Does accounting for within-individual trait variation matter for measuring functional diversity?

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ARTICLE INFO

ABSTRACT

Trait-based approaches to disentangle assembly processes in ecological communities typically rely on average trait values obtained from the literature or databases. Recently, ecologists have shown growing concern in accounting for intraspecific variation in trait-based metrics. Besides intraspecific variation, plants and animals exhibit functional trait variation within the same individual (within-individual variation), which may exceed intraspecific variation and constitute a functional trait itself, influencing ecosystem functioning through individual performance variation. However, the role of within-individual variation in functional diversity (FD) remains unexplored. Here, we used sequential foraging observations of four bird species to quantify the magnitudes of interspecific, intraspecific and within-individual functional trait (foraging item, maneuver and stratum) variation. Then, we estimated functional richness using different hierarchical levels of increasing data resolution: (1) average trait values (based on our own literature search, on a global dataset, on the first observation of each foraging sequence and on complete foraging sequences), (2) average trait values plus intraspecific trait variation, and (3) average trait values plus intraspecific and within-individual trait variation. We also performed a series of simulations accounting for different levels of within-individual trait variation. For the empirical data, both intraspecific and within-individual variation accounted for more than 84% of total variation in functional traits, and for one trait (foraging maneuver) within-individual variation accounted for 84.31%. Although all FD metrics showed significant positive correlations, their magnitude consistently decreased when intraspecific and within-individual variations were taken into account (Pearson's correlations from 0.99 to 0.28). Simulations also showed that not accounting for within-individual variation strikingly underestimated functional richness, even at the lowest levels (< 5%) of within-individual variation. Our results reveal that within-individual variation may represent a major source of functional trait variation. Overall, the inclusion of within-individual variation in trait-based approaches would improve our understanding and use of FD estimators and determine to what extent it matters for assembly processes.

1. Introduction

A long-standing challenge in community ecology is to understand how species and biological diversity influence community structure and ecosystem functions. In particular, trait-based approaches have been increasingly used in the last decade to address questions related to assembly processes of biological communities (Laureto et al., 2015). A functional trait can be any feature measurable at the individual level affecting fitness (Violle et al., 2007), which directly influences ecosystem functioning (Naeem and Wright, 2003; Hooper et al., 2005; Díaz et al., 2007). These traits are then used to describe the value and range of species-specific functional attributes in a given community under the term of "functional diversity" (hereafter FD; Tilman, 2001).

To estimate FD, researchers typically employ average trait values obtained from databases (e.g. Jones et al., 2009; Kattge et al., 2011; Wilman et al., 2014). This approach based on mean trait values has been fruitful in disentangling different processes of community assembly and ecosystem functioning, such as the effects of abiotic factors (Laliberté et al., 2010; Palacio et al., 2018) and biotic interactions (Schuldt et al., 2014). However, it has been a basic pillar of ecology that species exhibit phenotypic trait variation, recognized as a promoter of diversity and a condition for both local coexistence and adaptation

(Hallgrímsson and Hall, 2005; Bolnick et al., 2011; Dall et al., 2012). In this sense, intraspecific variation has almost been neglected in community ecology, under the assumption that interspecific trait variation is larger than intraspecific variation (Violle et al., 2012). Nevertheless, recently, ecologists have shown growing concern about the importance of accounting for intraspecific trait variation in FD measures (Albert et al., 2012; Violle et al., 2012; Des Roches et al., 2018). This is based on the evidence that within-species trait variation is relatively large and often exceeds between-species variation in biological communities (Messier et al., 2010; Siefert et al., 2015; Wood et al., 2017), and that ignoring intraspecific variation may strongly obscure the detection of ecological patterns or result in inaccurate interpretations (Jung et al., 2010; Bolnick et al., 2011; Des Roches et al., 2018). Furthermore, the use of average trait values to describe a local community overlooks the fact that the range of trait values used may be far from the actual observed trait values in the community under study, as a result of large trait variation (Bolnick et al., 2011; Albert et al., 2012). This would be particularly true for generalist species of large distribution ranges, which show high variation in many traits, such as size, diet or behavior (e.g. Sih et al., 2012; Slatyer et al., 2013). Therefore, the need of measuring traits in the community studied has been emphasized (e.g. Luck et al., 2013; Schuldt et al., 2014).

In addition to intraspecific trait variation, the same individual may also show functional trait variation (hereafter "within-individual variation"). For instance, plants show phenotypic variation among repeated structures such as leaves, flowers and fruits (Herrera, 2017). In the case of animals, individuals may change their diet or behave differently according to different ecological conditions (Podlesak et al., 2005; Jaeger et al., 2009; Zhao et al., 2017). Further, several studies have shown that within-individual variation of morphological and functional traits may be comparable to or even exceed intraspecific variation (Ordano et al., 2011; Kernaléguen et al., 2012; Palacio et al., 2014). Ignoring within-individual variation among species of a community misrepresents the fraction of resources that individuals can use, ultimately underestimating the different functions that species fulfil (Bolnick et al., 2002; Violle et al., 2012). Besides, within-individual variation may behave as a functional trait itself, influencing population persistence and community stability through individual performance variation (Herrera, 2009; Bolnick et al., 2011; Dall et al., 2012). This thereby suggests that within-individual variation may also represent an important source of functional trait variation with prominent effects on ecosystem functioning still neglected in community ecology (Bolnick et al., 2011; Herrera et al., 2015).

Although the use of available information on functional traits has provided valuable knowledge on disentangling different community assembly patterns and processes, the effects of using different levels of data resolution in functional traits (i.e. trait values based on global databases or literature vs traits measured in the community under study) remains almost unexplored in animal communities. Here, we assessed the role of both within-individual trait variation in FD and different data resolution by using bird foraging sequences to quantify different sources of functional trait variation (community, individual, and within-individual) and comparing FD metrics using traits based on different hierarchical levels of data resolution (data obtained from our own literature search, a global database, average trait values based on sequential observations, and intraspecific and within-individual trait variation). Like other functional traits, foraging behavior is a complex trait with a high level of variability (i.e. flexibility) and, therefore, an adequate functional trait to explore how within-individual variation affects the estimation of functional diversity. Similar to other directly recordable traits measured in many organisms, foraging behavior is a conspicuous trait, and it should be easily recorded in many study systems or communities. Although it is not usually a problem in regional or local studies (e.g. Petchey and Gaston, 2002; Petchey et al., 2007; Mendez et al., 2012; Ulrich et al., 2018), it is complex to compile this information on global databases. Specifically, we asked the following

questions: (1) How much functional trait variation is represented by intraspecific and within-individual variation (i.e. trait variation within the same individual)? (2) How many different levels of trait resolution (from average trait values based on the literature to intraspecific and within-individual trait variation based on field sampling) impair the description of ecological patterns? For a better understanding of the role of both within-individual trait variation in FD metrics and different data resolution, we complemented our analyses with numerical simulations using different levels of within-individual variation.

2. Materials and methods

2.1. Study area

The study was carried out at the San Isidro ranch (35° 09′ S, 57° 02′ W), located in the Biosphere Reserve "Parque Costero del Sur", near the shore of the Río de La Plata, Buenos Aires province, Argentina. The area is composed of grasslands (native and alien used for cattle grazing) and native forest patches, with nearly 10% forest cover. The landscape matrix has not elements hampering bird movements, as forest patches are approx. 200–600 m apart (Palacio, 2016). These patches are xeromorphic forests locally named "talares", and grow on calcareous soil deposits, parallel to the shore of the Río de La Plata (Goya et al., 1992). The dominant tree species are *Celtis ehrenbergiana*, *Scutia buxifolia*, *Schinus longifolia* and *Jodina rhombifolia* (Goya et al., 1992). In phytogeographic terms, this area corresponds to the "Provincia del Espinal", a region characterized by xeromorphic thorny forests at central Argentina (Parodi, 1940; Cabrera, 1971). The climate is wet temperate, with average minimum and maximum temperatures of 6.0° C and 26.0° C, respectively (averages estimated from data obtained for the 1980–2016 period from a weather station 20 km away from the study site). Annual mean rainfall is about 926 mm, mostly wet in January and February, but without a noticeable dry season.

2.2. Bird foraging observations

Fieldwork was carried out from 30 July to 3 December 2014 in an 81 ha plot (1,080 m × 750 m). Observations were made once a week or every two weeks in 14 native forest patches (sampling unit, 14 repeated measures). On a sampling day, one observer (FX Palacio) made intensive searches by walking along parallel 20 m-width transects in the longest dimension of each patch, up to finish the whole area of each (Palacio, 2016). We recorded foraging behavior data of four focal bird species: Rufous-collared Sparrow (*Zonotrichia capensis*), Rufous-bellied Thrush (*Turdus rufiventris*), Bay-winged Cowbird (*Agelaioides badius*) and Smalled-billed Elaenia (*Elaenia parvirostris*). These species were selected based on the following criteria: (1) they are relatively abundant at the study area, usually representing the first species in rank-abundance profiles (Cueto and López de Casenave, 2000), and (2) they belong to different families with drastically different life histories (del Hoyo et al., 2004, 2005, 2011). Relative abundances of these species (based on a sample of 45 species and 3671 individuals; Lacoretz, 2018) are: 14% (Rufous-collared Sparrow, rank = 1), 7% (Smalled-billed Elaenia, rank = 3), 4% (Rufous-bellied Thrush, rank = 7), and 3% (Bay-winged Cowbird, rank = 11). For each individual encountered, we recorded sequential observations of foraging behavior. Observations ceased when the observer could no longer see the bird or to a maximum of 30 min. When flocks were involved (Bay-winged Cowbird), data on one randomly selected individual was recorded to avoid dependence between foraging observations (Morrison, 1984; Recher and Gebski, 1990). For each observation, we recorded the foraging maneuver, food item, and foraging substrate following Remsen & Robinson (1990). All these functional traits impact main aspects of resource use by birds and thus are linked to their ecosystem functions (Luck et al., 2012). Food item (i.e. diet) represents a direct effect on ecosystem functions such as nutrient flow, pest control, and seed dispersal (Whelan et al., 2008;

Luck et al., 2012). Foraging substrate becomes relevant when it reflects spatial segregation (i.e. competition) among individuals or species searching for different prey or dietary items (Mouchet et al., 2010; Luck et al., 2012). Besides, variation in foraging substrate would also affect ecosystem functions, with the conspicuous case of seed dispersal, whose efficiency relies on the arrival of seeds to specific sites (Whelan et al., 2008). In turn, foraging maneuver could represent an indirect effect on ecosystem functions, and the result of the interaction between food item and foraging substrate. All field observations were made within four hours after sunrise and three hours before sunset (approx. seven observation hours per sampling day). Patch order was randomized each day to reduce bias due to sampling hour.

2.3. Data analysis

2.3.1. Magnitude of intraspecific and within-individual variation in functional traits

To quantify the magnitude of interspecific, intraspecific and intra-individual variation in functional traits, we used linear mixed models fitted by restricted maximum likelihood, with the corresponding trait as the response variable and four hierarchical levels (i.e. patch, species, intraspecies and within individual) as random factors (Messier et al., 2010; Violle et al., 2012). The ratio between the variance component and the sum of variance components represents the proportional contribution of the variation due to each level (Crawley, 2012). Given that variance partitioning can only handle continuous variables, we first performed separate Principal Coordinate Analyses (PCoA) on each functional trait (food item, foraging substrate and maneuver) based on a Gower distance matrix and then used the first PCoA axis (72.60–86.18% variance explained) as functional traits (Violle et al., 2012). One major caveat of this approach is that foraging observations of unmarked birds are potentially dependent, as the same individual may be observed in subsequent days. This is likely to occur, given the proximity among forest patches, the ease of dispersal of these species (e.g. Small-billed Eleania migrates to northern South America in the non-breeding season; McNeil & Itriago, 1968) and the relatively high matrix permeability (Stupino et al., 2015). So, it is likely for some within-individual variation to be included as intraspecific variation, underestimating the magnitude of within-individual variation yet making our approach conservative. Finally, we also computed 95% bootstrap confidence intervals for each level of variation using 1000 samples per trait (Messier et al., 2010).

2.3.2. Intraspecific and within-individual functional diversity

To assess the impact of average trait values and trait variation on functional diversity, we quantified FD of forest patches under six different hierarchical levels of increasing resolution of functional traits: (1) average trait values (presence-absence) based on our own literature search, (2) average trait values (proportions) based on the global dataset of Wilman et al. (2014), (3) average trait values (proportions) based on our data using only the first observation of each foraging sequence, (4) average trait values (presence-absence) based on our data using complete foraging sequences, (5) average trait values plus intraspecific trait variation (using only the first observation of each foraging sequence; presence-absence), and (6) average trait values plus intraspecific and within-individual trait variation (using complete foraging sequences, presence-absence). Traits used were: diet (invertebrates, fruits, seeds, other plant material), foraging stratum (ground, understory, mid and high strata, canopy, air). Foraging maneuvers included: glean, flake, lunge, peck, probe, reach, sally, and scratch (Remsen and Robinson, 1990). In an attempt to homogenize databases, we did not include body size, as it was not measured in this study (but see Discussion). In levels 3 and 5, we decided to use the first observation of each sequence based on a methodological criterion. Although we acknowledge that any observation in the sequence can be selected, the first sighting matches the field technique termed "single-point observation", a standard practice in bird foraging studies (Recher and Gebski, 1990). Besides, repeated observations are needed to then choose any particular observation of the sequence, representing much more effort than single-point observations. For the first four scenarios, we computed functional richness ($FRic_1$ to $FRic_4$, respectively) which represents the (convex hull) volume of functional traits space occupied by a community (Mason et al., 2005). We here focus on FRic because it is one of the most commonly used FD metrics (Luck et al., 2013) and facilitates comparison of our results with those of past studies. To visually inspect functional relationships among bird species, species by traits matrices were converted to Gower distance matrices and clustered through UPGMA (unweighted pair group method with arithmetic mean) algorithm to produce dendrograms.

For the last two scenarios (intraspecific and within-individual FD), we used the recent approach of Carmona et al. (2016), which relies on the probabilistic nature of functional trait distributions to quantify different components of FD. Basically, a trait probability density (TPD) function is fitted to each species (TPD_S) using kernel density estimators, which are then combined to create a community TPD (TPD_C) as the sum of abundance-weighted TPD_S values (Carmona et al., 2016). Similarly, within-individual variation in TPD can be included into FD by estimating a TPD for each individual (individual TPD -TPD_I-), which are then summed to create a TPD_S and then, a TPD_C (Carmona et al., 2016). Under this framework, FRic is the amount of functional volume occupied by TPD_C and is therefore analogous to FRic computed using the convex hull volume approach (Carmona et al., 2016). The TPD approach has the advantages of being able to be computed for any type of ecological unit, explicitly considering intraspecific trait variation, being sensitive to gaps in the functional volume, and being less sensitive to outliers (Carmona et al., 2016). To include intraspecific variation in FRic (iFRic), we built a TPD for each species (TPD_S) using the first observation of each foraging sequence. We finally accounted for within-individual variation in FRic (wiFRic) by fitting a TPD for each foraging sequence (TPD_I; Appendix A). We computed Pearson's correlation coefficients to assess relationships and potential redundancy between FD metrics.

2.3.3. Simulations of the effect of within-individual trait variation on FD

To investigate the impact of both intraspecific and within-individual variation on FRic, we developed three simulation scenarios. For each scenario, we used the same artificial community matrix (**A**) arbitrarily composed of 10 sites by 10 species, in which species abundances were modelled using a log-normal distribution (Magurran, 2004), with a coefficient of variation CV = 2.0. Then, we simulated three species by trait matrices (**T**), reflecting different levels of functional trait variation.

"Within-individual FRic (wiFRic)": an artificial matrix **T** was generated considering two normally distributed traits with parameters μ (drawn from an arbitrary uniform distribution with minimum = 1.0 and maximum = 10, one per species) and $\sigma = CV \times \mu$. For the first trait, the CV was arbitrarily fixed to 0.3. For the second trait, 50 evenly distributed CV values from 0.1 to 1.0 were used. To simulate within-individual trait variation, five measurements were randomly sampled per individual and species. wiFRic was estimated using the TPD approach.

"Intraspecific FRic (iFRic)": for each individual, the five random measurements derived from the first scenario were averaged and the TPD approach was used.

"Average FRic": for each species, all the measurements of all the individuals derived from the first scenario were averaged.

For each CV value, we computed and plotted the percentage of within-individual variation (resulting from variance components) vs. FRic. The three scenarios were thought to control for most factors affecting FRic, so we only varied within-individual variation of one trait. Given that FRic represents the volume of functional trait space, it is expected that accounting for no intraspecific or within-individual trait variation underestimates FRic, because trait values are summarized in

mean values. Similarly, it is expected that iFRic underestimates FRic, because now individuals are characterized by mean values. Finally, iFRic and wiFRic should increase with increased within-individual variation, whereas average FRic should remain constant (as trait values do not change regardless of trait variation). The R code is available at Appendix B.

All analyses and graphs were performed in R 3.4.0 (R Core Team, 2017) using the packages lme4 (function *lmer* for variance components; Bates et al., 2015), boot (function boot.ci for bootstrapped confidence intervals; Canty and Ripley, 2016), FD (function *dbFD* for FRic; Laliberté et al., 2014), ape (function *pcoa* for principal coordinate analyses; Paradis et al., 2004), TPD (functions *TPDs*, *TPDc* and *REND* for the TPD approach; Carmona, 2017), mobsim (function *sim_sad* for simulations of species assemblages; May, 2017), vegan (Oksanen et al., 2016) and ggplot2 (Wickham, 2009).

3. Results

A total of 87 foraging sequences and 736 foraging events were recorded for the four species: 49 foraging sequences for Rufous-collared Sparrow (mean number of foraging events per sequence = 13.27, range = 1–229 foraging events), 17 for Rufous-bellied Thrush (mean number of foraging events per sequence = 1.94, range = 1–3 foraging events), 12 for Bay-winged Cowbird (mean number of foraging events per sequence = 3.33, range = 1–6 foraging events) and 9 for Small-billed Elaenia (mean number of foraging events per sequence = 1.44, range = 1–5 foraging events). Plant material different from fruits and seeds (52.87%), and invertebrates (41.37%) were the most common item diets. Ground (62.42%) and glean (79.84%) accounted for most foraging strata and maneuvers, respectively. A graphical summary of foraging sequences of each species is shown in Fig. 1. Taken together, both intraspecific and within-individual variation accounted for at least 84% of total variation in functional traits (Appendix C). In particular, intraspecific variation was largest for foraging stratum, whereas within-individual variation accounted for most variation in foraging maneuver (Appendix C). For food item, similar levels of intraspecific and within-individual variation were found (Appendix C). High levels of intraspecific variation relative to interspecific variation were also evidenced in the 2-dimensional TPDs, showing high overlap between most species (Fig. 2; see also Appendix A).

All FRic metrics showed positive relationships (Table 1). In particular, the three FD metrics based on average trait values showed strong correlations (*r* > 0.96), but they consistently decreased when intraspecific and within-individual variation were taken into account (Table 1). That is, iFRic showed lower correlations with FDs based on average trait values (*r* > 0.60), and wiFRic showed even lower correlations (*r* = 0.28–0.48). This was also evidenced in functional relationships between species (Fig. 3), where including complete foraging sequences barely altered the dendrogram compared to that including only the first observation of each sequence.

Simulations showed that, as expected, increasing within-individual trait variation increased iFRic and wiFRic, whereas average FRic remained constant (Fig. 4). More importantly, excluding intraspecific or within-individual trait variation strikingly underestimated FRic (Fig. 4). Finally, iFRic always underestimated wiFRic, even at the lowest levels (< 5%) of within-individual variation (Fig. 4).

4. Discussion

4.1. Intraspecific and within-individual variation in trait-based approaches

Our results revealed that both intraspecific and within-individual variation represent major sources of functional trait variation among species within a community. Recently, the importance of intraspecific trait variation on the quantification of FD metrics has been highlighted (Violle et al., 2012). This is because ignoring intraspecific trait variation
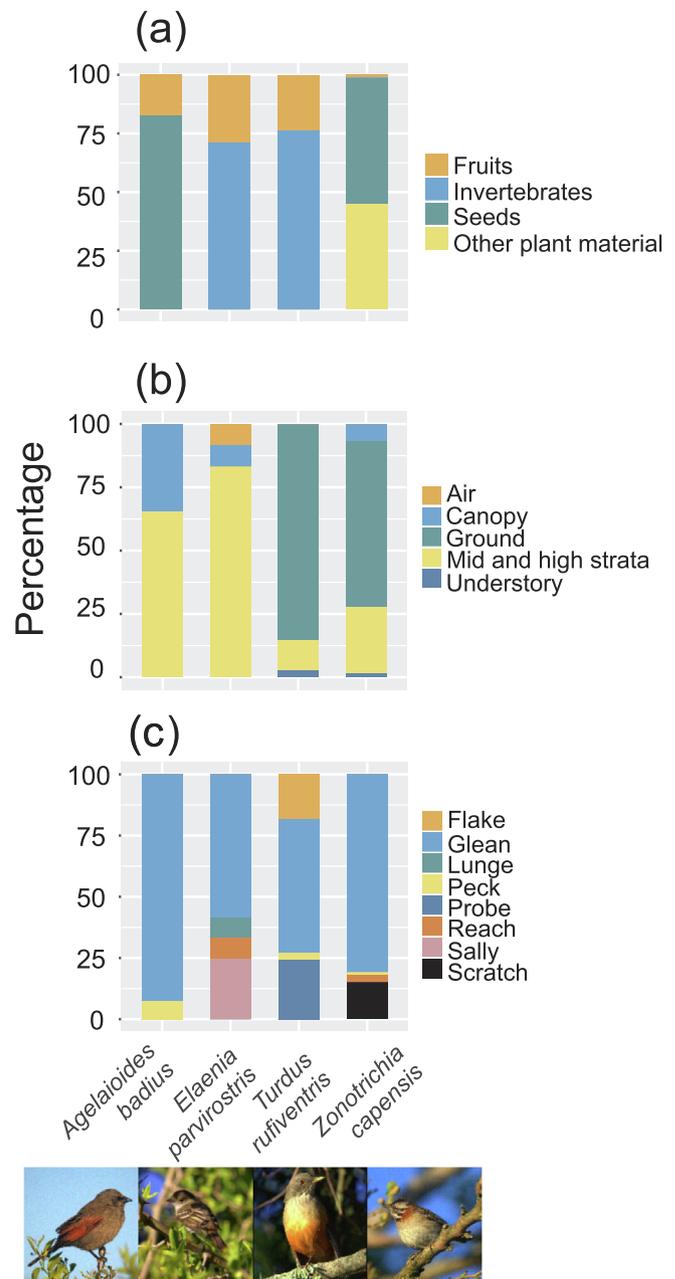

Fig. 1. Description of functional traits (percentage of species that each category of functional trait space has) of four bird species from "talares" of Buenos Aires province (Argentina). (a) Food item, (b) foraging stratum, (c) foraging maneuver.

may strongly alter the estimation of FD and obscure the description of ecological patterns (Albert et al., 2012; Ross et al., 2017). This would be particularly true when assessing patterns of FD at local scales, because intraspecific variation is expected to gain in importance as the scale of study decreases (Albert et al., 2011). On the other hand, broadening the study scale tends to increase variability, and interspecific trait variation is thus expected to be relatively larger than intraspecific variation (Albert et al., 2011).

In contrast to intraspecific trait variation, much less attention to within-individual variation in community assembly has been paid (Herrera et al., 2015). In this sense, within-individual variation (Herrera, 2009; Arceo-Gómez et al., 2017; Palacio et al., 2017) has the potential to contribute to ecosystem functioning and is thus a feature that should be included in FD metrics. Our theoretical reasoning and simulations supported the idea that using traits as mean values per
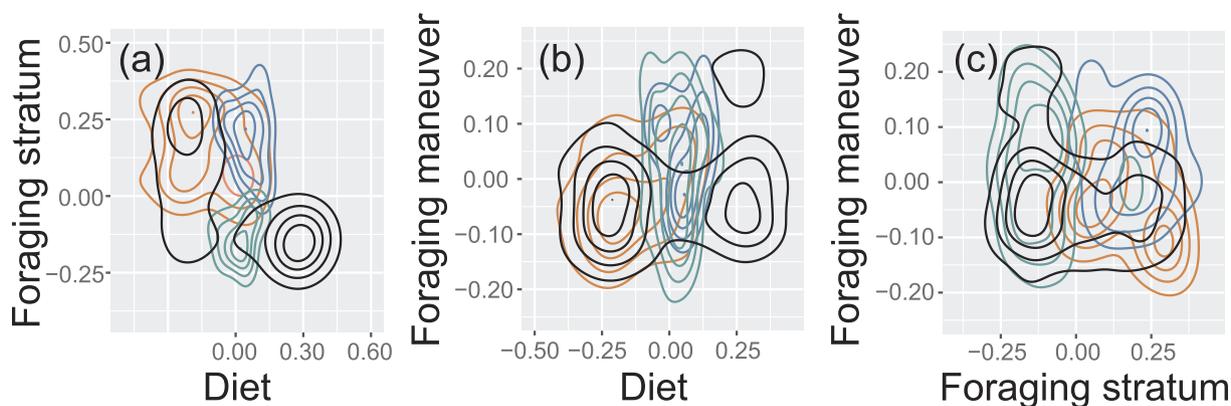
Fig. 2. Kernel density plots of functional traits of four bird species from "talares" of Buenos Aires province (Argentina). Values of the first axis resulting from Principal Coordinate Analyses are shown. Under a trait probability density (TPD) framework, each density plot represents a species TPD (TPD$_S$); the TPD$_S$ functions of the species present in a given community are then combined to create a community TPD (TPD$_C$). Functional richness is the volume occupied by a given TPD$_C$. Colors depict species (brown: *Agelaioides badius*, blue: *Elaenia parvirostris*, green: *Turdus rufiventris*, black: *Zonotrichia capensis*).

Table 1

Pearson correlation matrix of functional diversity metrics measured at different levels of data resolution. Functional richness at the species (FRic), individual (iFRic) and within-individual levels (wiFRic) is shown ($n = 61$). Subscripts one to four indicate the following data resolution in the species by trait matrix: (1) average trait values based on literature, (2) average trait values based on Wilman et al. (2014), (3) average trait values based on our data using only the first observation of each foraging sequence, and (4) average trait values based on our data using complete foraging sequences. Values in bold indicate $P < 0.0001$.

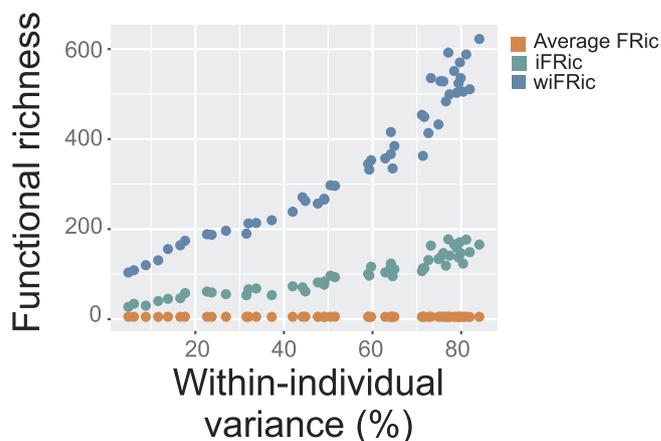|	FRic$_2$	FRic$_3$	FRic$_4$	iFRic	wiFRic
FRic$_1$	**0.992**	**0.968**	**0.966**	**0.607**	0.276
FRic$_2$		**0.991**	**0.990**	**0.610**	0.288
FRic$_3$			**0.999**	**0.604**	0.285
FRic$_4$				**0.604**	0.285
iFRic					0.480

Fig. 4. Impact of within-individual variation on functional richness (FRic). Points result from simulating three scenarios of 10 assemblages × 10 species (see Materials and Methods): (1) FRic accounting for within-individual and intraspecific variation (wiFRic), (2) FRic only accounting for intraspecific variation (iFRic), FRic and (3) accounting for no variation (average FRic).

species cannot capture patterns of at least one component of FD (i.e. functional richness). In turn, not accounting for within-individual variation also underestimates FRic, particularly under scenarios of high within-individual variation. This would translate into the underestimation of the number of ecosystem functions (Violle et al., 2012). Nevertheless, within-individual trait variation for many animal taxonomic groups or sampling methods may be difficult, or even impossible, to account for (e.g., insect traps, mist nets). This task also becomes strongly difficult in hyper-diverse communities (e.g. tropical systems) or large-scale projects. Despite these difficulties, several individual-level traits can be obtained from captured organisms (e.g. arthropods) or from? technical devices, such as camera traps.

Overall, we recognize that obtaining trait data on individuals is a labor-intensive task, but, hopefully, it will enhance our understanding on ecosystem functioning. Although further studies need to address the effect of within-individual variation on other FD components (evenness, divergence, redundancy), our results suggest that the inclusion of within-individual variation would improve approaches relying on FD metrics.

4.2. The importance of data resolution in quantifying FD

Although we have used only four species, our results show that different data resolutions changed the estimation of FD. Surprisingly,
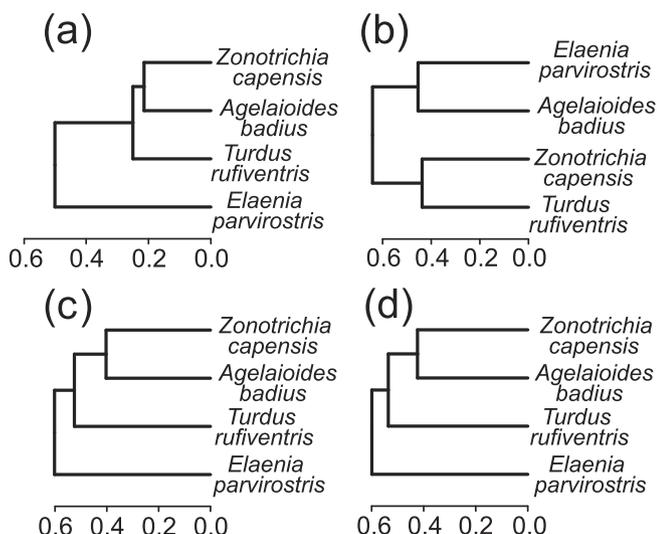

Fig. 3. Functional relationships between four bird species from "talares" of Buenos Aires province (Argentina). Dendrograms were produced by UPGMA algorithm of Gower distance matrices computed from the functional traits of species. Horizontal distance represents separation in trait space. Letters indicate the following data resolution in functional traits: (a) average trait values based on our own literature search, (b) average trait values based on Wilman et al. (2014), (c) average trait values based on our data using only the first observation of each foraging sequence, and (d) average trait values based on our data using complete foraging sequences.

trait data resolution has been an issue seldom addressed in studies of FD, particularly in animal communities (but see Griffiths et al., 2018). In a simulation study of different sampling strategies of several plant functional traits, Baraloto et al. (2010) showed that using a database with average trait values led to poor performance of FD estimation. By contrast, quantifying traits of at least one individual per plot performed relatively well, probably due to regional genetic variation, environmental plasticity or both (Baraloto et al., 2010). On the other hand, Cordlandwehr et al. (2013) found that the accuracy of traits retrieved from a regional database relative to local trait measurements in plant communities from the Netherlands depended on the level of aggregation (lower at community level), the trait (lower in plastic traits) and habitat type (lower in extreme habitats). Although further studies are needed to determine the effects of using different trait data resolutions, these results underscore the importance of measuring traits of at least some individuals in the field (Griffiths et al., 2018), rather than blindly relying on global databases as proxies for on-site measurements. This procedure has become more common in plant communities given the immobile nature of plants (e.g. Cadotte et al., 2009; Schuldt et al., 2014; Luo et al., 2016), although efforts have also been made in animal communities as well (e.g. Luck et al., 2013; Griffiths et al., 2016). Nevertheless, all authors agree that studies carried out at local scales would be strongly impaired by the use of large scale databases, which therefore justifies appropriate sampling of functional traits in these scenarios (Baraloto et al., 2010; Albert et al., 2011; Cordlandwehr et al., 2013).

4.3. Links between foraging behavior, ecosystem functioning and FD

As we stated in the Methods section, the three functional traits included in our study (foraging maneuver, food item, and foraging substrate) are linked to ecosystem functions (Luck et al., 2012). For our study species, food item showed high levels of both intraspecific and within-individual variation, foraging substrate showed a high level of intraspecific variation, and foraging maneuver showed a high level of within-individual variation. If intraspecific effects are strong when indirect interactions alter community composition (Des Roches et al., 2018), it is expected that foraging behavior will affect ecosystem functions. Therefore, the estimation of FD metrics based on functional traits becomes relevant for the understanding of community dynamics and ecosystem functions. Altogether, further studies are necessary to precisely estimate the magnitude of direct and indirect effects of intraspecific and within-individual functional variation on ecosystem processes.

4.4. The role of body size in FD

Body mass was not included as a functional trait in our study, due to sampling limitations. To achieve this goal at the within-individual level, individuals should be ringed, so one can both capture birds to repeatedly measure body mass and perform observations on foraging behavior. We highlight, however, that body size is a key trait reflecting many other traits including metabolic rate, foraging behavior, longevity and territory size (Luck et al., 2012; Moretti et al., 2017). Also, body size correlates with flight distance, which determines the contribution of species to pollination and seed dispersal functions. In practice, body size tends to be the more readily available trait for animals (e.g. Dunning, 2007; Jones et al., 2009; Olson et al., 2009; Wilman et al., 2014), which explains the fact of being the most commonly used trait in animal FD studies. Despite some redundancy between morphology and behavior is often expected, it has been shown that one set of traits (e.g. morphological traits) may not necessarily correlate with other set of traits (e.g. reproductive or habitat-related traits; Tsianou and Kallimanis, 2016). Therefore, we should interpret our results cautiously and underscore the need of including body size in FD studies.

4.5. Conclusions

The preceding considerations indicate that ecologists should be careful when computing FD indices and designing studies about FD, in particular when intraspecific and within-individual variation may be relatively high to such a degree that it dissolves taxonomic boundaries. Indeed, we found high overlap between species traits resulting from high intraspecific and within-individual variation. Even though within-individual variation is probably underestimated (see Materials and Methods) and despite the use of drastically different species (i.e. high *a priori* interspecific variation), it reached extremely high levels in some cases (> 84%). It would be therefore a key step for researchers to first quantify the magnitude of both intraspecific and within-individual trait variation before conducting a FD study, and then evaluate whether these should be accounted for or not (Albert et al., 2010). Our results support the idea that within-individual variation represents another level of intraspecific trait variation, and advocate the need to integrate variation at within-individual, intraspecific and interspecific levels. To this end, detailed descriptions of functional traits of species within communities using standardized protocols are needed (Baraloto et al., 2010; de Bello et al., 2011; Pérez-Harguindeguy et al., 2013; Moretti et al., 2017). In scenarios logistically unfeasible (e.g. regional or global scales), simulations to test the effects of intraspecific and within-individual variation on FD should accompany empirical studies as recommended by Albert et al. (2011). Overall, the inclusion of both intraspecific and within-individual variation in trait-based approaches would improve our understanding of the patterns and processes that govern ecological communities.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.02.018.

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