

PASSIVE ACOUSTIC MONITORING AS A TOOL FOR STUDIES OF FUNCTIONAL DIVERSITY IN BIRDS

Facundo X. Palacio^{1,2} , Daniela Zaffignani³  & Maila Scheffer^{1*} 

¹Sección Ornitología, Facultad de Ciencias Naturales y Museo, La Plata, Buenos Aires, Argentina

²Consejo Nacional de Investigaciones Científicas y Técnicas, La Plata, Buenos Aires, Argentina

³Laboratorio de Ecología de Aves, Instituto 'Dr. Raúl A. Ringuelet' (ILPLA) – UNLP/CONICET, La Plata, Buenos Aires, Argentina

*maila.scheffer@gmail.com

ABSTRACT: Passive acoustic monitoring (PAM) has become a key tool for studying avian ecology. However, studies applying PAM to functional diversity analyses remain scarce. Here, we describe the advantages of PAM for estimating functional diversity, as well as its limitations. We also review available approaches for incorporating imperfect detection into the estimation of functional diversity metrics, present a mathematical demonstration highlighting some limitations of currently used methods, and conduct simulations to evaluate the effects of using occupancy probabilities and true occupancy states as proxies for species occurrence in these estimations. As a case study, we analyzed bird assemblages obtained from an intensive acoustic monitoring survey (10 consecutive days) conducted in two forest types (native and exotic). Simulations showed that estimates based on occupancy probabilities more accurately recovered expected functional diversity than those based on observed matrices or latent occupancy states. In the empirical case study, accounting for imperfect detection altered inferences for some functional diversity metrics, particularly functional regularity. Overall, our results highlight the potential of PAM to explicitly integrate detection processes into functional diversity studies and suggest that occupancy probabilities provide a robust alternative for estimating functional diversity in bird communities.

KEYWORDS: *acoustic trait, autonomous recording unit, imperfect detection, Ligustrum lucidum, occupancy models, talaes*

The study of sound and vocalizations has a long tradition in avian ecology and behavior. From classic work on song learning and function (Kroodsma & Miller 1982) to more recent applications in community ecology (Farina & Gage 2017), bioacoustics has been a key tool for understanding communication processes, vocal activity, and assemblage structuring, establishing sound as an essential dimension of ecosystems and biodiversity (Ross et al. 2023). In this context, passive acoustic monitoring (PAM) has emerged as a technological extension of this tradition, enabling systematic and standardized recording of avian vocal activity across different spatial and temporal scales, and introduced soundscape ecology as a subdiscipline within bioacoustics (Pijanowski & Farina 2011).

In recent decades, this approach has also begun to integrate with perspectives from functional ecology. This discipline seeks to understand how the functional traits of species — that is, how morphological, physiological, phenological, genetic, or behavioral characteristics linked to survival and fitness — determine community responses to the environment and their effects on ecosystem functioning (Violle et al. 2007). Within this framework, functional diversity describes the degree of ecological differentiation among the species of a community based on attributes linked to their performance and resource use (Palacio 2024). Because vocalizations and the use of acoustic space reflect the ecological and behavioral attributes of species, the sounds produced by birds can also be considered potential sources of functional information. In this context, so-called acoustic traits

can be obtained from spectrograms, graphical representations of sound that show, for a given acoustic signal, the temporal variation (X axis) of frequency (Y axis) and its energy (amplitude; Z axis). In this way, the soundscape can be understood not only as a measure of presence or biological activity, but also as an expression of the functional diversity of communities (Ross et al. 2023).

Advantages of passive acoustic monitoring

In recent years, PAM has become an effective tool for studying avian bioacoustics (Shonfield & Bayne 2017, Darras et al. 2018, Wood et al. 2019), with an exponential increase in the use of autonomous recorders (Shonfield & Bayne 2017, Bruyninckx 2018, Darras et al. 2019). This is because this technology offers many advantages compared with more traditional sampling methods in avian ecology, such as point counts and transects. First, the data obtained through these devices produce diversity estimates comparable to those generated by trained observers (Darras et al. 2018, 2019), and the sustained reduction in equipment costs has favored its widespread adoption in ecological studies (e.g., Hill et al. 2018). Second, recent advances in machine learning are beginning to facilitate the automatic detection and identification of vocalizations, allowing hundreds of species to be rapidly classified from large volumes of audio (Wood et al. 2021, Somervuo et al. 2025). Likewise, recordings constitute a permanent record that can be reviewed by multiple observers, which reduces observer-associated bias and allows detection probabilities to be estimated and the factors affecting them to be evaluated (Campbell & Francis 2011, Darras et al. 2019). This feature is especially advantageous in species-rich communities (Hobson et al. 2002, Campbell & Francis 2011), particularly during the dawn chorus (Haselmayer & Quinn 2000), since files can be listened to repeatedly to improve identification accuracy. In addition, having an archived record is essential for corroborating the presence of rare or cryptic species (Jones et al. 2007, Swiston & Mennill 2009, Darras et al. 2019, Bota et al. 2023) and for comparing current vocalizations with historical records (e.g., Luther & Derryberry 2012). Finally, a central advantage of automated recorders is their natural integration into occupancy modelling frameworks (e.g., Campos-Cerqueira & Aide 2016, Zaffignani et al. 2026). These devices allow repeated samples to be standardized and synchronized at comparable times of day, reducing temporal variability in detection probability and improving the precision of estimates (Furnas & Callas 2015). On the other hand,

processing the large volume of data generated usually demands a considerable investment of time, although this cost is being mitigated by automated and accessible analysis tools such as the Automated Remote Biodiversity Monitoring Network (ARBIMON; Acevedo et al. 2009, Aide et al. 2013, Vega et al. 2016), Animal Sound Identifier (Ovaskainen et al. 2018), BirdNET (Kahl et al. 2021), or Bird Sounds Global (Lauha et al. 2025).

Acoustic monitoring and its application to functional diversity

In parallel with the development and expansion of PAM, the study of biodiversity has increasingly incorporated the trait-based approach to functional diversity (Guillerme et al. 2025). This approach has been widely used in recent years to determine how environmental gradients and disturbances act as filters on particular traits, thereby modifying the functional composition and assembly rules of communities (Palacio et al. 2022). It has also gained increasing relevance in biogeography and conservation, allowing spatial patterns of functional diversity to be assessed, priority conservation areas to be identified, biotic homogenization processes to be detected, and potential losses of ecosystem functions in the face of environmental change to be anticipated (Stewart et al. 2022, Ali et al. 2023, Martínez-Núñez et al. 2023). In this context, linking PAM with functional diversity studies makes it possible not only to estimate the taxonomic composition of communities, but also to characterize their functional structure based on the species detected and their vocal activity, opening new possibilities for assessing changes in assemblage functioning across different spatial and temporal scales. This approach, however, assumes that the recorded vocal activity adequately represents community composition and that a consistent relationship exists between acoustic signals, species presence, and their ecological attributes. Despite its potential, studies applying PAM to the analysis of functional diversity in birds remain scarce.

OBJECTIVES

In this work, our aim was to review the integration of PAM into studies of functional diversity in birds. To this end, we (1) synthesized how species detection can be incorporated into the estimation of functional diversity metrics, (2) discussed the potential of acoustic traits as functional traits, (3) evaluated through simulations the consequences of including occupancy proxies in functional metrics, and finally

(4) illustrated these concepts through a case study analyzing the functional diversity of bird assemblages based on an intensive acoustic monitoring survey in two forest types (native and exotic). We expect that explicitly incorporating detectability will reduce bias in the estimation of functional diversity, particularly in communities with species of low detectability or infrequent occurrence.

Estimating functional diversity from passive acoustic monitoring

Every estimate of functional diversity requires at least two sources of information (de Bello et al. 2021, Palacio 2024): a community matrix (sites by species or any other taxonomic unit) and a functional trait matrix (species by functional traits). In this sense, PAM offers certain advantages for characterizing the community matrix, by improving the detectability of cryptic or hard-to-observe species, reducing observer-associated bias, and providing standardized, reproducible sampling (Darras et al. 2019), despite representing only a fraction of the community — the species that vocalize (acoustic assemblage; e.g., Blake 2021). Its high temporal resolution allows daily and seasonal variation in species' vocal activity to be captured, which facilitates a better estimation of occupancy and imperfect detection (Singer et al. 2025). In addition, PAM is easily scalable to large spatial extents and is compatible with automated analysis methods, generating permanent records that enable long-term comparisons (Szymański et al. 2021, Symes et al. 2022). It should be noted that PAM still faces serious limitations for estimating abundance, since it records vocal activity rather than individuals per se. In this case, detection probability depends on vocalization rate, species behavior, distance to the microphone, and environmental conditions, which makes it difficult to translate the number of vocalizations into the number of individuals present (Knight et al. 2024, 2026; but see Fiss et al. 2024 and Navine et al. 2024). Consequently, metrics derived from PAM tend to reflect the frequency or intensity of acoustic activity rather than abundance, and their interpretation requires the use of explicit detection models or additional assumptions that cannot always be verified (Knight et al. 2026). Likewise, the explicit incorporation of detectability into estimates of functional diversity derived from acoustic data has received little attention (Schillé et al. 2024). In addition to the challenges associated with imperfect detection, the integration of PAM and functional diversity raises further conceptual and methodological questions regarding

how to define and select functional traits in an acoustic context.

Acoustic traits as functional traits

Although PAM facilitates the large-scale acquisition of acoustic information, conceptual questions remain as to whether acoustic traits can be considered true functional traits or whether they represent only indirect proxies for other ecological attributes. In general, acoustic traits tend to be obtained from the literature, online databases, or individuals captured in the field. In this context, PAM has begun to facilitate the incorporation of so-called 'acoustic traits' — that is, characteristics of a sound signal produced by an organism that describe its temporal, spectral, or energetic structure (e.g., duration, frequency, entropy, or modulation) and reflect properties of the emitter or the communication context (Odom et al. 2021). Operationally, these traits correspond to variables extracted from spectrograms that describe the frequency, duration, and complexity of species' songs (Moreno-Contreras et al. 2019, Prieto-Torres et al. 2021, Schillé et al. 2024). Despite growing interest in functional diversity, the use of acoustic traits in this context remains relatively scarce. Available examples include studies that used vocalization-derived variables, such as song duration, frequency, or entropy, to estimate functional diversity metrics (Moreno-Contreras et al. 2019, Prieto-Torres et al. 2021, Schillé et al. 2024). In some of these cases, this information was obtained directly from PAM-derived recordings (Schillé et al. 2024), while in others it came from online databases such as Macaulay Library and Xencanto (Moreno-Contreras et al. 2019, Prieto-Torres et al. 2021).

Before considering their functional role, it is useful to distinguish between 'effect' and 'response' traits (Lavorel & Garnier 2002). Effect traits determine the impact that organisms have on ecosystem functioning, whereas response traits indicate how organisms respond to environmental factors (de Bello et al. 2021). These categories are not mutually exclusive, and in this sense, acoustic traits can be conceptualized as both effect and response traits. As effect traits, acoustic characters can influence ecological processes such as territory establishment, mate attraction, interspecific competition, and acoustic niche partitioning (e.g., Tobias et al. 2016, Hart et al. 2021). At the same time, as response traits they can reflect species-specific adjustments to environmental conditions such as habitat structure or ambient noise (e.g., the 'acoustic adaptation hypothesis'; Tubaro et al.

1993, Boncoraglio & Saino 2007, Gil & Brumm 2014). Another useful heuristic for classifying functional traits is the dichotomy between ‘hard’ and ‘soft’ traits (Hodgson et al. 1999, Nock et al. 2016). ‘Hard’ traits are precise indicators of species’ functions within ecosystems and tend to be physiological or ecological traits (e.g., basal metabolic rate, annual survival). In contrast, ‘soft’ traits are proxies or approximations of those functions and tend to be morphological (e.g., body size, wing length). ‘Hard’ traits are generally difficult or costly to measure in practice (Hodgson et al. 1999), so they are often replaced by ‘soft’ traits, which are less costly to obtain. In the case of acoustic traits, in principle, they could be either ‘soft’ or ‘hard’, depending on how closely they relate to the ecosystem process of interest. If an acoustic trait is directly linked to a measurable ecosystem function and does not act merely as a proxy, it could then be considered a ‘hard’ trait. Vocalization is not itself an ecosystem function in the way that seed dispersal or the removal of decomposing matter is, but it could affect processes that scale up to the community level. For example, song rate could directly affect reproductive success, population density, or territorial occupancy. If this in turn modifies the rate of seed dispersal per unit area, then the acoustic trait directly affects the fitness of the individuals expressing it and indirectly influences an ecosystem function, in which case it could be considered a ‘hard’ trait. In the literature, however, most of these traits are dominant frequency, song duration, and the complexity of the tonal range, which are proxies for body size, reproductive strategy, and habitat structure, and could therefore be considered ‘soft’ traits instead. In this context, the use of PAM offers a valuable opportunity to assess how different acoustic traits influence assemblage structure and how these variations can be linked to specific ecosystem functions, an approach that remains scarcely addressed in the literature.

On the other hand, conceptual questions remain regarding whether acoustic traits can be considered true functional traits or whether they represent only indirect proxies for other ecological attributes. In fact, none of the studies cited above explicitly mention the (direct or indirect) relationship of these acoustic characters with ecosystem functions; rather, they are used as proxies for differences in habitat use, owing to the transmission properties of sound. Although different acoustic traits influence reproductive success, territory defense, and social cohesion (Tobias et al. 2016), with possible effects on abundance, habitat occupancy, and community structure (Alcocer et al. 2022), there

is little information on how these traits contribute directly to ecosystem functions such as pollination, seed dispersal, or arthropod control. On the contrary, they appear to indicate which species — and, therefore, which functions — are present. Consequently, their inclusion as functional traits should be explicitly justified on the basis of clear ecological hypotheses about the functions they might mediate (Palacio et al. 2022). For example, are low-frequency songs associated with larger-bodied, frugivorous, or granivorous species that make a relevant contribution to seed dispersal? Or do species whose songs have characteristics that favor detection in noisy environments (e.g., high minimum frequencies, greater amplitude, changes in singing time) maintain higher abundances in urban areas, translating into a greater contribution to arthropod control?

Functional diversity incorporating imperfect detection: a synthesis

As mentioned above, the ability to monitor birds over time through PAM makes it possible to explicitly incorporate detection as an observation process in the estimation of species diversity (Campos-Cerqueira & Aide 2016). Regardless of the use of PAM, estimating avian species diversity while accounting for imperfect detection has become common practice in recent years. This has been made possible by the development of hierarchical models that explicitly incorporate detection probability, such as occupancy models for presence/absence data and N -mixture models for count data in multispecies contexts (MacKenzie et al. 2017, Royle et al. 2005, Royle & Dorazio 2008, Iknayan et al. 2014, Devarajan et al. 2020). Despite this substantial development, most studies incorporating imperfect detection have focused on species richness estimators, leaving aside other dimensions such as functional and phylogenetic diversity (Si et al. 2017, Palacio et al. 2020, 2022).

To address this problem, Jarzyna & Jetz (2016) proposed building a dendrogram based on functional characters (or a phylogeny in the case of phylogenetic diversity) following Petchey & Gaston (2002), and assigning weights w_j to branches j (terminal and internal) using the following criteria: (1) if species i is detected at a site, the weight of its corresponding terminal branch is $w_j = 1$ (true presence), (2) if species i is not detected at a site, then the weight of its corresponding terminal branch is $w_j = \psi_i$, where ψ_i is the occupancy probability of species i (which can be derived, for example, from an occupancy model), and (3) the weight of internal branches is

given by the probability that at least one species in the group is present $w_j = 1 - \prod_{i \in I} (1 - \psi_i)$, where I represents the set of all species included at the internal branch node. If an internal branch is shared by at least one detected species, its weight equals 1, since $w_j = 1 - (1 - 1) \prod_{i \in I} (1 - \psi_i) = 1$, where species k has $w_j = 1$ (see Figure 1 in Jarzyna & Jetz 2016). In contrast, if an internal branch is shared by two undetected species, its weight will be $w_j < 1$. The functional (or phylogenetic) diversity, corrected for detection or 'true' $\overline{FD}$ is then calculated as $\overline{FD} = \sum_{j=1}^n L_j w_j$, where L_j is the length of branches j , and n is the total number of species in the assemblage considered ($I = n$ only at the root of the dendrogram; in any other case, $I < n$ because I represents the number of descendant species associated with a particular internal branch of the dendrogram; Jarzyna & Jetz 2016). In this way, undetected species contribute less than detected species to functional diversity. It is then possible to calculate what fraction of diversity has been detected through the detectability of biodiversity q , as $q = \frac{FD_{obs}}{\overline{FD}}$, where FD_{obs} is the functional diversity obtained from the observed species matrix (Jarzyna & Jetz 2016).

Although this approach has been novel for the discipline in explicitly incorporating detection into the estimation of functional diversity, it presents several conceptual and methodological problems: (1) the dendrogram tends to be a poor representation of the functional space, since it converts a continuous distance matrix into a discretized hierarchical structure (Maire et al. 2015, Villéger et al. 2017), (2) the dendrogram-based index is strongly influenced by species richness (Poos et al. 2009), (3) when an internal branch is shared by numerous undetected species and a single detected species, its weight equals 1, which causes an overestimation of functional diversity; and (4) the detection of multiple rare species can substantially inflate functional diversity estimates, owing to the discrepancy between the detection of a rare species ($w_j = 1$) and its occupancy probability ($w_j \ll 1$; Fig. 1). In addition, the weight of internal branches increases rapidly with the number of descendant species, such that branches shared by many taxa tend to reach values close to 1 even when individual occupancy probabilities are low. In Supplementary Material S1 we develop an original mathematical demonstration showing the strong dependence of internal branch weights on the number of descendant species that share them.

Finally, this approach combines philosophically distinct concepts by integrating, within a single metric, empirical information based on direct species

observation with probabilistic inferences about undetected species. Whereas observed species constitute empirical realizations of the assemblage, undetected species are latent entities whose presence is inferred through a statistical model. This mixture introduces a conceptual inconsistency, as it treats entities with different ontological status as equivalent, which can lead to ambiguous interpretations of estimated functional diversity.

Which is better: the occupancy probability or the latent process?

As an extension of the ideas of Jarzyna & Jetz (2016), Palacio et al. (2020) proposed calculating any functional diversity metric using the observed matrix, and replacing non-detections with their respective occupancy probabilities (or detection-corrected abundances if individual counts are used). Essentially, these values function as weights or substitutes for relative abundances in the analysis, which are combined with the functional trait matrix (Palacio et al. 2022). In practice, however, it is possible to use the occupancy matrix directly (e.g., Penjor et al. 2022), the latent-state matrix (true presences and absences; e.g., Si et al. 2017, Jones et al. 2021), or the observed matrix with non-detections replaced by their latent states (Fig. 2, Table 1). Although these approaches coexist in the literature, their implications for the estimation of functional diversity are rarely discussed explicitly, and there is no clear consensus on which one most adequately represents species occurrence in this context. This raises the following question: which values of w_j are most appropriate for correctly estimating functional diversity from passive acoustic data? To try to answer this question, it is first necessary to explore an occupancy model and its ecological interpretation in detail.

In a single-species occupancy model, z_i is the true latent occupancy state of the species at site i , which depends on the occupancy probability ψ_i :

$$z_i \sim \text{Bernoulli}(\psi_i)$$

If $z_i = 1$, the species is present; if $z_i = 0$, the species is absent. It is not directly observed, which is why it is called latent. The model links z_i to the detections y_{ij} as follows:

$$y_{ij}|z_i \sim \text{Bernoulli}(z_i p_{ij})$$

Where $y_{ij} = 1$ if the species was detected, or $y_{ij} = 0$ otherwise, and p_{ij} is the detection probability at site i and replicate j , given that the species is present. This last part is key to the model, since if the site is not

occupied ($z_i = 0$), then it necessarily cannot be detected ($y_{ij} = 0$). In other words, the model assumes there are no false positives. Conversely, if the site is occupied ($z_i = 1$), then y_{ij} can be 1 or 0, depending on the detection probability. It follows that, if a species was observed at least once at a site, then necessarily $z_i = 1$: if it was detected, it must have been present. This assumes demographic closure during the sampling period, that is, that the species' occupancy state does not change between temporal replicates (MacKenzie et al. 2017). In this way, the model does not estimate z_i when there are detections; in those cells $z_i = 1$ deterministically.

In this sense, the effect of detection will depend on the diversity metric used. For example, functional richness is usually estimated as the volume occupied by species in functional space (Mammola et al. 2021). Because this metric only takes extreme values into account, it always increases or remains the same, by definition, with the addition of new species. Furthermore, it is independent of the values of w_j (abundance, presence-absence, occupancy): if $w_j > 0$, the species is present and is assigned a value of 1; if $w_j = 0$, the species is considered absent and is assigned a value of 0. In the latent-state matrix, many cells are 0 because the model assigns presence or absence in binary form. In the occupancy matrix, however, even if the species was not observed, it can have an intermediate probability (e.g., 0.3 or 0.4) of being present. Thus, the occupancy matrix will always have

a greater number of occupied cells, resulting in higher functional richness values. Using a combination of detections with occupancy probabilities (Jarzyna & Jetz 2016) will give the same diversity value, since the number of occupied cells will be the same.

As mentioned above, detected species receive a maximum weight ($w_j = 1$), while undetected species are weighted with values $w_j < 1$. As a result, detected species can have a disproportionate influence on diversity indices, especially when combined with relatively low occupancy probabilities (Fig. 1). This is because detecting a species during sampling does not necessarily mean it has a high occupancy probability. This method therefore tends to over- or underestimate diversity values compared with those obtained by using the occupancy matrix directly. In contrast, when the latent-state matrix is used directly, detected species still receive maximum weight, but in addition, some undetected species can also receive maximum weights. It should be noted that the latent-state matrix is only one possible outcome of the assemblage, whereas the occupancy matrix represents the expected distribution of species presence in space, given the environmental covariates and the detection process (Guillera-Aroita et al. 2019). Therefore, calculating a functional diversity metric with the latent-state matrix estimates the functional diversity of the realized assemblage, representing one possible version of the assemblage of species that actually coexist at the site, given the environmental conditions and model uncertainty. Calculating an index with the occupancy probability matrix, in contrast, yields the expected or potential functional diversity of the assemblage, given the probability that each species occurs at the site. This produces more stable estimates and allows the average functional diversity to be compared across sites or conditions, without the noise of discrete realizations.

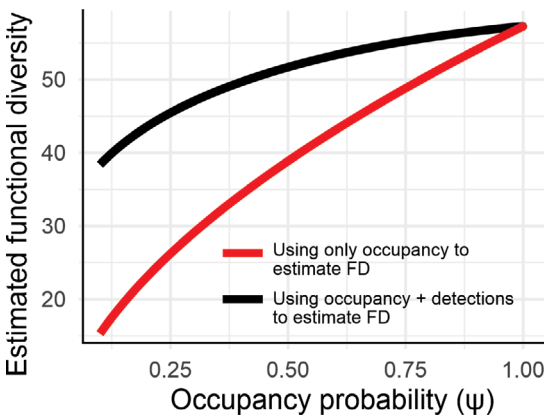


Figure 1. Effect of using the presence matrix for detected species and occupancy probability for undetected species in the estimation of functional diversity (Jarzyna & Jetz 2016 approach; black line) vs. using only occupancy probability (red line). Lines represent 1000 simulated values of functional diversity, derived from a dendrogram of 50 species and two traits with a normal distribution ($\mu_1 = 10$ y $\sigma_1^2 = 4$, $\mu_2 = 20$ y $\sigma_2^2 = 25$), calculated as $\widehat{FD} = \sum_{j=1}^n L_j w_j$, where L_j is the length of branch j , and n is the number of species in the assemblage. For each species in a given assemblage, a constant occupancy probability ψ was assumed (1000 values between 0 and 1), and a detection probability derived from a binomial distribution with $p = 0.7$. If many rare species are detected (low average occupancy probability), functional diversity will be strongly overestimated.

Furthermore, we mathematically demonstrate that, under the assumption of a constant occupancy probability among species, there is an analytical expression describing the relationship between occupancy probability and dendrogram-based functional diversity (Supplementary Material S1). This relationship is strictly monotonically increasing, indicating that as mean occupancy probability increases, so does expected functional diversity. Simulations show that, for assemblages with a moderate number of species ($n > 25$), the curve rapidly approaches an asymptotic value even at low occupancy probabilities ($\psi \approx 0.20$ – 0.25 ; Supplementary Material S1). This suggests that, even in small communities dominated by rare species,

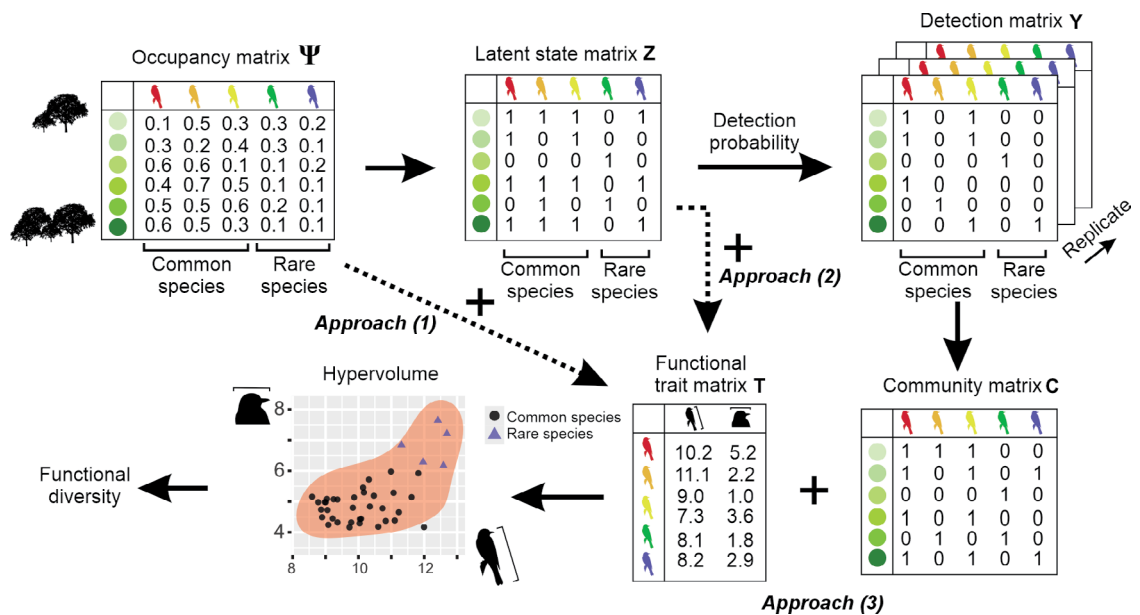


Figure 2. Workflow for simulating functional diversity under different approaches, explicitly accounting for imperfect detection.

Table 1. Description of the possible approaches for building the community matrix while explicitly accounting for detection in functional diversity studies. i = site, j = species, n = number of sites, J = number of species, ψ = occupancy probability, y = detection/non-detection, y^* = corrected detection/non-detection, z = latent state.

Approach for accounting for detection	Mathematical formulation	Type of information	Ecological interpretation	Main advantage	Main limitation
Using the occupancy matrix	$\Psi = [\psi_{ij}]_{n \times J}$	Probabilistic	Expected or probabilistic assemblage	Integrates occupancy uncertainty	Does not represent a realized community
Using the latent-state matrix	$Z = [z_{ij}]_{n \times J}$	Inferred binary realization	Realized or latent assemblage (a possible realization of the assemblage)	Represents a possible real community	Ignores posterior uncertainty
Combining the observed matrix with the occupancy matrix	$Y_\psi = [y^*_{ij}]_{n \times J}$ with $y^*_{ij} = \begin{cases} 1, & \text{if } y_{ij} = 1 \\ \psi_{ij}, & \text{if } y_{ij} = 0 \end{cases}$	Empirical observations + probabilities	Observed assemblage corrected for detection (probabilistic)	Preserves observed detections	Mixes observations with probabilities
Combining the observed matrix with the latent-state matrix	$Y_z = [y^*_{ij}]_{n \times J}$ with $y^*_{ij} = \begin{cases} 1, & \text{if } y_{ij} = 1 \\ z_{ij}, & \text{if } y_{ij} = 0 \end{cases}$	Empirical observations + inferred realization	Observed assemblage corrected for detection (realized)	Preserves observed detections and binary states	Mixes observations with inferred states

it is possible to obtain reasonably stable estimates of functional diversity using only the occupancy matrix.

Occupancy and functional diversity: coherence or circularity?

One of the ultimate goals of estimating functional diversity from passive acoustic monitoring is, in many cases, to link it with environmental gradients based on biological hypotheses. However, when building occupancy or abundance models, it is also common to incorporate environmental covariates. In practice, occupancy and detection are often modeled without including exactly the same environmental covariates that are later used to analyze their relationship with functional diversity. However, it is well known that bird species respond to environmental gradients, so failing to include these covariates in the occupancy model is expected to produce biased estimates of occupancy or abundance. This raises the question of whether it is methodologically appropriate to relate detection-corrected functional diversity estimates to the same covariates that were previously used to build the occupancy model. Conceptually, these covariates should be included because they are key determinants of species distribution and abundance; however, from a methodological standpoint, their inclusion could be interpreted as circular reasoning.

The key issue is that both occupancy and abundance of species depend on their response to the environment, and this response is usually mediated by their traits. When environmental covariates are not included in the occupancy model, they are treated as constant for each site and species. Functional diversity will therefore remain constant across any environmental gradient. Something similar will happen if covariates unrelated to the occupancy of the species are included, because such covariates do not generate substantial variation in occupancy probability. This can be seen by simulating the occurrence of multiple species under imperfect detection using a multi-species occupancy model (MSOM), in which the occupancy probability of each species depends on environmental covariates and species-level functional traits. For this, let us consider five species at 100 sites and three visits as a simulated case study. Let y_{ijk} be the detection at site i ($i = 1, \dots, 100$) of species j ($j = 1, \dots, 5$) during visit k ($k = 1, 2, 3$). We model detection conditional on the latent occupancy state z_{ij} :

$$y_{ijk} \sim \text{Bernoulli}(z_{ij}p_j),$$

where p_j is the detection probability of species j . We model the latent occupancy state as: $z_{ij} \sim \text{Bernoulli}(\psi_{ij})$.

We model the occupancy probability ψ_{ij} on the logit scale as a function of an environmental covariate x_i (e.g., building cover):

$$\text{logit}(\psi_{ij}) = \alpha_j + \beta_j x_i$$

where α_j is the species-specific intercept for species j , and β_j describes the response of species j to the environmental gradient, representing a continuous urbanization gradient. The covariate was simulated from a uniform distribution between 0 and 1. To link the species-specific responses to the environmental variable with functional traits, we modeled the coefficients β_j as a linear function of three continuous traits (Ovaskainen & Abrego 2020), representing relevant ecological axes (for example, degree of frugivory, body size, and habitat specialization):

$$\beta_j = \gamma_1 T_{j1} + \gamma_2 T_{j2} + \gamma_3 T_{j3}$$

where T_{jr} is the standardized value of functional trait r ($r = 1, \dots, 3$) for species j and γ_r quantifies how trait r modulates the occupancy response to the environmental gradient. Traits were generated as independent, standardized normal variables ($\mu = 0, \sigma = 1$), and were arranged in a T matrix of dimension species $\times$ traits. Contrasting values were set for the trait coefficients, such that the first and second traits had a negative effect on the response to urbanization ($\gamma_1 = -2, \gamma_2 = -1.5$), and the third trait (specialization) had no effect ($\gamma_3 = 0$). This parameterization generates species with positive, negative, or null responses to the environmental gradient, depending on their combination of functional traits. The occupancy intercepts were assumed constant, with $\alpha_j = -0.5$ for all species. Finally, the detection probability p was assumed constant per species, with a uniform distribution between 0 and 1. All parameter values were chosen to represent a simple, realistic scenario, with species exhibiting positive, negative, or null responses to the environmental gradient and a wide range of detection probabilities. The model was fitted in a Bayesian framework using Markov chain Monte Carlo (MCMC), implemented in the *spOccupancy* package (Doser et al. 2022). We used the package's default weakly informative priors for all community-level parameters (μ, σ, γ). These priors were chosen to exert minimal influence on the posterior estimates, allowing inference to be driven primarily by the simulated data. Using functional richness (the volume occupied by assemblages in functional space) as the diversity metric, the simulation shows a decrease in functional diversity with increasing building cover (Fig. 3A). At sites with low cover, the effect of the environmental gradient on occupancy was weak, resulting in similar occupancy probabilities among

species and relatively homogeneous occupancy of the functional space. At these sites, functional diversity was high (Fig. 3A). In contrast, at sites with high building cover, interspecific differences in response to the environment were accentuated: species with positive responses reached occupancy probabilities close to one, whereas those with negative responses showed probabilities close to zero (Fig. 3A). This pattern produced environmental filtering, giving rise to functionally redundant communities with lower functional diversity — a phenomenon widely observed in urban areas (Crocì et al. 2008, Silva et al. 2016, Evans et al. 2018, Palacio et al. 2018). In a model without covariates, or with other covariates unrelated to functional richness, there is by contrast no clear pattern between building cover and functional diversity (Fig. 3B). The analysis is thus structured at two levels: on the one hand, how species respond to the environment (through their functional characteristics) is evaluated; on the other, how communities as a whole respond to environmental conditions. Modeling occupancy and functional diversity using the same environmental covariates therefore does not constitute circular reasoning, but is instead ecologically coherent, since it explicitly links species distribution with their functional traits and with diversity, giving rise to ecologically testable predictions.

How does detection affect functional diversity? A simulation

To analyze the effect of detection on the estimation of functional diversity derived from potential passive acoustic monitoring, we simulated 100 assemblages of 40 species under a multispecies occupancy model (Devarajan et al. 2020) with three sampling replicates per site, distinguishing 35 common species and five rare ones. For each site we generated an environmental covariate (forest cover) and modeled occupancy with species-specific effects, assigning rare species a positive response to forest and low occupancy and detection probabilities, while common species showed more variable responses (Davis et al. 2023, Fontana et al. 2025) and moderate detection. From the latent presence process and the simulated detections, we built an observed community matrix. We further simulated two continuous functional traits per species, assigning more central values to common species and more extreme values to rare ones, so that the latter showed greater functional originality (Leitão et al. 2016, Affleck et al. 2020, Loiseau et al. 2020). In this way, common species had higher occupancy and detection probabilities, as well as more central trait values within the functional space. In contrast, rare or specialist species showed low occupancy and detection probabilities, together with more extreme or original traits, more realistically reproducing the

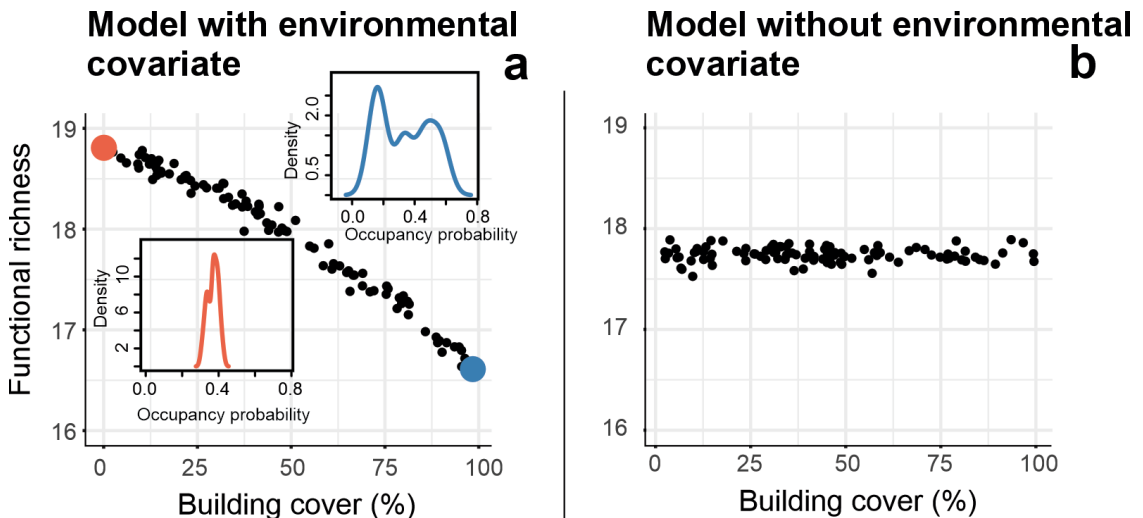


Figure 3. Effect of using the same environmental covariate to estimate occupancy and to relate it to detection-corrected functional diversity. Each point represents a hypothetical assemblage of five species and three simulated functional traits. The curves represent density plots of occupancy in assemblages at low- and high-cover sites. When the same environmental covariate is used (A), a pattern of functional diversity consistent with environmental filtering is recovered. The colored points and density curves show two extreme scenarios, one with low building cover (red) and one with high cover (blue). Not including the covariate to estimate occupancy produces a constant relationship between functional diversity and the environmental gradient (B).

structure and functional heterogeneity typical of bird assemblages in many terrestrial systems (Jarzyna & Jetz 2016, Palacio et al. 2020, 2022). Using the occupancy (Ψ), latent state (Z), community (C), and functional trait (T) matrices, we estimated functional diversity indices (richness, regularity, and divergence) using probabilistic hypervolumes (Mammola & Cardoso 2020). Although numerous approaches exist for estimating functional diversity in the literature (Mammola et al. 2021), we used the same approach to calculate different metrics so that they would be comparable (Mammola et al. 2021, Palacio et al. 2022). We then fitted a multispecies occupancy model in a Bayesian framework using *spOccupancy* (Doser et al. 2022), and combined different estimated and observed matrices with the functional traits to calculate the indices and compare them with population values using the root mean square error (RMSE) as an estimator of overall bias and dispersion (a lower value indicates greater accuracy). The detailed workflow, along with the parameters used, is provided in Supplementary Material S2. The code used to perform the simulations is available at <https://github.com/facucpalacio/diversidad-funcional-y-deteccion>

When comparing the simulation results across the different approaches, we found that RMSE was lowest when the occupancy matrix was used to estimate all three functional diversity metrics (with deviations of 3.0–4.6% from the functional diversity values estimated from population occupancy probabilities), and highest when the observed matrix was used (with deviations of 19.6–37.0% from the functional diversity values estimated from population occupancy probabilities; Table 2). This was expected, since the simulations were based on known population occupancy probabilities. The approach based on combining the observed matrix with the occupancy matrix yielded RMSE values comparable to those obtained using the occupancy matrix alone (with deviations of 3.5–5.5% from the functional diversity values estimated from population occupancy probabilities), consistently across metrics (Table 2). In contrast, using the latent-state matrix, either alone or combined with the observed matrix, produced considerably larger RMSE values (with deviations of 19.5–42.7% from the functional diversity values estimated from population occupancy probabilities; Table 2). Regarding functional diversity metrics, richness and regularity were much more sensitive to not incorporating detection (35.7 and 37.0%, respectively, relative to the functional diversity values estimated from population occupancy probabilities) than divergence (19.6%).

However, biodiversity detectability q (observed functional diversity / estimated functional diversity) was relatively high and similar whether the observed matrix or the observed-plus-occupancy matrix was used, for richness ($q = 0.96$ in both cases) and divergence ($q = 0.95$ and 0.96 , respectively), indicating a good representation of the assemblage's functional diversity, but overestimated in the case of regularity ($q = 1.51$ in both cases). Using the latent-state matrix, whether alone or combined with the observed matrix, produced a systematic overestimation of functional diversity across all metrics analyzed ($q = 1.06$ – 1.32).

Empirical example

To illustrate the empirical application of the approaches presented, we developed a case study at the 'El Destino' Private Reserve (35°08'S, 57°25'W) and the private ranch 'Lomas Overas' (35°09'S, 57°23'W), Magdalena district, northeastern Buenos Aires province. The reserve lies within a matrix of natural grasslands dominated by native species such as *Nassella* sp., *Paspalidium* sp., and *Leersia hexandra*, with sectors dominated by *Baccharis* sp. shrubs. Within this matrix are remnant patches of native forest known as '*talares*', dominated by *Tala* (*Celtis tala*) and Coronillo (*Scutia buxifolia*; Arturi & Goya 2004). The area also has a strong presence of exotic tree species in plantations (*Eucalyptus*, *Fraxinus*, *Cupressus*, *Platanus*, *Populus*, and *Quercus*), with sectors heavily invaded by Glossy Privet (*Ligustrum lucidum*), whose expansion has profoundly modified the structure and dynamics of the *talares*, giving rise to nearly monospecific forests up to 20 m tall, known as '*ligustrales*' (Franco et al. 2018). The climate is humid temperate, with a mean annual temperature of 16 °C and annual rainfall close to 1000–1030 mm.

Between 28 September and 8 October 2025, we conducted continuous passive acoustic monitoring of birds ($n = 10$ days) using two automated recorders (Audiomoth v1.2.0), placed at least 1.25 km apart and mounted at a height of 1.5 m, one in a *ligustral* and the other in a *talar*. The devices recorded for 10 consecutive days in 10-minute cycles every 10 minutes, from 19:00 h to 9:30 h, in mono format (*wav*), with a sampling frequency of 48 kHz, 16-bit resolution, and medium gain (Sedláček et al. 2015, Moreno-Gómez et al. 2019). Files were stored on 32 GB memory cards. Recordings were processed by the three authors through listening and spectrogram visualization using the software Kaleidoscope Pro v. 5.4.7 (Wildlife Acoustics Inc. Maynard, MA, USA) and Raven Pro v. 1.6.5 (K. Lisa Yang Center for Conservation Bioacoustics at the

Cornell Lab of Ornithology). Species identification was carried out by the three authors; for the few cases in which vocalizations could not be recognized (three species), BirdNET (Kahl et al. 2021) was used as a complementary tool and, subsequently for validation, Xeno-canto (www.xeno-canto.org).

The data consisted of detections/non-detections for $S = 40$ species. Each sampling ‘day’ (total recordings from 19:00 to 9:30 h) was treated as an independent sampling unit (in combination with the recorder used), and was subdivided into $K = 44$ temporal replicates of 10 minutes each ($k = 1, \dots, 44$). In total, $D = 20$ sampling units were considered (‘site’ = recorder $\times$ day = 20). Species rarefaction curves for each recorder are shown in Supplementary Material S3. In the recorder located in the *talar* we identified 52 species, representing 84% of the estimated asymptotic richness (62.1 species). In the recorder located in the *ligustral* we identified 24 species, corresponding to 92% of the estimated asymptotic richness (26.2 species). We modeled occurrence using a multispecies occupancy model, in which occupancy was modeled as:

$$z_{jd} \sim \text{Bernoulli}(\psi_{jd}).$$

Daily occupancy probability was modeled on the logit scale as:

$$\text{logit}(\psi_{jd}) = \beta_{0j} + \beta_{1j} \text{Habitat}_d + \beta_{2j} \text{Date}_d,$$

where β_{0j} is a species-specific intercept, β_{1j} and β_{2j} represent the species-specific additive effect of habitat type (0 = *ligustral*, 1 = *talar*) and sampling date on daily occupancy. The observations y_{jdk} of species j on day and recorder d and replicate k were modeled conditional on true presence:

$$y_{jdk} \sim \text{Bernoulli}(z_{jd} p_{jdk}),$$

where z_{jd} is the daily latent occupancy state, and p_{jdk} is the detection probability conditional on presence. Detection may depend on whether the species was detected in the preceding 10 min; we therefore included a categorical covariate indicating whether

species j was detected in the preceding interval within the same day (y_{jdk-1} ; 0 = not detected, 1 = detected; Lloyd et al. 2019). For the first replicate of the day, this covariate was set to zero. Detection was thus estimated as:

$$\text{logit}(p_{jdk}) = \gamma_{0j} + \gamma_{1j} \sin(\text{Hour}_{dk}) + \gamma_{2j} \cos(\text{Hour}_{dk}) + \gamma_{3j} \text{Precipitations}_{dk} + \gamma_{4j} y_{jdk-1}$$

where γ_{0j} is a species-specific intercept, γ_{1j} , γ_{2j} and γ_{3j} represent species-specific additive effects of sampling time and the presence of rainfall (0 = absence, 1 = presence), and γ_{4j} quantifies the effect of detection in the preceding 10-min interval on the current detection probability. We included time of day as circular variables (sine and cosine functions) to model daily cyclical variation in detection. The parameters γ_{0j} , γ_{1j} , γ_{2j} , γ_{3j} , γ_{4j} , β_{0j} , β_{1j} and β_{2j} were assumed to be drawn from community-level hierarchical normal distributions, and non-informative priors were used for the means and variances of the hyperparameters at the community level. The model was fitted in a Bayesian framework with the *rjags* package (Plummer 2025), using three MCMC chains, 20,000 iterations per chain, a ‘burn-in’ period of 5000 iterations, and a ‘thinning’ interval of 10. It should be noted that, although the analysis included 20 sampling units (recorder $\times$ day), these do not constitute independent spatial replicates, since days recorded by the same recorder share the same location and, therefore, a fraction of the spatial variation (see Discussion).

We used bird traits known for their relevance to ecosystem functions, including pollination, arthropod control, seed dispersal, and waste removal (Luck et al. 2012), from the EltonTraits database (Wilman et al. 2014): mean body mass, percentage of diet items (invertebrates, vertebrates, fruit, nectar, seeds), and percentage of foraging strata used (ground, understory, mid-high, canopy, air). These functional traits are commonly used as indicators of ecosystem functions in studies of avian functional diversity. Body mass is associated with metabolic rate and foraging

Table 2. Simulations showing how different approaches for building the community matrix, while explicitly incorporating detection, approximate functional diversity based on population occupancy probabilities. Root mean square error values are shown (see ‘How does detection affect functional diversity? A simulation’). C: detection or observed matrix, $\hat{\Psi}$: occupancy matrix (derived from the multispecies occupancy model), $\hat{Z}$: latent-state matrix (derived from the multispecies occupancy model). Root mean square error values and the standard deviation of the errors (in parentheses) are reported.

Functional diversity metric	C	$\hat{\Psi}$	C + $\hat{\Psi}$	$\hat{Z}$	C + $\hat{Z}$
Richness	4.52 (4.41)	0.59 (0.37)	0.72 (0.42)	4.13 (0.77)	3.71 (1.20)
Regularity	0.25 (0.07)	0.01 (0.01)	0.02 (0.01)	0.21 (0.02)	0.18 (0.05)
Divergence	0.38 (0.35)	0.09 (0.06)	0.10 (0.06)	0.38 (0.11)	0.35 (0.12)

behavior. Diet reflects nutrient flow, pest control, pollination, and seed dispersal (Whelan et al. 2008). Foraging substrate, in turn, influences resource use, spatial distribution, and segregation among species searching for different types of food, and affects vegetation composition and structure through pollen and seed dispersal (Luck et al. 2012). Of the total species recorded during monitoring, we excluded those that mainly occupy open or aquatic environments (representatives of the families Tinamidae, Ardeidae, Anatidae, Anhimidae, Charadriidae, and Scolopacidae, and some members of the family Icteridae), as well as individuals that were merely flying overhead.

Over the 10 days of monitoring, we recorded a total of 3437 detections and 68 species from 28 families. In the *ligustral* we recorded 936 detections of 31 species, while in the *talar* we had more than double the number of detections (2501) of 58 species. In the *ligustral*, the dominant species were Grey-cowled Wood Rail (*Aramides cajaneus*, 122 detections), Picazuro Pigeon (*Patagioenas picazuro*, 114 detections), Rufous-bellied Thrush (*Turdus rufiventris*, 107 detections) and Golden-crowned Warbler (*Basileuterus culicivorus*, 99 detections), while in the *talar* the dominant species were Rufous-collared Sparrow (*Zonotrichia capensis*, 145 detections), Rufous Hornero (*Furnarius rufus*, 136 detections) and Southern House Wren (*Troglodytes musculus*, 125 detections). The multispecies occupancy model showed adequate convergence ($\hat{R}$ maximum = 1.05). At the community level, detection probability was influenced by environmental and temporal variables. In particular, the presence of rainfall showed a negative relationship with detection (Fig. 4a), while activity showed a marked daily pattern, with a peak around 8:30 h and a smaller peak of activity around 19:00 h (Fig. 4a and b). In addition, prior detection of a species in previous recordings increased the probability of detecting it again (Fig. 4a). Regarding occupancy, habitat type influenced species' probability of presence. On average, occupancy was 40.73% higher in the *talar* than in the *ligustral* (Fig. 4c). In contrast, sampling date had no relevant effect on daily occupancy (Fig. 4c). At the species level, responses to habitat type were heterogeneous (Fig. 4d), and several species were recorded exclusively or almost exclusively in one of the two environments. For example, White-necked Thrush (*Turdus albicollis*, 47 detections), Chestnut-backed Tanager (*Stilpnia preciosa*, 21 detections), Chivi Vireo (*Vireo chivi*, 20 detections) and Euler's Flycatcher (*Lathrotriccus euleri*, 9 detections) were detected only in the *ligustral*. In contrast, species such as Rufous Hornero, Southern House

Wren, White-crested Tyrannulet (*Serpophaga subcristata*, 91 detections), Common Starling (*Sturnus vulgaris*, 91 detections), Red-crested Cardinal (*Paroaria coronata*, 79 detections) and Tufted Tit-Spinetail (*Leptasthenura platensis*, 51 detections) were detected only in the *talar*. This was also clearly reflected in the site-by-species occupancy matrix: species frequently detected in a single habitat type had high occupancy probabilities in that environment (typically > 0.95), and low probabilities in the other (typically < 0.05). This had important consequences for the estimation of functional diversity, since the observed matrix was very similar to the latent-state matrix, as a result of the marked differences in occupancy probabilities between habitats.

Regarding functional richness and divergence, we did not detect significant differences between the two habitat types for any of the approaches ($t = -1.59$ – 1.83 , all p 's > 0.05). In contrast, observed functional regularity was significantly higher in the *ligustral* ($t = 12.57$, $p < 0.00$). This same pattern was observed when using the latent-state matrix ($t = 20.14$, $p < 0.0001$) and the matrix combining the observed and latent-state matrices ($t = 23.57$, $p < 0.0001$). However, using the occupancy matrix or the observed matrix combined with the occupancy matrix showed no differences between the two environments ($t = -0.40$ – 0.65 , $p = 0.53$ – 0.59). Despite the marked differences in richness and species composition, these results suggest that there are no major differences in functional diversity between the two habitat types. The lower number of species in the *ligustral* appears to be compensated for by the presence of species that tend to be located toward the extremes of the functional space (Fig. 5). When analyzing the structure of the functional space, the *talar* appears dominated by small-bodied species (mainly Passeriformes) that forage on invertebrates in the understory and canopy (e.g., Southern House Wren, Rufous-collared Sparrow, Red-crested Cardinal, White-crested Tyrannulet, and Tufted Tit-Spinetail). In contrast, the *ligustral* is dominated by species that feed in the mid-story and canopy (e.g., Golden-crowned Warbler; Rufous-browed Peppershrike, *Cyclarhis gujanensis*; Narrow-billed Woodcreeper, *Lepidocolaptes angustirostris*), together with larger species that forage on the ground (e.g., White-tipped Dove, *Leptotila verreauxi*; Grey-cowled Wood Rail). Therefore, the differences between the two habitat types appear to occur at the level of functional composition rather than diversity.

Mean per-site biodiversity detectability was relatively high for all three metrics ($q = 0.93$ – 1.00),

regardless of the approach used, although it was slightly lower in the case of functional regularity ($q = 0.93\text{--}0.99$). However, for a given metric and approach, considerable variability was observed between days, with cases of both underestimation and overestimation. For example, in occupancy-based functional richness, detectability of biodiversity ranged between 0.88 and 1.14, while for functional regularity it ranged

between 0.82 and 1.09. Functional divergence, in turn, was the metric least influenced by the approach ($q = 0.94\text{--}1.07$). However, in no case did we detect substantial correlations between the measures of detectability of biodiversity derived from the observed matrix and those derived from the occupancy matrix ($r = -0.28\text{--}0.13$). In contrast, using the latent-state matrix yielded strong positive correlations ($r = 0.83\text{--}0.97$),

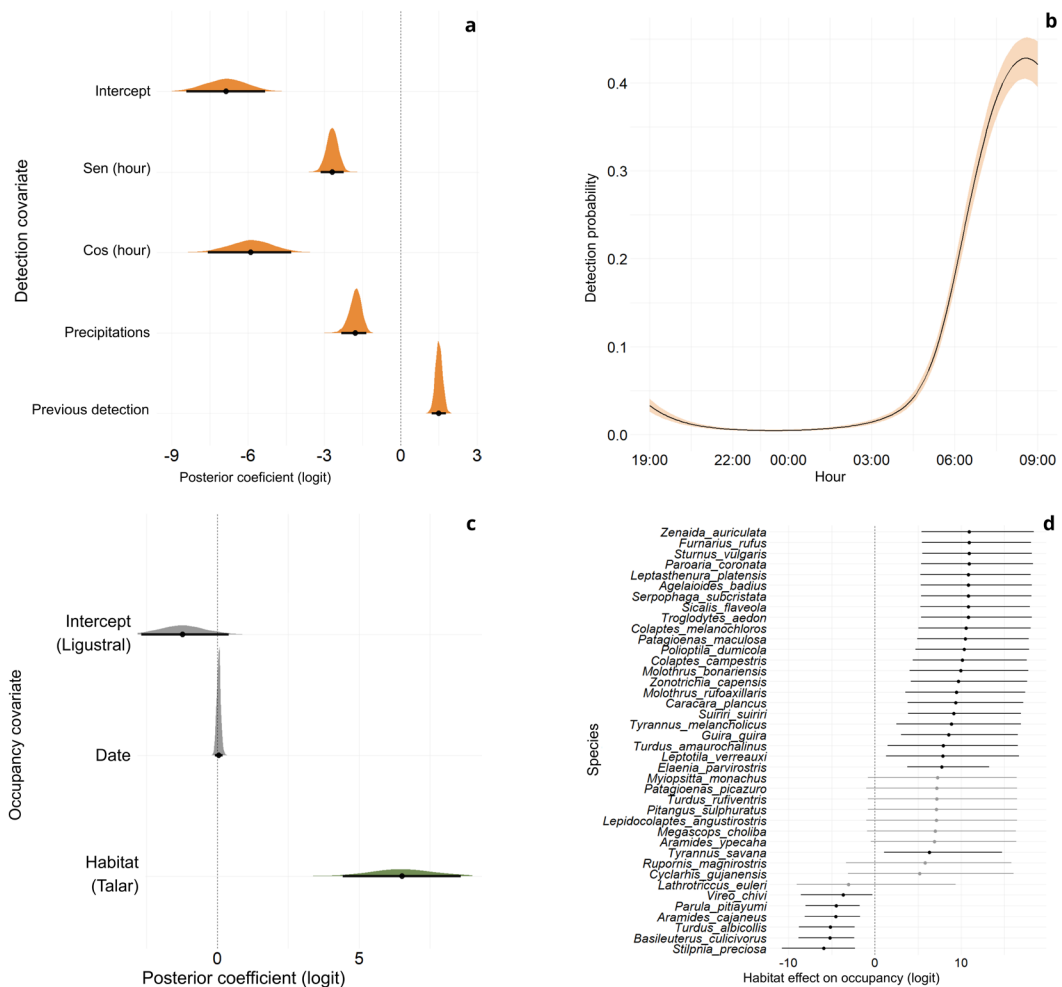


Figure 4. Multi-species occupancy model results. (a) Community-level posterior distribution of the detection coefficient (logit scale). Shaded areas represent posterior densities, points indicate means, and horizontal lines show 95% credible intervals. (b) Relationship between detection probability and sampling time; the solid line represents posterior predictions and the shaded bands show 95% credible intervals. (c) Community-level posterior distribution of the occupancy coefficient (logit scale). Shaded areas represent posterior densities, points indicate means, and horizontal lines show 95% credible intervals. (d) Species-specific responses to habitat type (ligustral vs. talar); points indicate means and horizontal lines show 95% credible intervals.

as a consequence of the marked differences in occupancy probabilities between habitats. Together, these results show that higher observed functional diversity does not necessarily translate into higher detectability of biodiversity.

DISCUSSION

Passive acoustic monitoring (PAM) is becoming an increasingly widely used tool for studying and monitoring bird communities. Because many species are highly vocal, the use of autonomous recorders makes it possible to record a substantial proportion of the community without requiring the constant presence of observers in the field, which helps reduce observer-associated bias and standardize sampling protocols (Darras et al. 2018, 2019, Knight et al. 2026). In this context, PAM represents a promising tool for improving species detection, assessing changes in community composition, and strengthening long-term bird monitoring programs.

In the particular case of functional diversity analysis, PAM offers several relevant advantages. First, it facilitates the detection of rare, cryptic, or hard-to-observe species (Scheffer et al. 2026), which tend to occupy particular positions within the functional space by performing distinctive or less redundant ecosystem functions. It also allows recording at times that, for safety, logistical, or practical reasons, would not be easy to carry out in person, such as nocturnal surveys. For example, in our case we detected three species of nocturnal raptors: Tropical Screech Owl (*Megascops choliba*, 18 detections), American Barn Owl (*Tyto furcata*, 3 detections) and Striped Owl (*Asio clamator*, 1 detection). Since daily activity pattern (diurnal/nocturnal) is often used as a functional trait, the inclusion of these species expands the volume of the functional space, leading to a better characterization of diversity. However, rare or cryptic species do not always present unique or distinctive functional traits. For example, species considered rare for the study area, such as White-necked Thrush (Scheffer et al. 2026) and Chestnut-backed Tanager (Malagisi & Quintela 2019), were located near the centroid of the functional space, while common species such as Narrow-billed Woodcreeper and Rufous-browed Peppershrike were located at its extremes, owing to their particular morphological and ecological characteristics. On the other hand, PAM allows for a considerably greater sampling effort per sampling unit compared with traditional surveys (hours of recording versus minutes of direct observation) and tends to contribute to a better representation of community

functional space (Kümmet et al. 2025, Doohan et al. 2026). However, although PAM reduces the bias associated with imperfect species detection by incorporating occupancy probabilities, the functional representation of the acoustic assemblage continues to depend on limitations inherent to acoustic sampling, such as differences in vocal activity among species.

Second, PAM offers the possibility of explicitly incorporating detection probability into the estimation of this diversity component through occupancy models (Jarzyna & Jetz 2016, Palacio et al. 2020). This makes it possible to separate the ecological process of interest (occupancy or the true presence of species) from the observation process, since the probability of detecting a species during a visit is rarely equal to one and can vary with factors such as time of day or weather conditions (MacKenzie et al. 2017, Devarajan et al. 2020). Ignoring this variation implies assuming perfect detection, which can bias presence estimates and, consequently, diversity metrics (Jarzyna & Jetz 2016). In this way, incorporating detection improves both the ecological interpretation of results and the predictive capacity of the model. Although the possibility of incorporating imperfect detection is not exclusive to PAM, this methodology allows a large number of replicates to be considered to correct occupancy estimates for detectability with relatively little effort, compared with more traditional surveys such as point counts and transects (Rhinehart et al. 2026). Nevertheless, defining temporally independent replicates requires careful evaluation, since consecutive recording intervals may show autocorrelation in detection. In our empirical study, for example, detection in the previous interval had a positive effect on detection probability, showing that consecutive 10-minute intervals do not necessarily constitute independent replicates. In these cases, sampling days may be considered more appropriate replicate units, while within-day temporal variation can be modeled explicitly through covariates or temporal dependence structures. We therefore recommend explicitly evaluating temporal independence among replicates (e.g., through temporal autocorrelation in detections) before defining the sampling unit used in occupancy models.

When estimating a functional diversity index, there are different alternatives for building the community matrix on which the calculations are based. Some initial approaches proposed combining observed detections with estimated occupancy probabilities for undetected species (Jarzyna & Jetz 2016, Palacio et al. 2020). Our simulations show that

using the observed matrix can produce substantial bias compared with using the occupancy matrix. As Jarzyna & Jetz (2016) point out, using the observed matrix is not necessarily a problem in itself, since the same ecological patterns could be detected if detection probability varied constantly along an environmental gradient. However, this condition can rarely be assumed a priori and can only be evaluated by explicitly considering the effect of detection on the estimate. Therefore, although we do not question the use of observed matrices in functional diversity studies, we recommend that, whenever possible, they be corrected for imperfect detection, especially when using PAM. In this sense, we argue that it is important to strike a balance between sampling effort and the time required for analysis. Our results show that intensive monitoring (44 replicates per day) markedly increases the ability to adequately characterize different dimensions of functional diversity. In such cases, biases are considerably reduced, and consequently the observed data matrix may be sufficient to describe functional diversity. We do not, under any circumstances, recommend using the model-derived latent-state matrix, because it represents only one possible realization of the assemblage. The occupancy matrix, by contrast, offers a more appropriate representation of the expected distribution of species in space, by incorporating both environmental information and the detection process affecting observations. Although until a few years ago implementing multispecies occupancy models used to be arduous, their use has become increasingly accessible in recent years, thanks to the

development of statistical packages and computational tools that facilitate their implementation (Doser et al. 2022, Kellner et al. 2023).

Third, the recordings obtained make it possible to characterize the vocalizations of the different species detected and to extract, from the spectrograms, various acoustic variables that could be used as acoustic functional traits in the estimation of functional diversity. Although some studies have begun to incorporate acoustic traits to estimate functional diversity metrics (Moreno-Contreras et al. 2019, Prieto-Torres et al. 2021, Schillé et al. 2024), their use is still relatively scarce and it is not yet entirely clear how they relate, directly or indirectly, to specific ecosystem functions. In this context, characterizing an acoustic functional space in bird assemblages opens new opportunities to explore its relationship with other, more commonly used functional dimensions, such as morphology, diet, or foraging behavior. In the future, we plan to make use of the recordings obtained to build this acoustic functional space and evaluate its congruence and complementarity with other functional dimensions, to determine whether it provides novel information for understanding the structure and functioning of bird communities.

One limitation of our empirical case study is that sampling was carried out using only two autonomous recorders, one per habitat type, with each recording day treated as an independent sampling unit. Consequently, the replication obtained mainly represents temporal variation within each environment

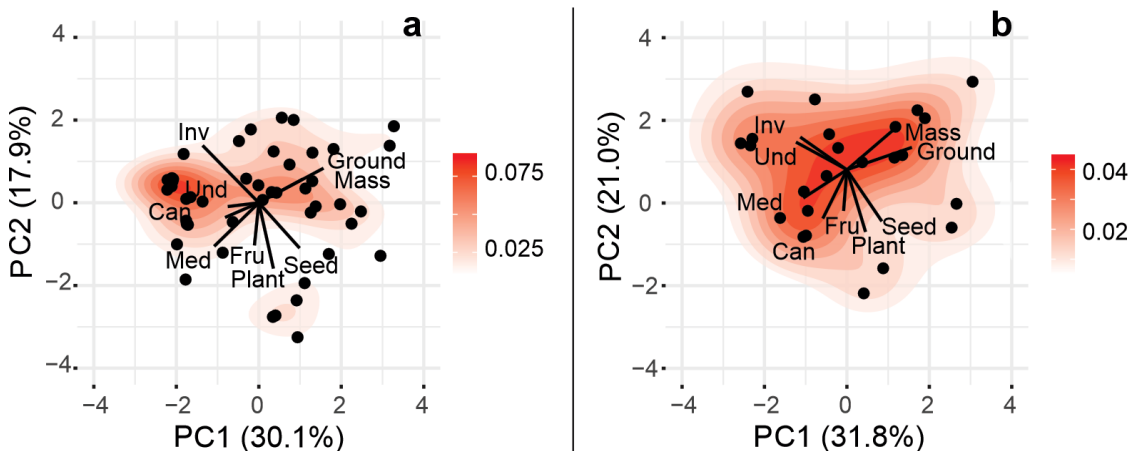


Figure 5. Functional spaces of the talar (a) and the ligustral (b) based on principal component analysis applied to the species-by-functional-trait matrix. Shaded areas represent kernel densities, vertical bars represent density values, and points represent the species detected in each habitat type. Percentages of variation explained by each principal component (PC) are shown. The color scale represents species density. Mass: body mass, Inv: proportion of invertebrates in the diet, Fru: proportion of fruit in the diet, Seed: proportion of seeds in the diet, Plant: proportion of other plant-derived items in the diet, Ground: proportion of ground use during foraging, Und: proportion of understory use during foraging, Med: proportion of mid-story use during foraging, Can: proportion of canopy use during foraging.

rather than spatial replication across multiple *talar* and *ligustral* patches. Although species accumulation curves showed values close to the asymptote (Supplementary Material S3), the observed differences between habitats should be interpreted with caution. However, independent analyses based on 106 point counts distributed across both environments (53 per environment) show ecological patterns consistent with those observed from the recordings (Palacio, unpubl. data), suggesting that the results obtained are not exclusive to the sites sampled. Since the main objective of this work was to evaluate how incorporating detectability affects estimates of functional diversity derived from acoustic data, this design allowed us to generate an intensive dataset, adequately replicated over time, to illustrate these methodological issues.

An aspect that deserves greater attention in future studies is intraspecific variation in acoustic traits. Traditionally, functional diversity has been quantified using the arithmetic mean of traits for each species, under the assumption that variation among species is considerably greater than variation among individuals of the same species (Albert et al. 2012, Violle et al. 2012). However, in recent years this approach has been widely questioned, since intraspecific variation can represent a substantial fraction of total functional variation, and its omission can bias estimates of functional diversity and the ecological inferences derived from them (Palacio et al. 2025). In the case of acoustic traits, the structure of vocalizations can vary among individuals, populations, sexes, ages, and behavioral contexts (e.g., Mates et al. 2015, Sementili-Cardoso et al. 2018, Smeele et al. 2025, Pérez-Granados et al. 2026), so incorporating this variability could improve the estimation of acoustic functional diversity and contribute to a more mechanistic understanding of the patterns detected through ecoacoustic approaches. Although this aspect is beyond the scope of the present study and has still been scarcely explored in the context of acoustic functional diversity, it represents a promising line of research for future work.

Finally, although automated bioacoustic classifiers have greatly expanded the ability to process large volumes of recordings and can achieve good levels of accuracy for individual species, their performance at the assemblage scale still has limitations. Several studies show that false-positive and false-negative rates vary considerably among species and contexts, generating interspecific differences in detectability and potentially biased detection matrices (Goodman et al. 2025, Winiarska et al. 2025, Meliane et al. 2026).

For example, in controlled experiments with 43 European species, BirdNET showed large interspecific differences in detectability; some common species were not detected at all under realistic conditions, while others were detected accurately (Winiarska et al. 2025). In a comparison between human observers and Merlin Bird ID, observers detected 72% more individuals than Merlin Bird ID and had slightly higher accuracy (92 vs. 86%), while the app produced some false positives and showed inconsistencies between devices, although it also managed to detect some species that observers did not record (Goodman et al. 2025). In our particular case, only a few species that we had initially been unable to recognize were identified using BirdNET from the recordings (e.g., Sharpshinned Hawk, *Accipiter striatus* and Chestnut-backed Tanager). In most cases, however, vocalizations could not be identified or yielded relatively low confidence levels (0.3–0.4). Even common species were not identified on numerous occasions, presumably due to the low volume of the recorded vocalizations. These discrepancies may arise both from limitations inherent to acoustic sampling (for example, low-intensity or infrequent vocalizations) and from automatic classification errors. Collectively, these factors can translate into underestimation or overestimation of certain species, affecting estimates of richness, composition, and functional diversity. Consequently, results obtained through automated identification should be interpreted with these potential sources of error in mind and, whenever possible, complemented with manual validation procedures (Knight et al. 2017, Pérez-Granados 2023).

ACKNOWLEDGMENTS

We thank Claudia Gómez Martínez and Alejandra Gómez for logistical support within the ‘El Destino’ Private Reserve, and Mauricio Earnshaw for logistical support provided within the ‘Lomas Overas’ ranch. We thank Lucía Montesana, Natalia García, and two anonymous reviewers for their detailed and careful reviews, which substantially improved our manuscript.

FUNDING

FXP received funding from the American Ornithological Society (Kessel Research Fellowship 2023) and from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

ETHICAL PERMITS

Research within the 'El Destino' Private Reserve was carried out under a permit granted to FXP by the Ministerio de Ambiente de la Provincia de Buenos Aires, Argentina (DISPO-2022-116-GDEBA-DAPMAMGP).

USE OF ARTIFICIAL INTELLIGENCE

The authors used artificial intelligence tools solely during manuscript preparation. These tools were used to improve the writing and style of the text, assist with formatting the bibliography, and help develop and debug fragments of R code used for data processing and analysis. No artificial intelligence tools were used for study design, data collection, the generation or interpretation of results, or the formulation of conclusions. All results, interpretations, and the final content of the manuscript were reviewed and validated by the authors, who assume full responsibility for its content.

SUPPLEMENTARY MATERIAL

You can access the supplementary material for this article by visiting the link <https://doi.org/10.56178/eh.v41i2.1550>.

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