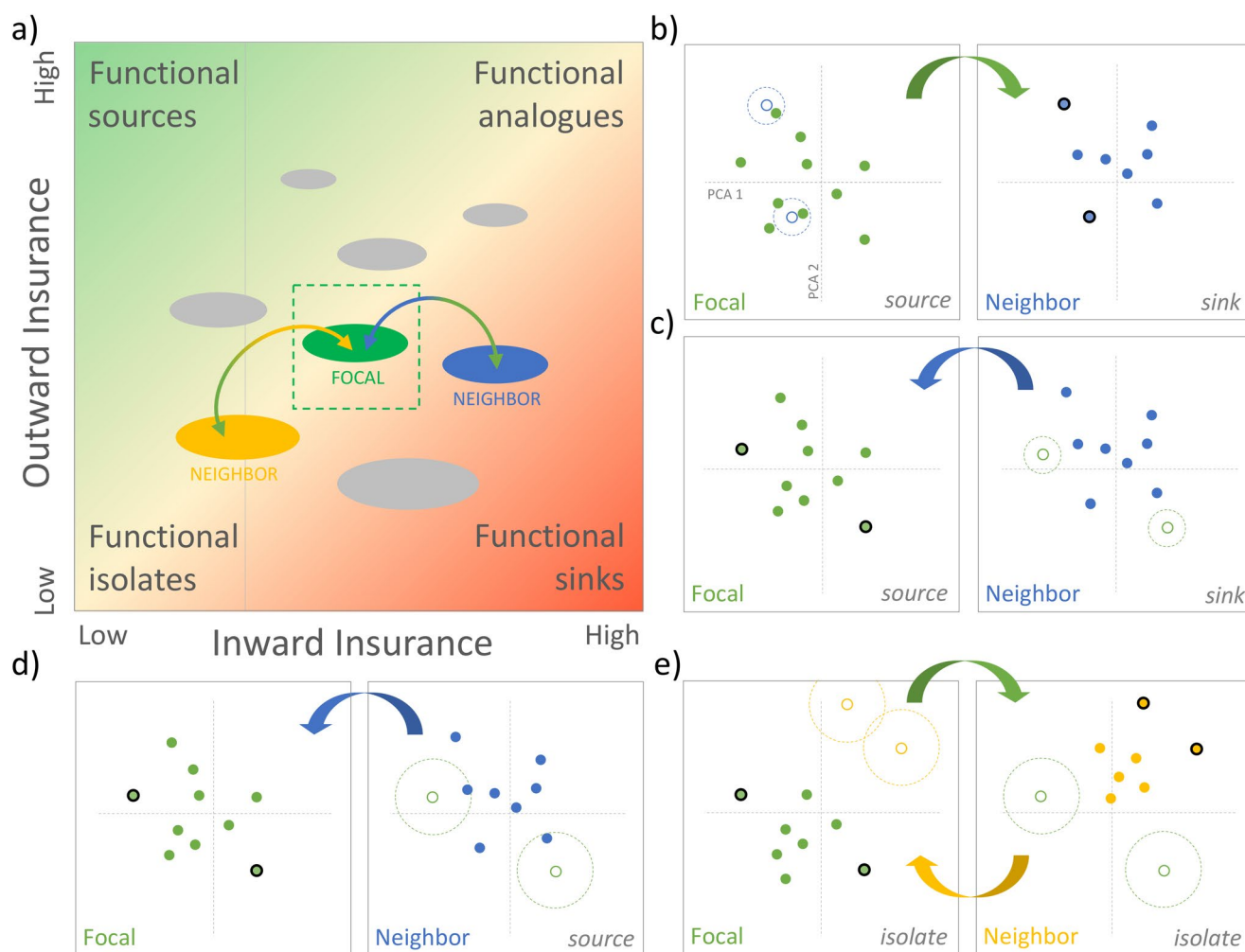


FIGURE 2 | (a) Communities can insure each other functionally when they share trait values across space. Functional insurance is quantified by comparing how much of a community's trait space is covered by neighbouring communities ('inward insurance') and how much of the neighbours' trait space is covered by the focal community ('outward insurance'). Communities can be classified based on this balance: *Sources* provide much more insurance than they receive, *sinks* receive much more than they provide, *analogues* both offer and receive high levels of insurance, and *isolates* neither receive nor provide insurance. (b–e) Functional insurance of distinct trait values is assessed within species trait space (represented here by only two functional axes for simplicity; dots denote species). The distinct species of a focal and a neighbouring community are shown as dots outlined in black; they are projected in the other communities (empty dots); the dashed circles represent the functional radius; the arrows represent the direction of the insurance. (b) The focal community is a source (green arrow, dispersal from left to right) while (c) the neighbour is a sink (blue arrow, dispersal from left to right). (d) Increasing the functional insurance radius can switch a sink community to a source. (e) Functional isolates do not provide or receive insurance.

community trait spaces. Conversely, *outward insurance* corresponds to the average proportion of neighbouring communities' trait spaces covered by the focal community, that is, the extent to which the latter contributes to insuring the former. We define a community as a *functional source* when its outward insurance is significantly higher than its inward insurance, and a *functional sink* when its outward insurance is significantly lower than its inward insurance (see below). Communities that are neither insured nor provide insurance are defined as *functional isolates*, while communities that exhibit both high levels of inward and outward insurance are considered *functional analogues* (i.e., communities with similar functional trait spaces).

When all species are considered, standard pairwise measures of functional dissimilarity, such as functional beta diversity between neighbouring communities (Villéger et al. 2011; Lengyel and Botta-Dukát 2023), could serve as a proxy for spatial functional insurance (de Bello et al. 2021). Lower functional beta diversity implies higher overlap in trait composition between communities, and thus a greater potential for mutual functional insurance. Inversely, high functional dissimilarity indicates a lower capacity for communities to functionally compensate for one another across space. Yet, functional beta diversity is not directional and cannot tease apart outward and inward components of functional insurance. Moreover, whether functional beta diversity adequately captures the spatial insurance of functionally distinct species remains unclear. Functional beta diversity measures differences in trait composition between communities, and is therefore inherently a community-level property (Villéger et al. 2012). In contrast, functional distinctiveness is a species-level attribute, reflecting how a given species' trait values are distinct to all other species (Violle et al. 2017). Functionally distinct species, by definition, occupy particular regions of trait space, often peripheral (Mouillot et al. 2021), and their redundancy across communities may not be reflected in aggregate dissimilarity measures such as functional beta diversity. On the other hand, some distinct species may also have one or a few redundant species at the regional level, all of which are functionally distant from all other species (e.g., ratite amongst birds, sirenians amongst marine mammals).

An alternative approach is to directly measure the functional insurance of distinct species in a trait space (Figure 2b–e), which has the advantage of solely focusing on species without a functional equivalent in their community. Functionally distinct species are identified using distinctiveness metrics (Grenié et al. 2017) within each community (dots highlighted in black in Figure 2b–e). The insurance potential of one community provided to a neighbouring community will be estimated by projecting the distinct species of the adjacent community into the trait space of the focal community (Figure 2b–e). In the example provided in Figure 2b,c, the focal community insures the distinct species of the neighbouring community (green arrows), but not vice versa (blue arrows), classifying it as a functional source and the neighbouring community as a sink. The insurance status also depends on the functional insurance radius (dashed circles in Figure 2b–e), which sets the trait distance below which one species can insure another. A large insurance radius increases potential insurance, and expanding the radius can even shift a neighbouring community

from a sink to a source (Figure 2b,d). In functional isolates (i.e., communities that are neither insured nor provide insurance), species of each community are found in different parts of the regional functional trait space (Figure 2e). In practice, the functional inward insurance of distinct species in a focal community, and its outward insurance to distinct species in neighbouring communities, can then be estimated respectively as, the proportion of its functionally distinct species insured by its neighbours, and the average proportion of distinct species in neighbouring communities that are insured by the focal community.

To illustrate this framework, we conducted a simulated case study of metacommunities composed of two communities. We defined a regional species pool of 5000 species, each with three traits for which values were drawn from a normal distribution (mean = 0, SD = 10). We then considered a set of 10,000 pairs of communities, each containing 10–300 species chosen randomly within the regional species pool. We computed the regional functional distance matrix with the function `compute_dist_matrix()` from the R package `funrar` v1.5.0 (Grenié et al. 2017). For each pair of communities, we considered all species present from the regional functional distance matrix and computed functional distinctiveness of species within each local community (using the `distinctiveness_global()` function from the R package `funrar` v1.5.0 (Grenié et al. 2017)). We considered species with local functional distinctiveness greater than 90% of the local species' distinctiveness values to be functionally distinct; other species were considered functionally common. A distinct species and the functions it provides were considered insured if at least one species within its functional insurance radius was present in the neighbouring community. To achieve this, we utilised the functional distance matrix of the neighbouring community, which included distinct species from the focal community. We considered three functional insurance radius values (0.4, 0.6 and 0.8), which were lower than the median functional distance between all species pairs (2.18). We then estimated inward and outward insurance as the percentage of focal community species (distinct and common) insured by neighbours, and vice versa. The functional beta diversity was measured for each metacommunity using the Jaccard-derived pairwise functional dissimilarity based on the overlap of the convex hulls shaping each community (Villéger et al. 2013; function `functional.beta.pair()` from the R package `betapart` v1.6 (Baselga and Orme 2012)).

We found that inward insurance of functionally distinct species was consistently lower than that of common species and diminished with decreasing functional insurance radius (Figure 3a). We found a weak negative correlation between inward insurance of functionally distinct species and functional beta diversity ($r = -0.16$, Figure 3b), while the correlation was stronger for common species ($r = -0.52$, Figure 3c). We observed that communities with the highest inward insurance of functionally distinct species tended to have lower species richness (Figure 3d). In contrast, those with the highest outward insurance had higher species richness (Figure 3d). These results show that although functional beta diversity is often thought to emphasise differences at the edge of trait space (Villéger et al. 2011), it fails to reflect the insurance status of distinct species (we found the same results when looking at the turnover component

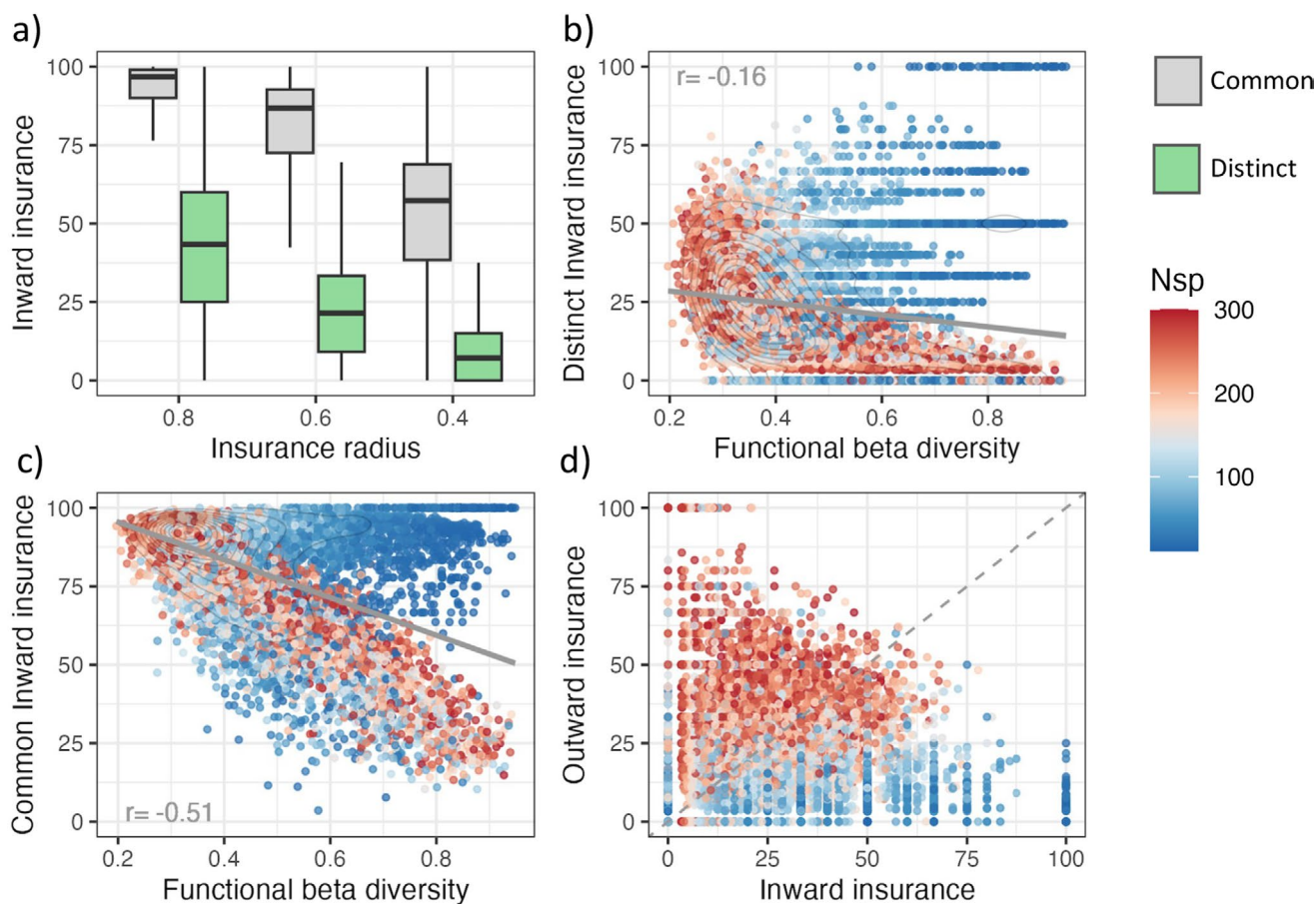


FIGURE 3 | Results of a simulation of multiple metacommunities with varying numbers of species and insurance radius (see main text). Inward and outward functional insurance are expressed as percentages (see main text). (a) The inward insurance of functionally distinct species (in green) is always lower than that of common species (in grey) and both decrease with the functional insurance radius. (b,c,d). Here, we focus on the simulation results using an insurance radius of 0.6. b and c show the correlation between the inward insurance and functional beta diversity (Jaccard-derived pairwise functional dissimilarity) for functionally distinct (b, Pearson correlation $r = -0.16$) and common (c, Pearson correlation $r = -0.52$) species. (d) Species-rich communities are more likely to provide outward insurance to functionally distinct species than to receive inward insurance (dashed line shows the 1:1 relationship). The colour gradient in b, c and d, corresponds to the species richness (N_{sp}) of focal communities (from high-red, to low-blue, values).

of functional beta diversity, and with taxonomic beta diversity indices, see Supporting Information S1). This can be explained by the high functional distinctiveness required for a species to be far from most other species in trait space, rather than simply being located at the edge.

Determining the potential for spatial functional insurance will also require three specific decisions: defining the metacommunity extent (i.e., in geographic space), establishing a threshold for classifying communities as functional sources or sinks, and determining the functional radius that limits functional similarity between species (i.e., in trait space). (i) In the geographic space, the spatial extent of a metacommunity (hereafter ‘*spatial buffer*’) depends on several key factors, including species dispersal capacities and behaviours, environmental heterogeneity and structural connectivity between communities (Mouquet and Loreau 2003; Leibold et al. 2004; Urban et al. 2009). (ii) Functional source and sink communities are defined, as for keystone species (Mills et al. 1993) and communities (Mouquet et al. 2013), as those that exhibit

significantly higher levels of inward or outward insurance relative to other communities within the metacommunity. This requires a reference—null model—that assigns a *potential* insurance status to each community based on its characteristics within the metacommunity (Mouquet et al. 2013). Choosing this null model implies weighting the contribution of each community based on specific characteristics (e.g., abundances, richness), which can be challenging to achieve in practice. A simple approach is to use a threshold based on the quantiles of the distribution of the inward-outward relationship. (iii) In the trait space, the insurance functional radius defines the threshold of functional similarity and limits how functionally redundant species must be to provide insurance to each other. It necessarily depends on the ecosystems, species and functions being studied. Setting the radius too low would result in a lack of insurance, while setting it too high would result in high redundancy and dilute the concept of distinctiveness. A more parsimonious approach might be to set up a threshold based on the mean or median values of regional functional pairwise distances, or to define the radius

empirically where known functions can be explicitly mapped into the functional trait space (e.g., nectar-feeding birds pollination, see Pigot et al. 2020).

3 | Measuring Functional Insurance at Biogeographical Scale

Measuring functional insurance at biogeographical scales is crucial for understanding and predicting ecosystem responses to global change. It also offers a pathway to integrate multi-scale dynamics in functional biogeography (Violle et al. 2014). However, scaling up from local to biogeographical levels remains challenging. It requires moving beyond the classical metacommunity framework to account for broader-scale processes, including landscape heterogeneity, dispersal barriers and species-specific dispersal capacities. While the metacommunity framework provides a mesoscale bridge between local ecological processes and regional species pools (Jenkins and Ricklefs 2011), it falls short of capturing macroecological dynamics and patterns (Leibold et al. 2022; Khattar and Peres-Neto 2024). A first step is to use large-scale biodiversity datasets of species distributions combined with available functional trait data, without considering landscape characteristics. This approach can produce maps of potential insurance, serving as references to compare against *realised* insurance, which could later be computed by incorporating more realistic landscape characteristics and species-specific dispersal strategies (if these are/become available).

To illustrate this first step, we chose two large-scale datasets with different settings (one regional with 'true' community plots, one global with broad-scale assemblages) and two different taxonomic groups (plants and birds): (1) a comprehensive database of herbaceous community plots (around 10×10 m plot) distributed across the French Alps (DIVGRASS, Violle et al. 2015; Gaüzère, Blonder, et al. 2023) and (2) the global distribution of birds mapped onto a 50×50 km grid-cell, representing broad-scale species assemblages (BirdLife 2019). Trait values were extracted from Gaüzère, Blonder, et al. (2023) for plants and from AVONET (Tobias et al. 2022) for birds. For both datasets, we defined the geographic and functional trait space. For plants, we chose a spatial buffer of 3 km to define metacommunities, whereas it was set at 350 km for birds (see Supporting Information S2 and S3). In other words, for each single plant community plot, its neighbouring community plots were located within a 3 km vicinity. For each bird cell assemblage, the geographic neighbourhood was represented within a 350 km spatial buffer, a scale consistent with long-distance bird dispersal and previous global analyses of avian beta diversity (McKnight et al. 2007). The functional radius was fixed to 20% of the median value of each global functional distance matrix for both datasets (see Supporting Information S2 and S3 for a full description of the data and methods). The global distribution of inward and outward insurance values was then used to classify each plot or cell as a potential source or sink, based on the 10th and 90th percentiles of the inward vs. outward relationships; other plots or cells were referred to as *intermediate*. Spatial aggregation of sources and sinks was tested by using the function `joincount.multi()` of the `spdep` v.1.3-10 R package (Pebesma 2018).

For plants, we found a widespread distribution of potential sources and sinks (Figure 4a) with significant spatial aggregation for sources (z -values = 3.53, $p < 0.001$) and no spatial aggregation for sinks (z -values = 0.51, $p > 0.05$). This difference in the patterns of spatial aggregation could result from the fine environmental grain and the distribution of species richness amongst plots, as well as the sampling strategy. As expected from simulations, sources were primarily found in species-rich plots (Figure 4b). The high spatial resolution of the DIVGRASS dataset allows a fine-scale analysis of herbaceous communities' insurance status (Figure 4c). Assuming that the vegetation sampling strategy is representative, these insights offer new perspectives for spatially informed conservation planning, enabling the identification of critical potential source plots essential for maintaining functional trait diversity across alpine landscapes. Additionally, our analysis computed functional distinctiveness at the plot level, which can highlight species that appear locally distinct but may not be so when considering the regional species pool. To illustrate this, we mapped local functionally distinct species in the functional trait space, and show that they occupy a broader portion of that space than species that are regionally the most distinct (Figure 4d). This highlights that local distinctiveness can reveal additional, spatially restricted strategies that are not captured when distinctiveness is assessed only at the regional scale (Gaüzère, Blonder, et al. 2023). Moreover, amongst the locally distinct species, some are weakly insured by neighbouring communities across the region (see examples in Figure 4d and Supporting Information S2). They represent functionally distinct and spatially isolated species, and should thus receive particular attention when prioritising conservation efforts aimed at preserving distinct ecological functions at broad spatial scales (Pollock et al. 2017). Note that the sampling strategy of the DIVGRASS dataset was not meant to be exhaustive. Combining a robust sampling strategy with ad hoc species distribution models will provide a more comprehensive picture of the spatial structuring of sources and sinks, especially for functionally distinct and spatially restricted species. We found our results to be robust to varying both the functional insurance radius and the extent of the metacommunity (Figures S2.3, S2.4 and Tables S2.1, S2.2 in Supporting Information S2).

For birds, we observed a strong spatial aggregation of both potential functional sources and sinks (Figure 5a; z -values of 238.5 and 249.2, respectively, $p < 0.001$). Sources were often located in coastal areas such as the coasts of North America, Australia, western South America and northern and southern Africa. At the same time sinks tended to be located near sources, mainly inland (except for the north Arctic coast, which had mostly sinks due to its very low species richness). Coastal areas indeed include marine birds, which are known to be functionally distinct (Loiseau et al. 2020). These areas likely contain a mix of marine and inland birds, which could insure mainland areas more than the reverse. Large mountain regions displayed contrasting patterns, with areas such as the Himalayas acting as sources and regions such as the Cordillera acting as sinks. This pattern can be attributed to the surrounding areas and, specifically, regions with a sharp gradient of species richness and turnover, which correspond to biogeographical boundaries (Holt et al. 2013) or ecotones (Ries et al. 2004). Source/sink status was linked to species richness (Figure 5b,c) but less strongly than for plants. Intermediate cells showed higher species richness than source

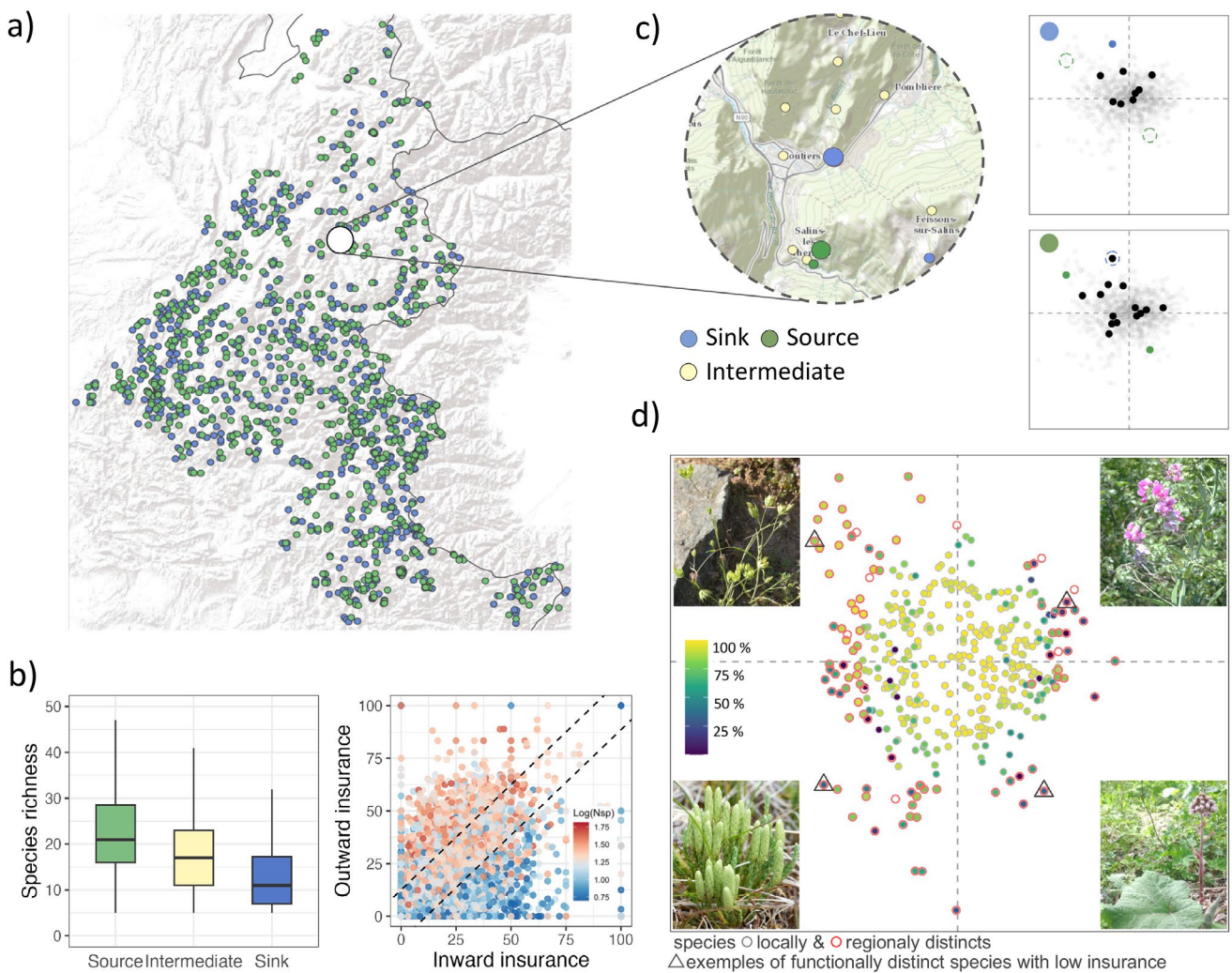


FIGURE 4 | (a) Regional distribution of spatial insurance for functionally distinct plants in the French Alps herbaceous communities, highlighting functional sources (in green) and sinks (in blue) plots. For clarity, plots with intermediate insurance status have been removed; a high-quality figure is provided in Supporting Information S2. (b) Left: Species richness for source (green), intermediate (yellow) and sink (blue) plots. Differences between insurance status are significant (Dunn's test, $p < 0.001$). Right: Outward vs. inward insurance for all plots. The two dashed lines show the 10th and 90th percentiles of the inward vs. outward relationship used to classify cells' insurance status. The colour gradient is the \log_{10} of plot species richness ($\text{Log}(\text{Nsp})$, from high-red, to low-blue, values). (c) Left: One sink plot (blue dot) within its 3 km radius neighbourhood, including other plots. Right: Species of the sink and of a neighbouring source (magnified in c left) are projected into the functional trait space (light grey empty dots show all species from the dataset, $n = 992$); the source insures the distinct species of the sink (blue dot) while the 2 distinct species of the source (green dots) are not (see also Box 1 b). (d) The first two principal components of the functional trait space (PC1 on the x-axis and PC2 on the y-axis, which represent, respectively, 59.9% and 31.6% of the total variance) computed with all species from the dataset ($n = 992$). For clarity, we only represent species (dots) that are either locally distinct (at least in one plot) or regionally distinct (dots surrounded in red). The colour gradient indicates the percentage of plots in which the species that are locally distinct are insured. The few empty dots are species that are regionally distinct but never locally distinct. The four triangles illustrate examples of functionally distinct species with contrasting trait value combinations, which exhibit low insurance: Upper left, *Bupleurum baldense*; upper right, *Lathyrus latifolius*; lower left, *Diphasiastrum alpinum*; lower right, *Petasites hybridus* (Photo credit: François Munoz, Public domain).

and sink cells (Figure S3.3 in Supporting Information S3). We found no clear latitudinal gradient in insurance status, unlike species richness, which peaks in the tropics (Figure S3.4 in Supporting Information S3). Regions such as the Sahara Desert, the sub-Saharan regions, and Central Australia, exhibit contrasting distributions of sources and sinks due to their low species richness (and thus low numbers of functionally distinct species). This leads to greater variability in insurance status between cells; for example, when the number of different species is very low (e.g., one or two), the presence of a single species in

a spatial buffer can significantly alter the status of a focal cell. At this global scale, one can also explore how closely the spatial distribution of potential sources and sinks aligns with both the human footprint and protected areas. We found that source cells were exposed to higher human footprint than intermediate and sink cells (Figure 6a, Supporting Information S3), the latter being found in areas with a higher proportion of protection (Figure 6b, Supporting Information S3). This pattern likely reflects the spatial distribution of source communities, which are often located in coastal areas that experience high population densities and

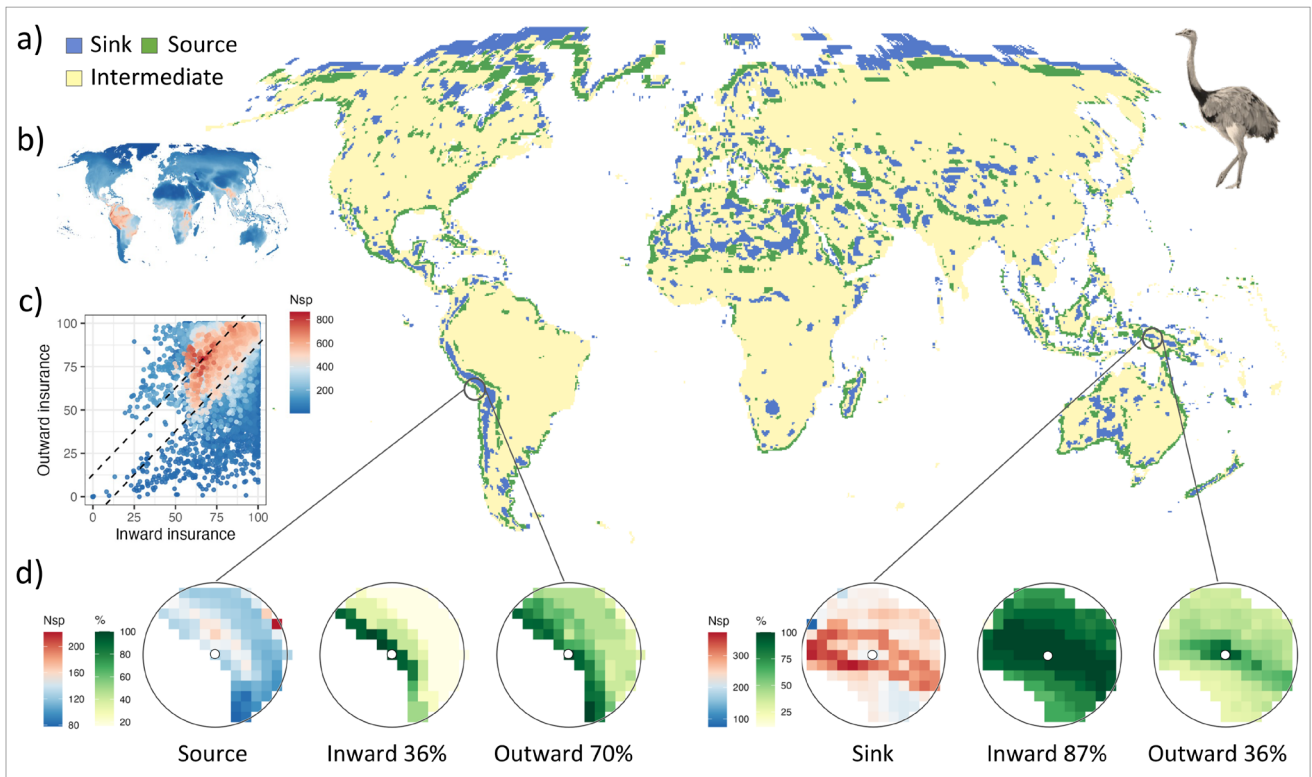


FIGURE 5 | (a) Worldwide distribution of spatial insurance for functionally distinct bird species, highlighting functional sources, sinks and intermediate cells. (b) Bird species richness. (c) Inward versus outward insurance, with dot colours indicating the species richness gradient across cells. The dashed lines show the 10th and 90th percentiles of the inward vs. outward relationship used to classify cells' insurance status. Panels b and c share the same colour scale for species richness (Nsp). (d) Examples of source (left) and sink (right) cells (white dots) within their spatial buffer. Species richness (Nsp) ranges from low (blue) to high (red). Inward (from neighbouring cells to the focal cell) and outward (from the focal cell to neighbouring cells) insurance values are expressed as percentages (%), ranging from high (dark green) to low (light yellow) values. Mean inward and outward insurance percentages are indicated below, with inward insurance \ll outward insurance for the source cell (left) and inward insurance \gg outward insurance for the sink cell (right). Image: *Rhea americana* is amongst the most functionally distinct birds worldwide (drawing has been produced digitally by the authors and is copyright-free).

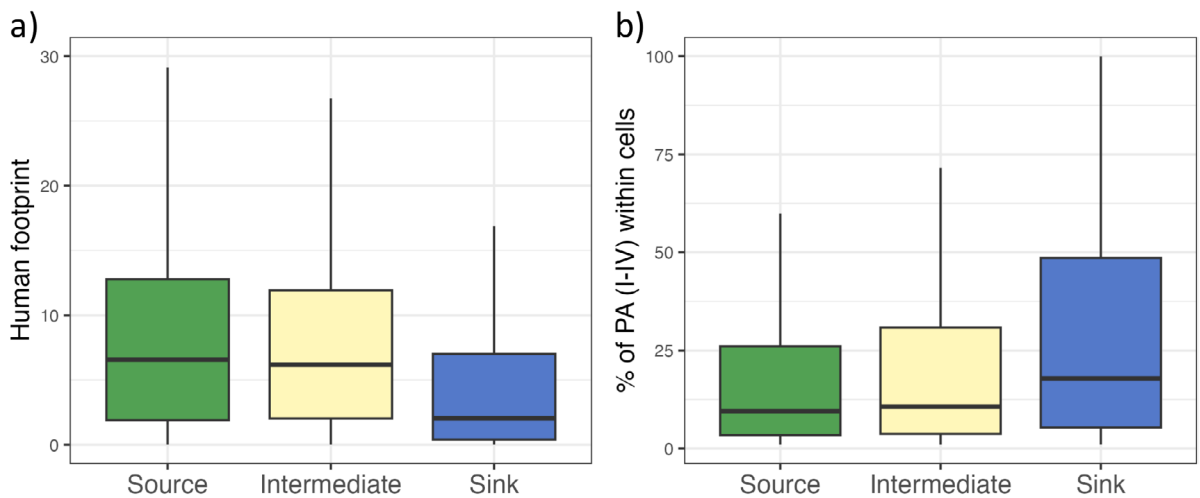


FIGURE 6 | (a) Human footprint vs. insurance status for birds. Mean human footprint, computed from Mu et al. (2022), within each spatial cell. Human footprint is based on eight variables, including built environments, population density, and infrastructure (see Supporting Information S3). Differences in human footprint between both source and intermediate with sinks are significant (Dunn's test, $p < 0.001$). (b) Protection level versus insurance status. Protection level is the mean percentage of cell area covered by protected areas (when considering only cells where at least 1% of the area was protected), including IUCN categories Ia, Ib, II, III, and IV (World Database on Protected Areas, UNEP-WCMC and IUCN 2025). Differences between all insurance statuses are significant (Dunn's test, $p < 0.001$). This pattern was consistent across the different IUCN categories of protected areas (see Supporting Information S3).

intense land-use change (Small and Nicholls 2003) but generally have lower protection levels than more remote inland regions (Watson et al. 2014; Mouillot et al. 2024). Overall, we found our results to be robust to varying both the functional insurance radius and the extent of the metacommunity (Figures S3.7, S3.8 and Tables S3.1, S3.2 in Supporting Information S3).

4 | Challenges and Perspectives

Our paper presents a generalizable and straightforward framework for assessing the spatial insurance of functionally distinct species across various scales. By embedding functional distinctiveness within a metacommunity perspective, we show that functionally distinct species are consistently less insured than more common ones. We highlight the role of spatially nearby communities, which can act as functional sources by hosting and ensuring trait values distinct elsewhere, thereby contributing to the persistence of unique ecological functions under potential local disturbances. When applied at biogeographical scales, as illustrated here for both plants and birds, our spatial insurance framework reveals layers of functional vulnerability not captured by traditional diversity metrics. By demonstrating how spatial connectivity contributes to the persistence of distinct functions, this approach can offer new insights into how spatial regional networks of communities can potentially mitigate the functional consequences of local species extirpations. The generality of our approach comes with obvious limitations that we view not as shortcomings, but as promising directions for future research: (i) bridging this framework with the complex realities of landscape structure and species dispersal; and developing more sophisticated measures of functional insurance, (ii) providing guidelines for conservation and prioritisation, (iii) integrating functional insurance in the ecological insurance framework and (iv) exploring the different ecological organisational scales at which functional insurance is likely to happen.

It is essential to acknowledge that the functional insurance measures reported here represent potential scenarios and do not fully account for the complexities introduced by landscape heterogeneity and species dispersal strategies. For instance, geographic barriers, such as mountains, can severely restrict species' ability to rescue functionally distinct counterparts from isolated communities, and assuming equal accessibility across all cells also overlooks the varying dispersal capacities of different species. Spatial functional insurance will not operate instantaneously; a species often requires time to disperse, colonise, and establish in nearby patches (Logue et al. 2011). We also assume that there is some kind of environmental continuity amongst habitat patches; that is, insurance cannot buffer complete state shifts (e.g., forest converted to cropland). To refine our framework, it would be essential to distinguish between potential and realised functional insurance, as the latter will be shaped by actual functional and structural connectivity (as for species distribution models, see, Thuiller 2024). Such refinement is within reach, as the latest methodological developments, combining circuit and network theories, allow us to define connectivity between cells or plots for the species of interest, or even more relevant, for the functional groups of interest defined by the functional insurance radius (Kervellec

et al. 2024; Prima et al. 2024). Another area of investigation concerns the definition of functional insurance. Here, we used a threshold distance in the functional trait space (i.e., functional insurance radius), but this requires choosing it somehow arbitrarily. An alternative approach could be to consider a continuous point of view, for instance, by incrementally varying the radius and recalculating the functional insurance to obtain a distribution of insurance values, rather than a single value for a given radius. A kernel decreasing function of both spatial and functional distances, reflecting the declining potential for insurance with increasing dissimilarity and dispersal cost could also be explored (Mammola and Cardoso 2020). Additionally, our framework categorises communities into discrete categories, such as sources and sinks, to facilitate comparisons, spatial aggregation measures and the development of operational guidelines for conservation prioritisation. While this approach provides clarity and practical value, it simplifies the continuous nature of inward and outward insurance, as communities may exhibit high or low values for both dimensions. Future extensions could integrate continuous measures that capture both magnitude and directionality, such as a normalised imbalance index or log-ratio. Using the realism of continuous metrics or the operational simplicity of categorical classifications will then be chosen depending on the research questions. Finally, it is important to note that because species occurrences can fluctuate over time, especially in dynamic communities, large-scale datasets that integrate observations from different periods or sampling protocols may introduce uncertainty into functional source-sink classifications. This underscores the need for careful interpretation of empirical results and the incorporation of temporal and sampling standardisation wherever possible. Altogether, these refinements will enhance the relevance and operability of functional insurance assessments at the biogeographic scale, informing conservation strategies that align more closely with ecological realities.

By understanding the distribution of functional distinctiveness and spatial functional insurance, we can refine conservation strategies that aim to mitigate the impacts of biodiversity erosion, habitat destruction, and climate change on functionally distinct species (Pollock et al. 2017). Our two case studies highlight some opportunities and challenges in maintaining distinct functional trait values (and associated functions). Their spatial extents (plants at the regional scale vs. birds at the global scale) demonstrate how the scale at which functional insurance is measured may lead to different conservation focuses. While the analysis at a biogeographical scale might help to determine general tendencies for global conservation priorities, downscaling at the regional level could lead to targeting particular sites that contribute the most to functional insurance or particular species that either show traits (and associated functions) that are never insured, or conversely, insure many others at the regional scale. This opens opportunities to design conservation prioritisation schemes that integrate not only the characteristics of local communities, such as species richness, phylogenetic or functional diversities (Pollock et al. 2017), but also how these communities contribute to functional insurance at a regional level. Global conservation prioritisation strategies (Brooks et al. 2006) have been instrumental in channelling efforts towards irreplaceable and vulnerable regions, and recent methodological advances

now allow acknowledging multiple biodiversity dimensions, including functional diversity metrics, in systematic conservation planning (Pollock et al. 2020). Embedding our framework into these approaches could inform strategies that ensure the persistence of distinct ecological functions and better account for spatial connectivity, especially under scenarios of species loss and habitat fragmentation (Brodie et al. 2025).

At the same time, identifying functional sources and sinks naturally raises the question of whether these critical communities are adequately protected or under threat. Our global bird analysis suggests that source sites, despite their importance, are more exposed to human activities and less protected in terms of spatial coverage. Yet, both source and sink habitats deserve particular attention. While source communities are crucial for maintaining regional functional diversity, sink communities cannot be neglected. If regional connectivity is disrupted, sink communities become even more vulnerable, as they can no longer rely on source communities to sustain their functions. Similarly, source communities may themselves contain functionally distinct species that, despite the overall high local species richness, are not well insured and thus require direct conservation action. Protecting both types of communities is therefore vital: by maintaining the links between sources and sinks and safeguarding locally unique functions, conservation strategies can balance the need to preserve regional connectivity with the protection of irreplaceable ecological functions.

A functional perspective complements existing prioritisation schemes such as Key Biodiversity Areas (KBAs, Eken et al. 2004), which are mainly defined by taxonomic criteria. Incorporating functional insurance into the KBA framework would highlight not only where biodiversity is most at risk, but also where it is essential to regional resilience. For example, sites that disproportionately insure distinct ecological functions, even if they do not host threatened species, could be recognised as conservation priorities, acting as functional supports as well as refuges. This echoes the concept of keystone communities, that is, local communities that disproportionately influence regional ecological properties within metacommunities (Mouquet et al. 2013). Amongst these, some may concentrate unique trait combinations or occupy central positions in the landscape, making them especially important for maintaining distinct ecological functions. In contrast, functionally isolated communities ('isolates' in Figure 2a) may represent overlooked ecosystems with little potential for functional rescue; these functional 'islands' would thus require specific conservation actions.

At the species level, our framework highlights taxa with unique functional trait combinations that may never be insured (see Figure 4d). Identifying such functionally vulnerable species is essential for targeted conservation measures. Likewise, some species may contribute disproportionately to functional insurance, though identifying them will require developing specific metrics to assess their importance within metacommunities (e.g., Rollin et al. 2024). This perspective could be particularly valuable for anticipating the future of biodiversity and adapting protected area networks to account for migratory species under and land-use change beyond country boundaries (Gatiso et al. 2022). Finally, our framework could be coupled with species distribution and macroecological models (Deschamps

et al. 2023) to predict both species and functional distributions. Together, these refinements could demonstrate how the functional insurance framework can be applied across scales, from communities to species, to inform conservation prioritisation based on functional distinctiveness.

By focusing on the spatial distribution of functional traits, our framework offers a complementary perspective to the ecological insurance theory (Yachi and Loreau 1999; Loreau et al. 2003; Wang and Loreau 2016), especially when the goal is to safeguard distinct ecological functions. Traditional ecological insurance emphasises biodiversity's stabilising effects through species asynchrony and complementarity between dominant species (Yachi and Loreau 1999; Loreau et al. 2003), typically associated with high taxonomic beta diversity (Wang and Loreau 2016). In contrast, functional insurance focuses on the spatial distribution and redundancy of traits, shifting the focus from species to functions: distinct ecological functions persist through the spatial insurance of functionally distinct species. Importantly, we show that low functional beta diversity is not a prerequisite for the spatial insurance of distinct traits; functionally distinct species can still be insured even in the presence of high turnover. This opens the door to a synergistic view, where temporal stability is enhanced by species asynchrony (and high taxonomic beta diversity), while some level of spatial functional redundancy supports the persistence of (locally) distinct functions.

Future work should also explore how different traits, those related to species' effects on ecosystem functioning and those reflecting their responses to environmental change (effect and response traits, respectively, Lavorel and Garnier 2002), interact to shape the spatial insurance of ecological functions. These interactions arise from the various physiological (e.g., allometry, Vasseur et al. 2022), genetic (e.g., pleiotropy, Arnold 1992) and evolutionary (e.g., natural selection, Endler 1995) constraints that shape the entangled phenotype (sensu Díaz 2025) of organisms. As a result, response and effect traits can be tightly linked, with critical impacts on long-term ecosystem functioning (de Bello et al. 2021). In particular, stronger correlations between response and effect traits can propagate the impacts of environmental change from species to ecosystem processes, whereas lower correlations may buffer such implications for ecosystem functioning (de Bello et al. 2021). Thus, just as these interactions have been key to understanding the temporal stability of ecosystems (de Bello et al. 2021), they could offer critical insights into how spatial trait distributions can support the persistence of functions under environmental change. However, deciphering the role of these interactions will require both a mechanistic understanding of trait–environment relationships and robust trait-to-function mapping, which remain major challenges in trait-based ecology (de Bello et al. 2025).

Ecological systems are organised hierarchically (Chave 2013), and functional insurance likely operates at multiple spatial and organisational scales, from individuals and populations to communities, ecosystems, and biomes. Spatially, the extent and grain of analysis will influence patterns of functional distinctiveness and insurance. While some distinct functions may be insured within local or regional assemblages, others may require broader, biogeographical perspectives to identify source communities capable of rescuing functionally distinct species.

Assessing functional insurance across trophic levels, rather than in isolated taxonomic groups, may also offer a more integrative approach. For instance, recent work by Gaüzère, Botella, et al. (2023) shows that while species interactions can be spatially unique, their functional roles often display redundancy across landscapes. Similarly, cross-taxon congruence in taxonomic beta diversity (McKnight et al. 2007) reveals that areas of high turnover for different taxa can coincide spatially, questioning whether such congruence also applies to functionally distinct species. Bridging broader spatial and organisational dimensions will be essential to advance our understanding of how distinct ecological functions are maintained or lost across scales. Future research should explore how functional insurance emerges when considering both spatial and trophic structures (Gravel et al. 2011), and how this understanding can guide conservation strategies to protect species, as well as the persistence of distinct ecological functions.

5 | Conclusion

Our study introduces a new conceptual framework to assess the spatial insurance of functionally distinct ecological functions. By integrating functional distinctiveness into a metacommunity perspective, we provide a simple way to identify communities that disproportionately insure (source) or depend (sinks) on neighbour communities to maintain unique ecological functions. This approach highlights hidden layers of functional vulnerability that cannot be detected using traditional biodiversity metrics. By focusing on the spatial distribution of traits, our framework complements traditional ecological insurance theory, which emphasised temporal stability and taxonomic diversity. The ability of neighbouring communities to counterbalance species extirpation calls for spatially explicit conservation planning that incorporates functional redundancy and connectivity. Our global bird analysis illustrates this point, showing that functional source communities potentially overlap with regions of intense human activity and limited protection, thereby revealing apparent mismatches between ecological importance and conservation efforts. This calls for advanced methodologies that will incorporate species dispersal behaviours, landscape heterogeneity, and the dynamic interactions shaping metacommunities, alongside an explicit consideration of the functional facets of biodiversity. Overall, our framework underscores the importance of a trait-based conservation perspective, where protecting biodiversity entails not only safeguarding local diversity but also preserving the spatial networks of communities that ensure the persistence of distinct ecological functions.

Author Contributions

N.M. initiated the research reported here. N.M. performed the analyses with some help from N.C. N.M. wrote the first draft. All authors participated in developing the ideas and contributed substantially to the manuscript.

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Data Availability Statement

All data and code needed to evaluate the conclusions in the paper are present on the Zenodo repository: <https://doi.org/10.5281/zenodo.17377513>. The EEA Alpine biogeographical shapefile is available at <https://www.eea.europa.eu/en/datahub/datahubitem-view/11db8d14-f167-4cd5-9205-95638dfd9618>. The Human Footprint dataset developed by Mu et al. (2022) is available at <https://doi.org/10.6084/m9.figshare.16571064>. The World Database on Protected Areas is available at <https://www.protectedplanet.net/>.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70266-sup-0001-Supinfo1.docx. **Data S2:** ele70266-sup-0002-Supinfo2.docx. **Data S3:** ele70266-sup-0003-Supinfo3.docx.