

RESEARCH ARTICLE

Network Analysis Highlights the Complementary Roles of Active and Passive Restoration for Birds in a Restored Landscape Mosaic

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ABSTRACT

Birds are essential in connecting conserved and restored habitats in anthropogenic landscapes, acting as ‘mobile links’ that enhance habitat connectivity. They contribute to key ecological functions that support habitat recovery. Despite their sensitivity to habitat changes, bird assemblages in restored landscapes show varied responses due to factors like the restoration technique employed. This study uses the species–habitat network approach to assess how different restoration techniques and bird functional traits influence bird habitat use and connectivity in the Atlantic Forest. We adapted network metrics—among-module connectivity and within-module degree (c - and z -scores, respectively)—to quantify how habitat types contribute to landscape connectivity and to assess how bird functional traits explain patterns of occupancy across restored fragments. We show that actively restored habitats tend to have more exclusive bird species compared to conserved forests, whereas naturally regenerated forests support a broader range of shared bird species. While active restoration often promotes species with specific habitat needs, it may have a more limited role in landscape connectivity, compared to natural regeneration, which better integrates habitat types. These findings suggest that combining active and passive restoration strategies can maximise landscape connectivity, with active restoration providing habitat for species with particular requirements and passive restoration enhancing broader ecosystem recovery through bird occupation. Additionally, our findings indicate that bird functional traits have low explanatory power for patterns of bird habitat use in restored landscapes, emphasising the value of a more detailed network approach that includes species-specific interactions. Still, the species–habitat network approach revealed key species that help connect different habitat types, highlighting the role of bird species in landscape cohesion. Future research should explore finer network resolutions and larger spatial scales to better capture species movement and habitat dynamics within restoration gradients.

RESUMO

As aves são elementos essenciais na conexão entre habitats conservados e restaurados em paisagens antrópicas, atuando como ‘elos móveis’ que potencializam a conectividade da paisagem. Elas contribuem para funções ecológicas-chave que sustentam a recuperação do habitat. Apesar de sua sensibilidade a mudanças no habitat, as assembleias de aves em paisagens restauradas apresentam respostas variadas, influenciadas por fatores como a técnica de restauração empregada. Este estudo utiliza a abordagem de redes espécie-habitat para avaliar como diferentes técnicas de restauração e os traços funcionais das aves influenciam o uso do habitat e a conectividade na Mata Atlântica. Foram adaptadas métricas de rede—conectividade entre módulos e grau dentro do módulo (valores c e z , respectivamente)—para quantificar como os tipos de habitat contribuem para a conectividade da paisagem e para avaliar como os traços funcionais das aves explicam os padrões de ocupação entre fragmentos restaurados. Demonstramos que habitats restaurados ativamente tendem a abrigar espécies de aves mais exclusivas em comparação com florestas conservadas, enquanto as florestas em regeneração natural sustentam uma gama mais ampla de espécies compartilhadas. Embora a restauração ativa frequentemente promova espécies com necessidades habitat-específicas, ela pode ter um papel mais limitado na conectividade da paisagem quando comparada à regeneração natural, que integra melhor os tipos de habitat. Estes resultados sugerem que a combinação de estratégias de restauração ativa e passiva pode maximizar a conectividade da paisagem: a restauração ativa provê habitat para espécies com requisitos particulares, e as restaurações passivas potencializam a recuperação mais ampla do ecossistema por meio da ocupação por aves. Adicionalmente, nossos resultados indicam que os traços funcionais das aves possuem baixo poder explicativo para os padrões de uso do habitat em paisagens restauradas, reforçando o valor de uma abordagem de rede mais detalhada que inclua interações espécie-específicas. Ainda assim, a abordagem de rede espécie-habitat revelou espécies-chave que auxiliam na conexão entre diferentes tipos de habitat, destacando o papel de espécies de aves na coesão da paisagem. Pesquisas futuras deveriam explorar resoluções de rede mais refinadas e escalas espaciais maiores para capturar de forma mais adequada o movimento das espécies e a dinâmica dos habitats dentro dos gradientes de restauração.

1 | Introduction

In anthropogenic landscape mosaics where conserved and degraded matrices intermingle, birds serve as vital ‘mobile links’. However, stressors such as fragmentation, land deterioration and urbanisation significantly impact the structure and function of bird assemblages within these mosaics (Morante-Filho et al. 2015; Castaño-Villa et al. 2019; Fontúrbel et al. 2022; Maruyama et al. 2024; Zhang et al. 2024), making the restoration of degraded forest lands a promising strategy to reintegrate bird assemblages into anthropogenic landscapes.

Nevertheless, forest habitat restoration initiatives have shown mixed results regarding bird responses, depending on the techniques and methods used. For instance, while active restoration can effectively recover forest-dwelling bird assemblages by increasing vertical structural complexity (Latja et al. 2016; Hariharan and Raman 2022; Joyce et al. 2024), it has sometimes been less effective than natural regeneration for faunal recovery (Crouzeilles et al. 2017; Mao et al. 2024; Zhang et al. 2024). Natural regeneration often facilitates the colonisation of locally adapted plants, promoting higher habitat heterogeneity compared to tree planting (Crouzeilles et al. 2017; Zhang et al. 2024), which commonly uses few tree species in overabundance (Ballarin, Hachuy-Filho, et al. 2022; Ballarin, Hachuy-Filho, Fontúrbel, et al. 2022; Ballarin, Amorim, et al. 2024).

Still, the complex coexistence of diverse land-cover types (e.g., human-induced fragmentation, restoration efforts and natural regeneration) within the same anthropogenic mosaic might imply that discrete comparisons among habitat types may oversimplify bird responses to land-cover changes, limiting our ability to predict assemblage dynamics (Chazdon et al. 2024). For instance, birds may move between different habitat contexts

(González-Varo et al. 2023), and distinct land-cover types within the same mosaic often support unique bird assemblages due to variations in ecosystem structure (Batisteli et al. 2018; Ikin et al. 2019; Rutt et al. 2019). In restored landscape mosaics, where conserved ecosystems blend with actively restored areas and naturally regenerating habitats, understanding how birds occupy and move through these spaces can guide the selection of restoration approaches that best promote the structural and functional recovery of bird assemblages (Rey-Benayas et al. 2010; Morrison and Lindell 2011; Barros et al. 2022). This understanding is particularly important given the significant differences in costs associated with implementing active versus passive restoration strategies (Brancalion et al. 2016, 2019).

Nevertheless, traditional methods for evaluating the effects of forest restoration on bird assemblages often focus on community-level metrics such as species abundance, richness, or, more recently, functional diversity (Barros et al. 2022; Hariharan and Raman 2022). While these approaches provide valuable snapshots of species composition across restored habitats, they offer limited insights into how unique species utilise these habitats and track environmental changes (Maas et al. 2009; Dong et al. 2025). Additionally, they place less emphasis on dynamics such as species movement between habitats or the identification of critical habitats and key species that enhance connectivity within the landscape mosaic (González-Varo et al. 2023). In contrast, species–habitat networks, an extension of the theory of Complex Networks, represent species and habitats as nodes within a network to analyse habitat use patterns (Marini et al. 2019; Dong et al. 2025). This approach overcomes the limitations of treating assemblages as single units, providing a deeper understanding of how restorative management practices and human-induced disturbances shape species responses (Emer et al. 2018; Clauzel et al. 2024).

Species–habitat networks enable the identification of preferred habitats within complex landscapes (Hackett et al. 2019; Lami et al. 2021; Dong et al. 2025), the tracking of species movements following environmental changes (Mendes et al. 2025) and the development of conservation strategies to protect threatened species (Gava-Just et al. 2024). Moreover, they allow identifying environmental properties of habitats that best support species, as well as specific functional traits that enable species to occupy different habitats and navigate the landscape. For instance, networks can be structured into compartments (i.e., modules) where nodes interact more strongly within compartments than with others (Olesen et al. 2007; Dehling 2018). Interactions within the network can also exhibit asymmetric dependencies between nodes (Bascompte and Jordano 2007), with some nodes depending more on their partners than vice versa.

In species–habitat networks where habitats are spatially explicit, habitat types can be interpreted as spatial compartments. Thus, as *c*- and *z*-scores have been widely used to describe how species interact within and between modules in interaction networks (Olesen et al. 2007), they can also be applied to assess how species connect distinct habitats (spatial compartments) in a landscape context (see Carstensen and Olesen 2009; Carstensen et al. 2012; Mendes et al. 2025). Specifically, *z* (within-module degree) quantifies how strongly a node—species or habitat—is connected within its spatial compartment, while *c* (among-module connectivity) captures how much it links different compartments. In this sense, these metrics can act as proxies of functional connectivity, reflecting either the properties of habitats (e.g., restoration technique) that facilitate their integration in the landscape mosaic or the traits of species that enable them to move across habitats and maintain connections among restoration sites (Mendes et al. 2025). These insights can help in understanding source–sink dynamics in complex landscapes, allowing accurate monitoring of biodiversity in anthropogenic mosaics.

The Atlantic Forest, home to over 65% of Brazil's population, has garnered remarkable attention from restoration initiatives due to its long history of land degradation and its vital role in providing ecosystem services (Rodrigues et al. 2009; Joly et al. 2014; Guerra et al. 2020). Despite this, long-term monitoring of restoration efforts remains rare, constrained by high costs, the temporal mismatch between restoration funding and the time necessary for ecosystem recovery, and the logistical challenges of sustaining long-term projects (Montoya et al. 2012; Chaves et al. 2015; Brancalion et al. 2019). Once restoration sites are implemented, few are revisited to assess critical factors that could hinder their progression along suitable successional trajectories (Viani et al. 2017; Brancalion et al. 2019), such as plant invasions (Parré et al. 2023) or the cascading recovery of functionally diverse higher trophic levels, including invertebrates, mammals and birds, and their accompanying ecological roles, such as herbivory, predation, pollination, seed dispersal (Montoya et al. 2012; Truchy et al. 2015; Rosenfield and Müller 2019).

In this study, we used a forest restored landscape mosaic with long-term restoration experiments alongside two reference forest ecosystems (see Engel and Parrotta 2001) to construct

species–habitat networks and evaluate how different restoration techniques influence habitat use and connectivity within the landscape. Birds were selected as a model group due to their sensitivity to habitat changes, their detectability through standardised methods and their role as indicators of ecosystem health (Gould and Mackey 2015). By representing bird species and habitats as nodes within the network, we assessed species-specific habitat preferences, bird movement dynamics and connectivity among habitat types. Specifically, we addressed: (i) which habitat types and their environmental and landscape properties (e.g., floristic composition and proximity to other fragments) influence patterns of bird occupancy; (ii) which habitats are critical for maintaining landscape cohesion by sharing bird species; and (iii) whether bird functional traits explain patterns of habitat use within the restored landscape mosaic. As in active restoration a subset of plant species is planted, which may not fully capture the diversity of the regional species pool (de Almeida et al. 2024, 2025), we hypothesised that these habitats would support only a subset of bird species found in reference fragments. In contrast, passively restored forests tend to develop a plant community more representative of the regional pool, allowing bird assemblages to more closely resemble those in reference habitats. Therefore, habitat type and floristic composition, in terms of tree diversity, would be important factors shaping bird occupancy patterns. In this context, active restoration would support a bird assemblage that represents a subset of the assemblages found in the other habitat types, implying lower frequencies of species shared with other habitats but higher frequencies of species shared with other active restoration areas, corresponding to high within-habitat connectivity (*z*) but low among-habitat connectivity (*c*). However, given birds' capacity to move across kilometres and use stepping-stone patches, the proximity of other fragments would probably not strongly influence occupancy patterns in the restored landscape mosaic. Hence, at the species level, no specific traits were expected to strongly explain variation in bird *c*- or *z*-scores.

2 | Methods

2.1 | Study Site and Habitat Types

The study was conducted in a restored landscape mosaic within the municipality of Botucatu, São Paulo State, Brazil (22°49'26" S, 48°25'09" W; 464–775 m a.s.l.). Botucatu is situated in an ecotonal zone between the fire-prone Cerrado (Brazilian savanna) (Ballarin, Mores, et al. 2024) and Atlantic Forest—global biodiversity hotspots (Myers et al. 2000), encompassing diverse vegetation types. These range from savanna-like ecosystems dominated by grasses, forbs and shrubs to forest ecosystems characterised by clearly defined vertical stratification of plant species. Botucatu has a humid subtropical climate (Köppen Aw) (Franco et al. 2023), with an average annual rainfall of 1500 mm concentrated between October and March, and a mean temperature of 20.5°C. The native vegetation of our study site is classified as Seasonal Semideciduous Forest within the Atlantic Forest domain (IBGE 2012). Seasonal Semideciduous Forests are characterised by the loss of 20%–50% of their tree foliage during the driest months of the austral winter and are the most threatened

Atlantic Forest formations (Carlucci et al. 2021). Seasonal Semideciduous forests dominate most forested habitats within the Edgárdia Experimental Farm (EEF), the site we used to represent the restored landscape mosaic. Covering an area of 1153 ha, equivalent to 1.4% of the municipality's total area, the EEF is surrounded by sugarcane fields, eucalyptus plantations, pasturelands, and, more recently, urban developments.

The restored landscape mosaic (Figure 1a) comprised four distinct habitat types (i and ii are about the same age): (i) a conserved reference Seasonal Semideciduous Forest (hereafter, Late-successional), which has remained undisturbed since at least 1962, when monitoring began; (ii) a transitional conserved forest (hereafter, Cerrado), where floristic elements of Cerrado forest profiles (e.g., Cerradão woodland) intermingle with species from the Atlantic Forest domain; (iii) a naturally regenerated forest (hereafter, Passive restoration), formed since 1982 through secondary succession as abandoned cattle pastures were colonised by forest tree species; and (iv) two actively restored sites (hereafter, Active restoration) located 1.5 km apart, where former coffee and bean plantations were converted into restoration experiments in 1997, covering a total area of 7.5 ha with various active restoration systems (Figure S1). Despite differences in soil properties, both Active restoration sites were established using the same mix of native plant species and restoration techniques.

2.2 | Bird Sampling

We conducted monthly systematic observations from September 2022 to August 2023. For each of the four habitat types, we selected two survey stations, ensuring a minimum distance of 1 km between them (Figure S1). Due to the small area, each active restoration had three point counts and represented one station. At each station, we established three point counts with a 50 m radius of detection (Bibby et al. 2000), spaced 150 m apart, and totalling 24 point counts (six per habitat type) in eight stations. Sampling was carried out by the same two observers at each survey station, equally distributed among point count stations. This resulted in a total of six observation hours at each of the eight survey stations over the 12 months (0.5 h per point count station and 1 h per habitat type), accumulating 48 sampling hours overall. To standardise the comparison of species diversity across samples, we constructed individual-based rarefaction and extrapolation curves using the iNEXT package (Hsieh et al. 2016). This approach interpolates diversity to smaller sample sizes and extrapolates it to larger sizes, predicting the asymptotic species richness. For our dataset, we captured approximately 90% of the estimated bird richness in each habitat type (Figure S2).

Surveys were conducted between 5:30 AM and 10:30 AM, due to the distances between stations. Bird species were identified visually using binoculars. We strictly focused on birds that occupied

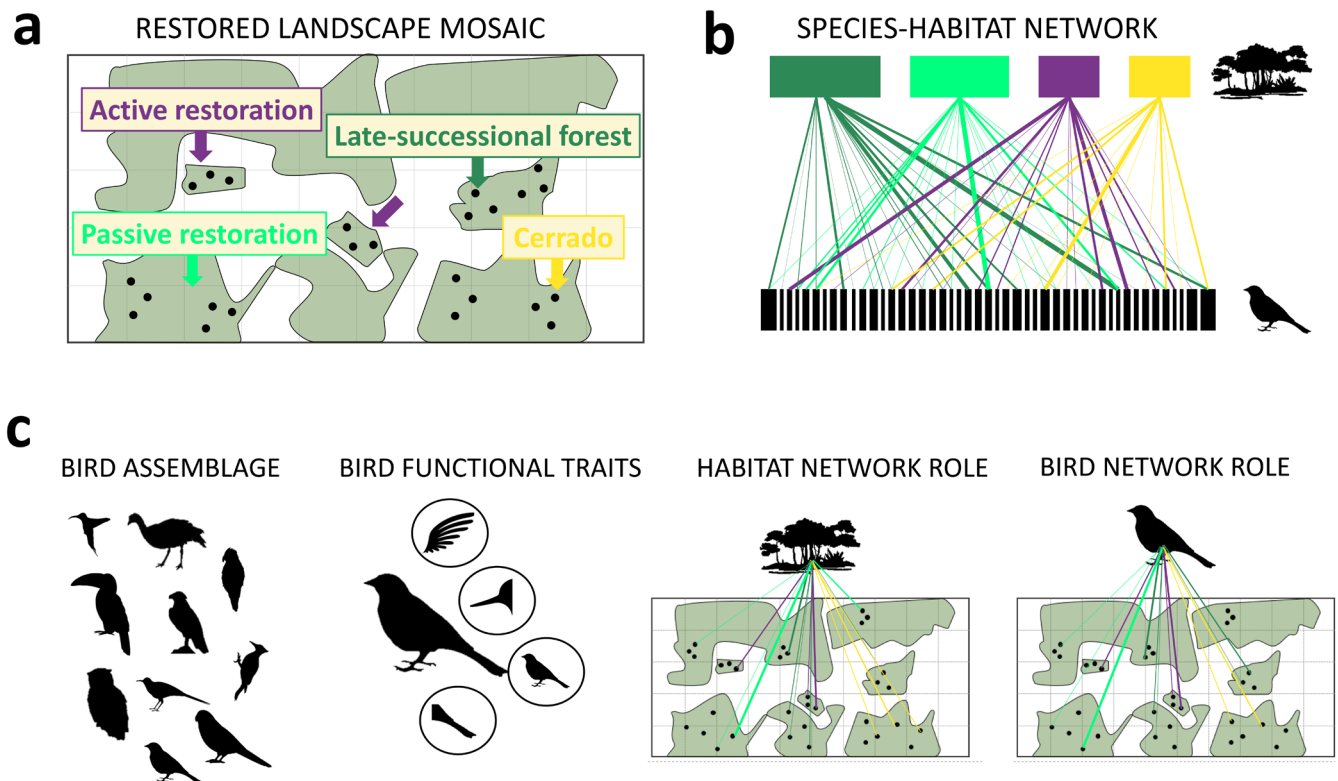


FIGURE 1 | General overview of the study design. Restored landscape mosaic showing the intermingling of different forest phytophysiognomies (i.e., habitat types; a): actively restored forests (purple), conserved forest (late-successional; dark green), naturally regenerated forest (passive restoration; light green), and transitional forest combining elements of Atlantic forest and Brazilian Cerrado (Cerrado; yellow; a). Species–habitat network constructed based on bird occurrences in each habitat type (b). Upper, coloured nodes represent habitat types, using the same colour scheme as in panel (a), while black nodes represent bird species. Ecological variables used to analyse patterns of bird occupation across habitat types within the restored landscape mosaic (c). Black dots in the upper-right panel (a) represent the point count stations used to sample bird species in our restored landscape mosaic.

the forest strata, not considering flyover species, mostly represented by the Cathartidae, Accipitridae and Psittacidae families. Audio recordings were made with a Tascam DR-05 recorder. All visual and audio data were subsequently uploaded to ornithological online platforms, including eBird (www.ebird.com), Wikiaves (www.wikiaves.com.br) and Xeno-canto (www.xeno-canto.org). Taxonomic classifications followed the most recent resolutions of the Brazilian Ornithological Records Committee (Pacheco et al. 2021).

2.3 | Bird Taxonomic and Functional Diversity Within Habitats

Due to inherent differential ecological aspects among habitat stands (e.g., successional stage, age, plant species composition, openness, and microclimatic and edaphic conditions) that might influence bird occupation through bottom-up (e.g., resource availability) and top-down (e.g., predation rates) effects, our primary goal was to evaluate how bird assemblage differs between habitat types. For this purpose, we calculated the taxonomic β -diversity of bird assemblages among point count stations, explicitly partitioning it into its two main components: β_{turn} (turnover) and β_{nest} (nestedness), following Baselga (2010). In our context, β_{turn} represents species replacement between bird communities at different habitat types, reflecting how species are replaced by others along environmental or spatial gradients. In contrast, β_{nest} captures differences in species composition that arise when one assemblage is a subset of another, indicating species loss or gain without replacement—essentially measuring how nested or ordered the bird communities are relative to each other. We used the Chao–Sørensen index to measure total β -diversity and partitioned it accordingly (Chao et al. 2006). These calculations were performed using the ‘betapart’ package in R (Baselga and Orme 2012), which is specifically designed to partition β -diversity into turnover and nestedness components.

Still, taxonomic differences in bird assemblages between habitats may not necessarily reflect a cascading impact on ecosystem functioning, as turnover between bird species can involve shifts in bird taxa with redundant ecological roles and similar functional traits. In this sense, we also inspected whether different habitat types harbour bird assemblages displaying distinct sets of functional traits. For this, we first assessed functional surrogates of distinct aspects of birds’ life-history. For diet breadth, we assessed bill width and length; for dispersal capacity we assessed wing chord and tail length, and corporal mass; for trophic position we categorised birds into their trophic level (e.g., herbivore) and feeding habit (e.g., nectarivore); and finally, for fine-grained birds’ spatial occupation within habitat we categorised them according to their natural history (i.e., insessorial, terrestrial, generalist and aerial). All bird functional traits were extracted from the AVONET database (Tobias et al. 2022).

We then used this set of bird functional traits to calculate functional diversity using two complementary indices: functional richness (FRic) and functional evenness (FEve). FRic quantifies the volume of the trait space occupied by the community, representing the range of trait values (Villéger et al. 2008). FEve measures the regularity with which species fill the trait space, indicating how evenly traits are distributed, and was calculated

using presence/absence data (Villéger et al. 2008). We selected these two indices because they capture complementary dimensions of functional diversity: FRic reflects the breadth of trait values within the community, while FEve describes the regularity of species’ positions in trait space, offering a comprehensive view of community structure without redundancy.

2.4 | Weighted Bird–Habitat Network

We built a weighted bird–habitat network (Figure 1b) as an adjacency matrix B , where rows i represent each point count station established within each habitat, columns j represent each bird species, and B_{ij} cells were filled with the abundance of a given bird species in each point count station (see Gava-Just et al. 2024 for a similar approach). As we had three point counts in an edge-to-interior gradient, and two stations per habitat type, the bird–habitat network contained 24 point counts j , six for each habitat. The bird–habitat network was created and then inspected to investigate patterns of bird occurrence in different habitats within the restored landscape mosaic using the ‘bipartite’ R package (Dormann et al. 2008).

2.5 | Habitat Type Roles in Harboursing Birds Within the Restored Landscape Mosaic

To evaluate how different habitat types perform in attracting and sustaining birds within the restored landscape mosaic as well as their connectivity with different habitat types through bird dispersal (Figure 1c), we used node-level metrics that reflect how much a single node (i.e., point count stations) cooperates for birds to permeate in the restored landscape mosaic (see Marini et al. 2019). For this, we used two distinct node-level metrics: among- and within-habitat connectivity (c - and z -scores, respectively).

Among- and within-habitat connectivity (c - and z -scores; formerly known as among-module connectivity and within-module degree) are adaptations of Guimerà and Amaral’s (2005) framework for evaluating the contribution of nodes to the formation of network compartments (i.e., subsets of nodes interacting more frequently within their subset—module—than with nodes from other subsets) (Olesen et al. 2007; Ballarin et al. 2020; Mendes et al. 2025). As in our study point count stations represented four different habitats within the restored landscape mosaic; c - and z -scores characterised the relative importance of each station in sharing bird species with other stations either within the same (z -score) or across different habitats (c -score; see Hackett et al. 2019 for a similar approach). Point count stations predominantly sharing bird species with others within the same habitat exhibited higher z -scores, whereas those sharing birds with stations from other habitats showed higher c -scores. To calculate these scores, we used the quadratic matrix (PAC_{ij}) obtained from the ‘PAC’ function in the ‘bipartite’ R package, which is based on an adaptation of the Müller index.

Originally developed to assess apparent competition, the Müller index quantifies how the consumption of one species can indirectly increase the consumption of another (Müller et al. 1999). Its application has since expanded to complex

mutualistic interaction networks, where nodes at the same level influence interactions with nodes at higher trophic levels (Carvalho et al. 2014; Bergamo et al. 2017; Ballarin, Amorim, et al. 2024). For example, in pollination networks, the Müller index can indicate how much a given plant species contributes to a pollinator's diet, thereby helping to retain the pollinator in the habitat and, consequently, increasing the likelihood that other plant species receive pollination services from these shared partners (e.g., plant–plant facilitation). We adapted the Müller index to species–habitat networks to quantify how much a given spatially explicit node (e.g., a point count station in our study, or a site or plot in other contexts) indirectly contributes to the occupation of organisms (e.g., birds) in other spatially explicit nodes. In other words, like in pollination systems, a habitat node (i.e., point count station) that hosts a given bird species can help maintain that species in the landscape, increasing the likelihood that it will occupy other habitat nodes. In our study, PAC_{ij} values represent the indirect interactions between pairs of point count stations through shared bird species. Each cell reflects the contribution of one node i to the presence of bird species in another node j . Summing the column values for a given node (the ‘ j values’) quantifies how much that node functions as a source habitat, sustaining species presence across other point count stations. This framework thus provides a proxy of functional connectivity within the restored landscape mosaic, capturing how habitats contribute to species occupation both within and across habitat types. To calculate these c - and z -scores, we used the summation of column values (‘ j values’) in the quadratic matrix (PAC_{ij}), and following the methodology proposed by Guimerà and Amaral (2005).

Based on their c - and z -scores, point count stations were categorised into four network roles. Two thresholds were defined to assign these roles: hubs were point count stations with high z -scores (z -score ≥ 2.576), indicating strong bird sharing within the same habitat, and connectors were point count stations with high c -scores (c -score ≥ 0.741), indicating substantial bird sharing with stations from other habitats. The threshold of z -score = 2.576 follows the traditional calculation of z -scores, where a z -score indicates how many standard deviations a value is above the mean. This threshold corresponds to a significance level of $\alpha = 0.005$, meaning that values above it are highly unlikely under the null expectation and thus minimise the probability of committing a type I error. The threshold of c -score = 0.741 depends on the number of habitats and was derived heuristically for this study (see Methods S1 for details). Using these thresholds, point count stations were classified as follows: Habitat hubs ($z \geq 2.576, c \leq 0.741$)—key to maintaining coherence within a specific habitat. Landscape hubs ($z \geq 2.576, c > 0.741$)—key to maintaining connectivity across the entire restored landscape mosaic. Habitat connectors ($z < 2.576, c > 0.741$)—important for linking different habitats. Peripherals ($z < 2.576, c \leq 0.741$)—limited bird sharing, primarily within their own habitat.

2.6 | Bird Roles in Connecting Habitats Within the Restored Landscape Mosaic

We used the species–habitat network (adjacency matrix B) to evaluate bird species’ roles in connecting different habitat types

within the restored landscape mosaic and to examine whether functional traits influenced these roles (Figure 1c). Bird roles were assessed by calculating among- and within-habitat connectivity (c - and z -scores, respectively), following the same rationale as applied to point count stations. Higher z -scores reflected preferential occupation of specific habitat types, while higher c -scores indicated birds occupying multiple habitat types. Based on c - and z -scores, birds were classified into four functional roles: (1) Habitat hubs ($z \geq 2.576, c \leq 0.587$)—species connecting stations within the same habitat; (2) Landscape hubs ($z \geq 2.576, c > 0.587$)—species enhancing coherence across the entire restored landscape mosaic; (3) Habitat connectors ($z < 2.576, c > 0.587$)—species linking stations in different habitats; and (4) Peripherals ($z < 2.576, c \leq 0.587$)—species primarily associated with a single point count station and present in low abundance.

2.7 | Data Analysis

To evaluate whether the β -diversity of bird assemblages differs among habitat types we performed two beta regression models, considering β_{turn} (species replacement) and β_{nest} (species loss/gain leading to nested patterns) as response variables. We considered the pairwise comparison among point count stations belonging to distinct habitat types as a fixed factor and the Sorensen taxonomic β -diversity (i.e., β_{turn} and β_{nest}) as the response variable for each model. To verify if distinct aspects of birds’ functional diversity differ between habitat types, we performed two regression models considering FRic and FEve as responses for each model. Habitat types were treated as a fixed effect. We log-transformed FRic to meet the assumptions of normality and homoscedasticity and modelled it using a Gaussian family distribution, while FEve was modelled using beta regression. We also included tree Shannon diversity, measured within a 1-ha plot of trees between the point counts at each survey station, and the distance to the nearest forest patch, calculated as the Euclidean distance from the point count station to the nearest forest fragment outside its own fragment, as alternative predictors to account for potential drivers of bird occupancy related to vegetation composition and habitat connectivity. Differences among pairwise β -diversity of bird assemblages (β_{turn} and β_{nest}), FRic and FEve between habitat types were assessed through a Tukey post hoc test using the package ‘emmeans’ in R (Lenth 2016).

We adopted a similar protocol to evaluate if the node role of point count stations within the species–habitat network differs between habitat types. We built two linear models considering among- (c -) and within-habitat connectivity (z -scores) as response variables. Habitat types were treated as fixed effects along with tree Shannon diversity and distance to the nearest forest patch. We performed a beta regression modelling the c -score as the response variable. The model including the z -score as response was built with a Gaussian error distribution. Differences in network roles played by point count stations of different habitats were assessed with a Tukey post hoc test.

Finally, to inspect the influence of bird functional traits on the network role played by bird species within the species–habitat network, we built two linear models considering c -score, and z -score as the response of each model. Initially, we included

all abovementioned functional attributes related to birds' diet breadth, dispersal capacity, trophic position, feeding habit and spatial occupation as predictors. A Gaussian error distribution was used for the model including z -score as response while we used a beta regression for the model including c -score as response. We used the Akaike information criterion corrected for small samples (AICc, $\Delta\text{AICc}=0$), by comparing the full model (considering all predictors), with the candidate models (including all combinations between predictors), and the null model (the intercept only), using the function dredge in the 'MuMIn' R package (Barton 2012). Collinearity among bird traits was assessed with the variance inflation factor (VIF) using the 'car' R package (Fox and Weisberg 2019). Many bird traits were correlated, showing $\text{VIF} > 3$. To avoid model multicollinearity, we repeated the same analytical routine only keeping bill width and length, wing chord, corporal mass and trophic level (e.g., herbivore), which generated models always with $\text{VIF} < 2.2$.

3 | Results

We observed 4571 bird individuals belonging to 152 species (130 with available trait data) within the restored landscape mosaic. The Late-successional habitat harboured the highest bird abundance (1335 bird individuals), followed by the Passive restoration (1166), the Cerrado (1096) and the Active restoration (974). Bird species richness was similar between habitats, with the Passive restoration and the Cerrado exhibiting 99 bird species, followed by the Late-successional (97), and the Active restoration (93). Nevertheless, different bird species, representing various trophic levels and feeding habits, occupied each habitat type at different abundances (Figures S3 and S4).

3.1 | Bird Taxonomic and Functional Diversity Within Habitats

We found intermediate levels of β -diversity within habitats ($\beta_{\text{Chao-Sorensen}} = 0.38 \pm 0.09$) with greater dissimilarities in bird species in comparisons between the Active restoration and the remaining habitat types, especially in the turnover component of β -diversity ($\beta_{\text{turn}} = 0.34 \pm 0.10$; $\chi^2_{1,215} = 591.55$; $R^2 = 0.73$; $p < 0.01$). The nestedness component of β -diversity was higher when considering the Cerrado and the Late-successional habitat types ($\beta_{\text{nest}} = 0.05 \pm 0.10$; $\chi^2_{1,215} = 22.98$; $R^2 = 0.08$; $p < 0.01$; Figure 2a; Table S1, Figures S5 and S6).

FRic ($\chi^2_{1,23} = 5.75$; $R^2 = 0.26$; $p = 0.12$) and FEve ($\chi^2_{1,23} = 6.53$; $R^2 = 0.25$; $p = 0.23$) did not differ between habitat types (Figure 2b,c; Table S2, Figures S7 and S8). Neither tree Shannon diversity nor distance to the nearest forest patch explained variances in bird functional diversity metrics ($p > 0.05$), and VIFs were always < 2.1 (Table S2).

3.2 | Habitat Type Roles in Harboring Birds Within the Restored Landscape Mosaic

Differences in the roles played by point count stations within the species-habitat network showed a generally consistent pattern, with the Active restoration differing from the remaining habitats (Figure 3). Among ($\chi^2_{1,23} = 50.31$; $R^2 = 0.792$; $p < 0.001$; Figure 3a) and within-habitat connectivity ($\chi^2_{1,23} = 18.75$; $R^2 = 0.59$; $p < 0.001$; Figure 3b) differed between habitat types (see also Table S3, Figures S9 and S10). While the Active restoration exhibits higher scores of within-habitat connectivity (z -score; Figure 3c), it showed lower scores of among-habitat connectivity (c -score; Figure 3c) in comparison with the remaining habitat types. In fact, while stations belonging to the Late-successional, Cerrado or Passive

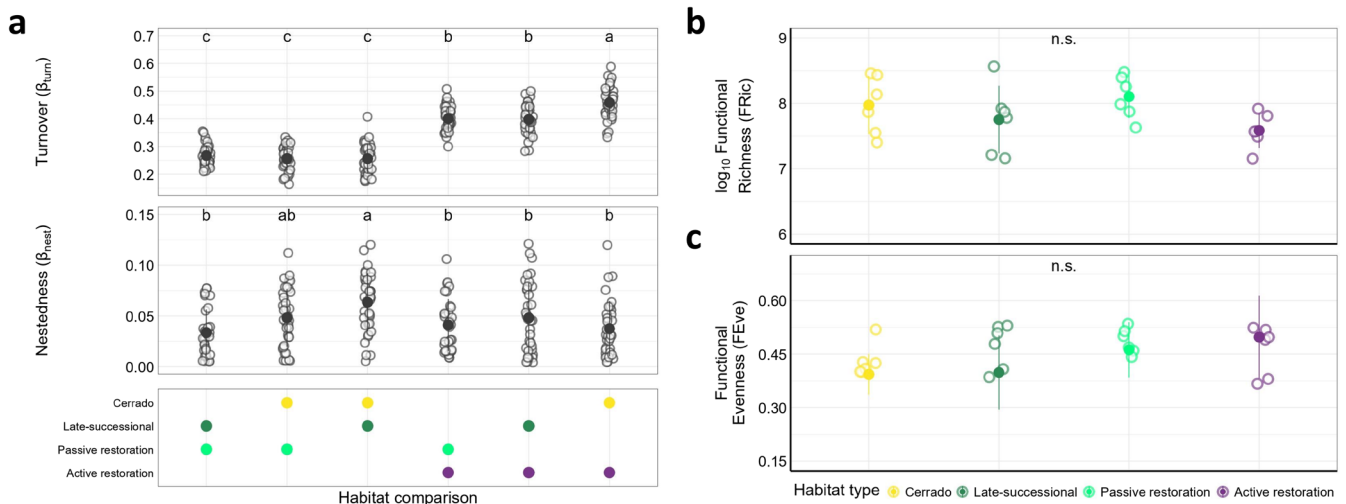


FIGURE 2 | Taxonomic and functional diversity of bird assemblages across different habitat types within a restored landscape mosaic. Beta diversity components of bird assemblages among habitat types (a), including turnover (β_{turn}) and nestedness (β_{nest}). Circles below the graph represent the habitat type pairs being compared. Actively restored habitats (purple) show different patterns of β_{turn} compared to passive restoration (light green), late-successional forest (dark green) and Cerrado (yellow). Functional diversity metrics of bird assemblages across habitat types, including functional richness (FRic; b) and functional evenness (FEve; c). Open circles represent point count stations, with colours corresponding to habitat type: Cerrado (yellow), late-successional forest (dark green), passive restoration (light green) and active restoration (purple). Compact letter displays indicate significant differences based on Tukey post hoc analyses. 'n.s.' denotes non-significant differences among habitat types.

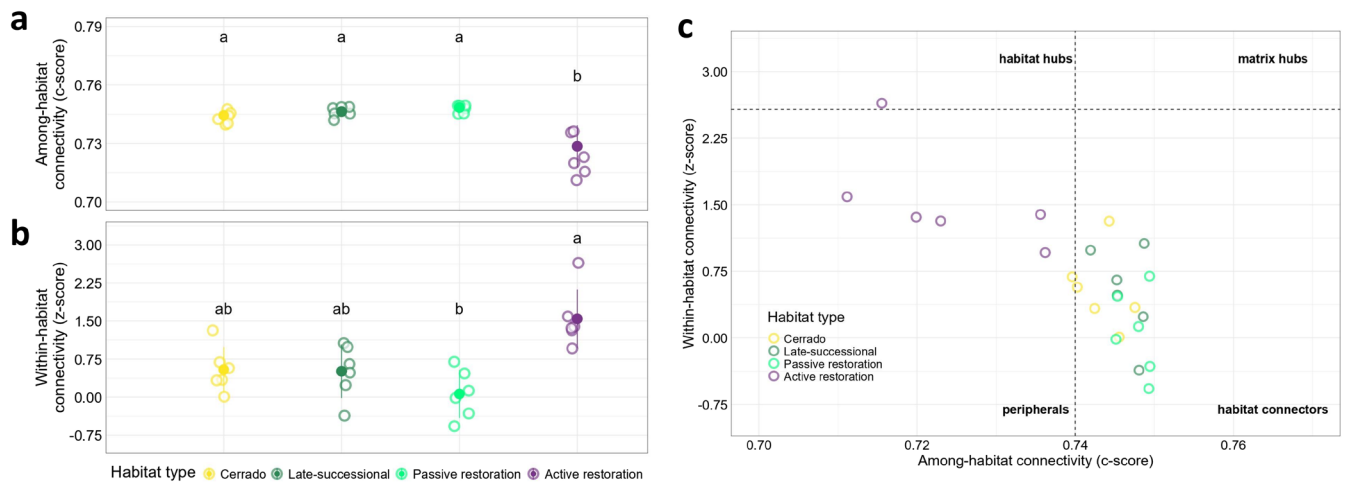


FIGURE 3 | Site network roles within the species–habitat network. Among-habitat connectivity (c -score; a) and within-habitat connectivity (z -score; b) of sites are shown, with compact letter displays indicating significant differences based on Tukey post hoc analyses. Habitat network roles (c) are classified into four categories according to their contribution to habitat connectivity, comparing connectivity within the same habitat type (z -score; y -axis) versus among different habitat types (c -score; x -axis), following Hackett et al. (2019) and Olesen et al. (2007). Open circles represent point count stations, with colours corresponding to habitat type: Cerrado (yellow), late-successional forest (dark green), passive restoration (light green) and active restoration (purple).

restoration were classified as habitat connectors, the Active restoration was generally classified as a peripheral or habitat hub (Figure 3c). Tree Shannon diversity and distance to the nearest forest patch did not explain variation in habitat roles within the network. VIF were < 2.1 in all models (Table S3).

3.3 | Bird Roles in Connecting Habitats Within the Restored Landscape Mosaic

No bird trait explained among-habitat connectivity (c -score; $R^2 = 0.06$; $p > 0.05$) nor within-habitat connectivity (z -score; $R^2 = 0.04$; $p > 0.05$; Table S4, Figures S11 and S12). Most birds played peripheral roles or acted as habitat connectors within the species–habitat network. The Southern House Wren *Troglodytes musculus* was the only exception, acting as a habitat hub. The Picazuro Pigeon *Patagioenas picazuro*, was the frugivore-granivore while the Rufous-browed Peppershrike *Cyclarhis gujanensis*, was the invertivore with more important roles in connecting the restored landscape mosaic (Figure 4).

4 | Discussion

Our findings show that actively restored forest stands harbour bird communities less similar to those of conserved reference forests than do naturally regenerated secondary forests. Furthermore, our results indicate that actively restored habitats are occupied by a distinct bird assemblage that appears to preferentially use these areas, potentially limiting their effectiveness as source or sink habitats within the landscape. Finally, although we did not identify any strong functional traits that could predict bird occupancy patterns across the restored landscape, certain bird species emerged as key players in connecting different habitat types.

Although active tree planting is essential in degraded forest landscapes due to the potential failure of natural species arrival

(Rodrigues et al. 2009; Reid et al. 2015; Shoo et al. 2016; Chazdon et al. 2024), in the highly fragmented Atlantic Forest, tree planting techniques often fail to incorporate locally adapted flora (de Almeida et al. 2024, 2025). Several factors may explain this low representativeness. For instance, current restoration practices often fail to represent the regional species pool, as tree nurseries typically focus on cultivating species with well-known developmental patterns, while neglecting those whose growth processes are less understood (Ladouceur et al. 2018). Furthermore, restoration programmes often prioritise planting fast-growing pioneer species or keystone and umbrella species due to cost and risk considerations (Brançalion et al. 2018; Ballarin, Amorim, et al. 2024). While species with broad ecological roles, fast growth and rapid biomass contribution are often prioritised for successful restoration, species with limited distributions, small populations and reliant on biotic services (such as pollination and dispersal) often face challenges in colonising restoration sites (Engert et al. 2020; de Almeida et al. 2024).

Nonetheless, restored landscapes often comprise a mix of habitat types and sites undergoing restoration through various strategies (Chazdon et al. 2024). Although the Active restoration shared fewer bird species with other habitat types, it hosted a functionally diverse bird assemblage, comparable to the Late-succession, Cerrado and Passive restoration. Due to its role in harbouring bird species that are less frequent in other habitats (i.e., higher β_{turn} , and low among-habitat connectivity), our data suggest that actively restored sites may play an important role at the landscape scale. While bird sharing between habitat types can facilitate landscape integration, actively restored sites could be key for supporting bird species that have not fully colonised the late succession or the passive restoration. For example, 13.7% of bird gamma diversity occurred only in actively restored habitats, including those bird species primarily associated with scrub-dominated habitats, such as the Rufous-collared Sparrow *Zonotrichia capensis*, the Blue-black Grassquit *Volatinia jacarina* and the Double-collared Seedeater *Sporophila caerulea*.

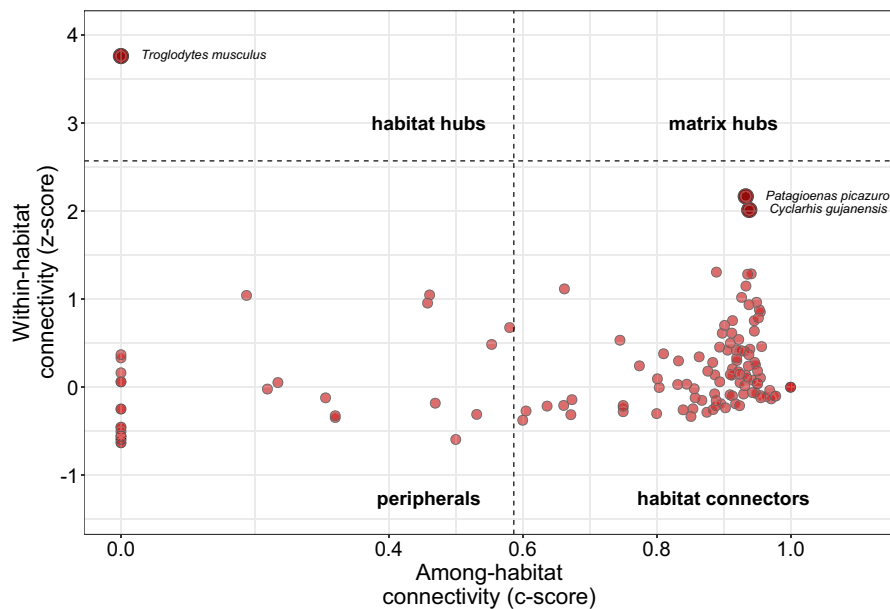


FIGURE 4 | Network roles of bird species within the species–habitat network. Each point represents a bird species positioned according to its among-habitat connectivity (x-axis) and within-habitat connectivity (y-axis, z-score). Most species occupy peripheral or connector roles, while a few species act as habitat or matrix hubs. Three species with particularly high among-habitat connectivity (*Picazuro* Pigeon and Rufous-browed Peppershrike) or within-habitat connectivity (Southern House Wren) are highlighted with larger, darker red circles.

(Figure S13). In contrast, sites undergoing natural regeneration shared many bird species with other habitat types. Hence, our results suggest that combining different restoration techniques can be advantageous by leveraging the strengths and cost-effectiveness of each strategy. Active restoration, for example, can facilitate the recruitment of medium-sized birds, such as the frugivore Surucua Trogon *Trogon surrucura* —a bird highly sensitive to habitat loss but capable of surviving in smaller fragments within a well-connected landscape (Pizo 2007). These birds contribute to restoring ecological functions that require greater human intervention, such as the recovery of large-seeded trees (see Holl et al. 2022). In contrast, we propose that passive restoration supports the recolonisation of species from the regional pool, promoting broader landscape regeneration (Zhang et al. 2024).

Despite habitat types partially explaining patterns of bird occupancy in the restored landscape mosaic through the species–habitat network approach, our results did not fully align with expectations. The nestedness component of bird β -diversity (β_{nest}) accounted for little of the variation in bird assemblage dissimilarities among habitat types, suggesting that, even if bottom-up effects influence bird occupancy (Cosset and Edwards 2017), planting a subset of native tree species resembling those in preserved sites does not necessarily attract a corresponding subset of bird species (see Munro et al. 2011). Moreover, establishing a representative assemblage of native trees at the onset of restoration does not guarantee that long-term tree densities and composition will converge towards those of nearby preserved forests, as ecological processes such as competition, herbivory and disturbance can alter trajectories over time (Suganuma and Durigan 2015). While distance to the nearest habitat patch had no effect on habitat roles, as anticipated, tree diversity also failed to explain these roles, contrary to our expectations. This suggests that tree diversity may be an overly

broad predictor of bird occupancy in small-scale landscapes (<15 km²), where birds can disperse throughout our restored landscape mosaic. More informative predictors may involve habitat attributes directly linked to resource availability, such as flowering and fruiting phenology, soil organic matter and canopy architecture. These factors could better explain the occurrence of resource-dependent guilds, including nectarivores reliant on nectar (Ballarin, Fontúrbel, et al. 2024), frugivores dependent on fleshy fruits (Quintero et al. 2020), invertivores feeding on ground-dwelling arthropods (Mansor et al. 2019) and canopy-nesting birds requiring complex canopy structure (Newell and Rodewald 2011). Therefore, long-term restoration monitoring should prioritise detailed documentation of tree functional traits and soil properties to improve predictions of the cascading effects of vegetation restoration on higher trophic levels, such as birds (Fraser et al. 2015).

In our study, bird functional traits had no influence on bird occupancy patterns within the species–habitat network. This result suggests that functional traits alone may be insufficient to predict bird occupancy patterns in mixed restored landscapes. Our upscaled network approach (i.e., bird–habitat networks) likely overlooks critical natural history aspects, such as the identity and timing of interactions within habitats. Previous research indicates that downscaled network approaches (e.g., individual-based networks) or traditional species–species networks are better suited to uncover niche-specific traits of interacting individuals or species, potentially improving predictions of bird habitat occupancy (Guimarães 2020; Quintero et al. 2025). For instance, finer network resolutions can capture trophic interactions, such as pollination, seed dispersal or predation, which are directly linked to traits like bill length and width that influence diet and nutritional intake (McFadden et al. 2022; Martins et al. 2024). We recommend future studies adopt these resolutions to identify bird functional traits

capable of predicting habitat occupancy within landscapes. A promising approach is the multilayer network framework, which integrates habitat and interspecies interactions (Mendes et al. 2025). This framework allows researchers to assess which resources birds commonly forage on (e.g., insects, flowers, fruits, seeds), link them to functional traits (e.g., bill morphology), and analyse how resource distribution influences habitat occupancy patterns. Furthermore, movement-related traits may not serve as strong predictors of bird roles within species–habitat networks in small-scale landscapes, where most bird species can easily traverse the spatial mosaic, regardless of their dispersal capacity. To address this, future studies should consider larger spatial scales to better capture differences in bird dispersal abilities and their influence on occupation patterns (Gava-Just et al. 2024).

Nonetheless, the species–habitat network provided a straightforward and valuable framework to identify key bird species contributing to site connectivity within the restored landscape. These included species important for connecting sites within the same habitat type or restoration strategy (habitat hubs), those linking distinct habitat types (habitat connectors) and those spanning the entire restored landscape mosaic (matrix hubs). Notably, our data suggest that very common and widespread edge-linked species with different trophic roles, such as the Picazuro Pigeon (fruit and seed disperser), and the Rufous-browed Peppershrike (invertivore), acted as important habitat connectors by moving among various habitat types (Figure S13). Conversely, the Southern House Wren (invertivore), for example, predominantly occupied actively restored habitats (Figure S13). These findings suggest that common and abundant urban-associated species, such as the Picazuro Pigeon, frequently visit urban-restored matrices, highlighting the need to carefully monitor the fruits they consume and the seeds they disperse, as these are likely to be deposited within the restored landscape. Supplementary strategies may be required to attract birds capable of consuming and dispersing large seeds and fruits not utilised by these urban-associated species. Additionally, the preference of open-country species like the Southern House Wren for actively restored sites may reflect their incomplete and less dense understory (de Oliveira et al. 2019), which facilitates access and frequent use of these habitats.

5 | Concluding Remarks

Our findings suggest distinct yet potentially complementary roles for actively restored and naturally regenerated habitats in recovering bird assemblages within restored landscape mosaics. While actively restored sites support specific bird species, naturally regenerated sites share a greater number of bird species with conserved patches. This suggests that employing complementary restoration strategies could help mitigate biotic homogenisation of bird assemblages (Holl et al. 2022). For instance, actively restored sites could focus on promoting plant species with limited colonisation capacity (Suganuma and Durigan 2022), whereas passively restored sites might enhance the representation of the regional species pool. Furthermore, although the network approach used here may not be ideal for identifying bird functional traits at the spatial scale and network

organisation employed (>15 km², species–habitat network), it remains a valuable tool for restoration planning by highlighting species and restoration strategies that play critical roles in connecting different habitat types, thus informing cost-effective and outcome-oriented restoration across restored landscape mosaics.

Still, we acknowledge some limitations in our study, including the small area and unbalanced sampling design, which stem from the labour and financial demands of establishing actively restored sites. These constraints may have introduced noise that our analyses could not fully capture. Moreover, species–habitat networks may be more accurate for assessing species occupancy patterns when applied over larger landscapes, where greater disparities among fragments and longer distances allow clearer identification of source and sink habitats, as well as the floristic, environmental, climatic and landscape properties that drive fragment importance and functional occupancy by birds. Despite these limitations, we believe that adapting network metrics to this spatial scale, as done in our study, provides valuable insights into the dynamic occupation of species across landscapes and the role of individual fragments in sustaining these organisms.

Author Contributions

Victor R. Antonelli: conceptualisation, methodology, investigation, data curation, writing – original draft, writing – review and editing, visualisation, resources, project administration. **Caio S. Ballarin:** conceptualisation, investigation, software, formal analysis, validation, writing – original draft, writing – review and editing, visualisation. **Vagner Cavarzere:** conceptualisation, methodology, investigation, writing – review and editing, visualisation, supervision. **Renata C. B. Fonseca:** conceptualisation, methodology, resources, investigation, writing – review and editing, visualisation, supervision, funding acquisition, project administration.

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Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** aec70145-sup-0001-AppendixS1.docx.