Why abundance-based indices of niche breadth are biased, and what can be done to improve them

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Abstract

Niche breadth is a central concept in ecology, and species with narrow niche breadth are believed to be more sensitive to anthropogenic factors than species with broad niche breadth. A myriad of methods to assess niche breadth have been suggested, many of them reliant on estimates of relative abundance (e.g., across habitats). We show, using both simulations and empirical data, that due to density-dependent habitat selection these niche breadth measures are inherently biased by abundance. Thus, rare species are perceived to have narrow niche breadth. We propose the "isodar-adjusted inequality" method, a new index with density-independent and density-dependent components, both of which are ecologically important. We show using simulations and empirical data that this index removes the inherent bias associated with abundance, while retaining the intuitive appeal of associating niche breadth with resource use variability. This method will hopefully improve niche breadth estimates and inspire reassessment of fundamental ecological patterns.

Keywords: Density-dependence; Habitat breadth; Isodars; Relative abundance; Specialization.

1. Introduction

1.1. Introducing the problem

Niche breadth is a central concept in ecology (Brown, 1984; Carscadden *et al.*, 2020; Hutchinson, 1957). For instance, it is widely believed that species with narrow niche breadth, or **specialists**, are more vulnerable to anthropogenic disturbance (Devictor *et al.*, 2008a; Feary, 2007; Stuart-Smith *et al*., 2021; Wilson *et al.*, 2008) and climate change (Colles *et al.,* 2009; Gaüzère *et al.*, 2015; Laidre *et al.*, 2008; Weaver & Mallinger, 2022), and are at higher risk of extinction (Ceretta *et al.*, 2020; Clavel *et al.*, 2011; Davies *et al.*, 2004; Munday, 2004). Conversely, species with wide niche breadth, or **generalists** capable of thriving under a wide set of conditions, are more likely to becoming invasive (Granot *et al.*, 2017; Hui *et al.*, 2023; Vazquez, 2006) and seem to be increasing in relative abundance (Alvarez-Filip *et al.*, 2015; Devictor *et al.*, 2008b; Le Viol *et al.*, 2012) and expanding their ranges (Stuart-Smith *et al*., 2021). Given its importance for basic ecology and conservation biology, it is vital that niche breadth is measured consistently and free of bias.

As a result of its broad definition (Futuyma & Moreno, 1988; Sexton *et al.*, 2017), it is usually not practical to fully describe the niche breadth of a species. Often, the species' relative abundance along one or a few prominent niche axes (e.g. habitat, diet, or temperature) is translated into an index of niche breadth (Devictor *et al.*, 2010), such as the coefficient of variation in abundance across habitats (Barnagaud *et al.*, 2011; Filippi-Codaccioni *et al.*, 2010; Jiguet *et al.*, 2007; Julliard *et al.*, 2006). For an extreme generalist, i.e. a species with the same abundance across all habitats, the coefficient of variation will be zero. Other indices to estimate niche breadth from abundance data have also been proposed (Poisot *et al.*, 2012), such as the commonly used Gini index of inequality (Morelli *et al.*, 2019), which conveniently scales the niche from zero (narrowest) to one (broadest). Alternative indices include relative habitat use (Larsen *et al.,* 2011; O'Reilly *et al.,* 2022), proportional similarity (Hernandez *et al.,* 2023), abundance-occupancy relationships (Drovetski *et al.*, 2014; Wells *et al.*, 2024), *n*-dimensional niche approaches integrating disparate niche components into a single hypervolume (Blonder, 2018; Blonder *et al.*, 2014; Pianka *et al.*, 2017; Swanson *et al.*, 2015), and more. Although some methods

are not directly centered on abundance, most are nonetheless fundamentally based on the occurrence or relative abundance along the niche axes (habitat, climate, host, etc.).

While these indices are intuitive and easy to use, we will show here using the isodar habitat-selection theory that estimating niche breadth from survey data is prone to severe biases resulting from density-dependent habitat selection. Fretwell and Calver (1969) first proposed the theory of ideal free distribution, which states that individuals will distribute themselves across habitats to equalize their fitness. Later, Morris (1987), used the idea of ideal free distribution to develop the **isodars**. An isodar is the line in a graph where each axis is the abundance (or density) of a species in a specific habitat (**figure 1**), and thus reflects the partitioning of total individuals between two habitats. The isodar has two components: (1) the **intercept**, which can be viewed as the density-independent difference between the habitats, or the true preference of the species at low densities, and (2) the **slope**, which can be viewed as the density-dependent difference between habitats, or the ratio available of resources between habitats (Morris, 1987). Isodars are used to understand how habitat use changes with density (Adams *et al.,* 2023; Ale et al., 2011; Rainville *et al.,* 2022; Tadesse & Kotler, 2010; Tarjuelo *et al.,* 2017). It is reasonable to assume that most species will show some density-dependent habitat selection as abundances increase and competition for resources becomes more severe (Haugen *et al.*, 2006; Kie & Bowyer, 1999; Planque *et al.*, 2011; Rosenzweig, 1991; Schilling, 2005; van Beest *et al.*, 2016). We show below that this density-dependence may have major consequences for the majority of current abundance-based estimates of niche breadth.

Niche breadth indices based on abundance (or relative abundance, such as those explained above) ignore density-dependent habitat selection. This may have two implications for estimating niche breadth. The first is a pure algebraic consequence of non-zero intercepts, which will cause species of higher abundance to display wider niche breadth. This is due to the non-zero intercept of isodars, i.e. most species have a preferred habitat at low abundances (intercept $\neq 0$). Under this condition, the proportional differences between habitats will decrease with the increase in total abundance, which yields a wider niche breadth estimate (**figure 1b**). This can have major ecological implications, as studies concluding an effect of niche breadth on other factors (e.g., the

widely perceived notion that generalist species are more common than specialists; Heino, 2005; Spitale, 2012; Faulks *et al.*, 2015; Rocha *et al.*, 2018) risk being partly an artifact of the way niche breadth is quantified.

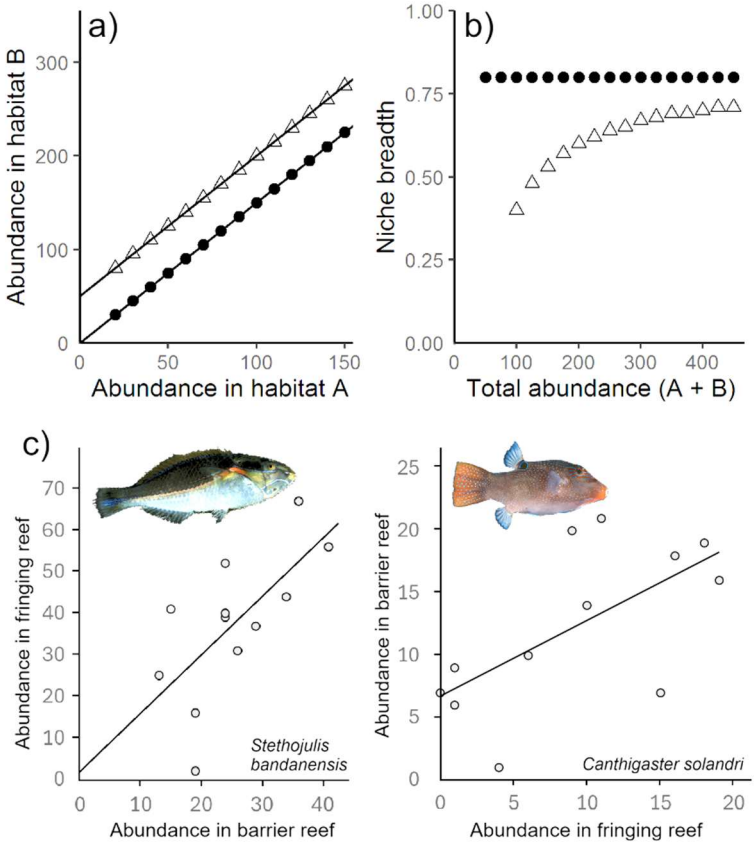


Figure 1. A demonstration of the abundance-dependence of niche breadth indices. **(a)** Points along two distinct isodars, one with a zero intercept and a slope equal to 1.5 (circles), and another with the same slope but with a positive intercept (50, triangles). **(b)** Corresponding niche breadth calculated using the complementary of the Gini index (so 0 corresponds to extreme specialist and 1 to extreme generalist) plotted against the total abundance. As clearly seen, niche breadth, which simply depends on the ratio of densities between habitats, is abundance-dependent when the isodar intercept is non-zero, displaying a positive relationship with total abundance. However, the same index is abundance-independent when the intercept is zero. **(c)** Empirical isodars for reef fishes across habitats in Moorea island (Dornelas *et al.*, 2025) indicate that *Stethojulis bandanensis* (images from FishBase) has minimal habitat preference at low densities (isodar intercept = 1.4), but the fringing reef is twice as preferred as density increases (slope = 2.06), whereas *Canthigaster solandri* prefers the barrier reef at low densities, but after the abundance in the fringing reef

increases above some level (intercept = 6.8), the barrier reef is nearly twice as preferred (slope = 0.61). Both isodars had $R^2 > 0.4$ and had one extreme-abundance outlier removed for clarity.

The second consequence of density-dependence, not addressed by existing alternative estimation methods, is that by ignoring the two separate components of habitat preference, important information is lost. Habitat preference at low densities (the density-independent habitat preference, represented by the isodar intercept) may differ considerably from the habitat preference at high densities (the density-dependent habitat preference, represented by the isodar slope). For instance, a habitat might be rich in high-quality food resources but poor in shelters (Blüthgen & Feldhaar, 2010; Dupke *et al.*, 2017; Mysterud & Ims, 1998). Hence, at low density the food-rich habitat is preferred, but at high densities when shelters become limiting, individuals may actually numerically dominate an alternative habitat with more available shelter. This will result in a positive intercept (indicating that the food-rich habitat is quantitatively preferred at low densities) and a slope shallower than one (indicating that the shelter-rich habitat is qualitatively preferred at high densities, see **figure 1c**). Ignoring these two distinct components results in losing critical information regarding the biological meaning behind the niche breadth of the species.

In this paper, we first use simulations to quantify the impacts of abundance on niche breadth, emphasizing that even small isodar intercepts yield substantial dependence on abundance, and therefore bias in niche breadth. We continue by evaluating the potential impact of current indifference to the abundance-dependence problem, by performing a literature review and examining a large dataset of real abundances. We then propose a simple and intuitive niche breadth index, combining existing indices with isodar theory, and evaluate its performance. Finally, we apply our new R package 'isoniche' (Dubiner *et al.*, 2026) to demonstrate the merits of this index on simulated and real abundance data.

1.2. Demonstrating the problem

1.2.1. Simulating the effect of isodar parameters on niche breadth estimates

We simulated data in order to examine the extent of the bias associated with dependence on abundance. The simulated data is based on isodars between habitat pairs, with a set intercept and slope. We tested a variety of slope and intercept combinations. For each simulation run, we created 1000 populations of different sizes, which were divided into four habitats using the isodars (three isodars in total: between habitats one and two, two and three, and three and four). Variation was added by adding random noise (Gaussian with an SD of 2) to the populations within each habitat. We calculated the classic Gini index for each of the 1000 populations and plotted it against the total abundance of the population across all four habitats. We then varied the slope and intercept values of the isodars and reexamined the patterns. When the intercept equals zero (**figure 2**, top row) there is no relationship between niche breadth and abundance (despite large variation in niche breadth estimation at low abundance). However, when adding even a small intercept of 5 to the isodars (**figure 2**, bottom row), which means that individuals will start density-dependent habitat selection from the sixth individual onward, a dramatic underestimation of niche breadth at lower population size is seen. Only around a population size of 200-300 do niche breadth estimates start to converge to those without an intercept. While this is a simple algebraic outcome, it is quite striking that even small intercepts may affect the niche breadth estimation in relatively large populations. Thus, whenever a density-independent habitat preference (the intercept) is accompanied by density-dependent habitat selection (any non-zero slope), current niche breadth indices will depend on total population abundance.

1.2.2. The potential bias in published niche breadth estimates

We conducted a literature review to assess the number of niche breadth studies that use occurrence or abundance data and hence may suffer from abundance-dependence. We examined all studies published throughout one decade (January 2015 to January 2025) which had “niche breadth” OR “niche width” OR “specialisation” in their title, within 10 leading ecology journals (see **table S1** for details). This search yielded 150 studies, of which 111 focused on empirical quantifications of ecological niche breadth. Of these, 70 studies (63%) used abundance or occurrence data in at least one step of calculating niche breadth. As occurrence and abundance are highly correlated (Wright, 1991; Verberk et al.,

2010; Weber et al., 2017), using occurrence instead of abundance does not alleviate the problem of density-dependence. This is because at low densities some habitats will not be occupied, the same habitats may contain some individuals when total densities increase. Thus, the majority of current niche breadth studies appear to suffer from this problem. We note that none of the studies have any mention of isodars.

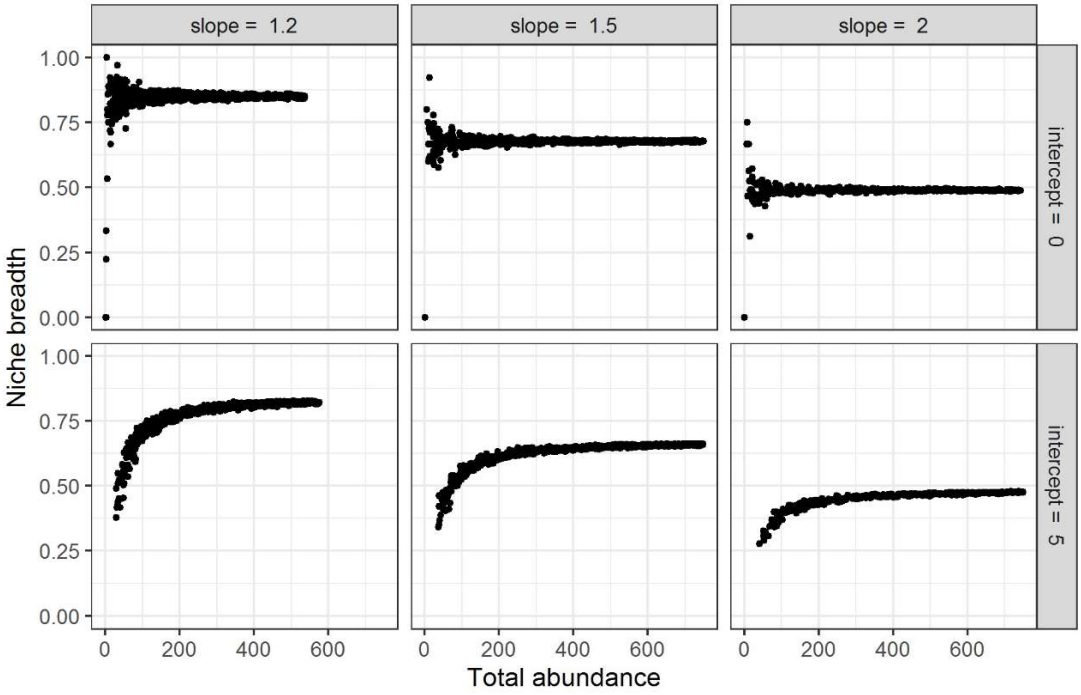


Figure 2. Classic niche breadth calculation (1 –Gini index) of simulated populations plotted against their total abundance. Each population was divided among four habitats using three consecutive isodars using slopes of 1.2, 1.5, or 2, and intercepts of 0 or 5 (same parameters between habitat A-B, B-C, and C-D). We simulated 1000 populations overall per each combination of intercept and slope. When isodar intercepts are non-zero, niche breadth may be vastly underestimated at low abundances.

1.2.3. Estimates derived from empirical data are density-dependent

It is of course conceivable that abundance-dependence of niche breadth indices would not constitute a problem in empirical data because (1) the intercept in the isodar in natural

populations is close to zero, (2) densities of species are so high that the non-zero intercept have only a small impact on niche breadth estimates, or (3) species do not display density-dependent habitat selection. We tested if niche breadth is abundance-dependent in real data using reef fish surveys from Moorea Island. Here, the basic sampling unit is a belt transect (counting the number of fish seen along the transect up to a fixed distance from both sides of the line). This data was collected by the researchers of CRIOBE from 2004 to 2018, at 13 sites around the island. The data can be found under the "MCR LTER Coral Reef Long-term Population and Community Dynamics Fishes" database in BioTIME 2.0 (Dornelas *et al*., 2025). We filtered the data for species occurring in 5 or more sites (223 species, see **table S2**). Most importantly, each site was surveyed across three distinct habitats: barrier reef, fringing reef and outer slope, which allows estimation of habitat breadth (Granot *et al.*, 2025). Since within each site these reef types are fairly close, movement of individuals between them is possible, and habitat selection among habitats must be accounted for.

We ran a zero-inflated beta GLMM (generalized linear mixed model), with 1–Gini for each site as the dependent variable, and total abundance (log-transformed, nested in site of survey) as a predictor. We added species identity as a random effect (random slope and intercept). There was a positive correlation between the abundance and niche breadth estimates ($n = 2457$, $z = 14.1$, $p < 0.001$, **figure 3**). When restricting the analysis to species occupying 10 or more sites, and that had occurrences in all habitats, this result remained qualitatively unchanged ($n = 1352$, $z = 10.7$, $p < 0.001$). These results serve as evidence for abundance-dependence in niche breadth indices and undermine the three possible justifications to continue using classic indices noted at the start of this section (namely if intercepts are all near zero, densities are never low, or the isodars are not significant). Since a non-zero intercept will inevitably cause abundance to bias the niche breadth estimate (**figures 1b & 2**), the presence of these relationships across species supports the need to develop a new approach to account for the density-dependence of niche breadth.

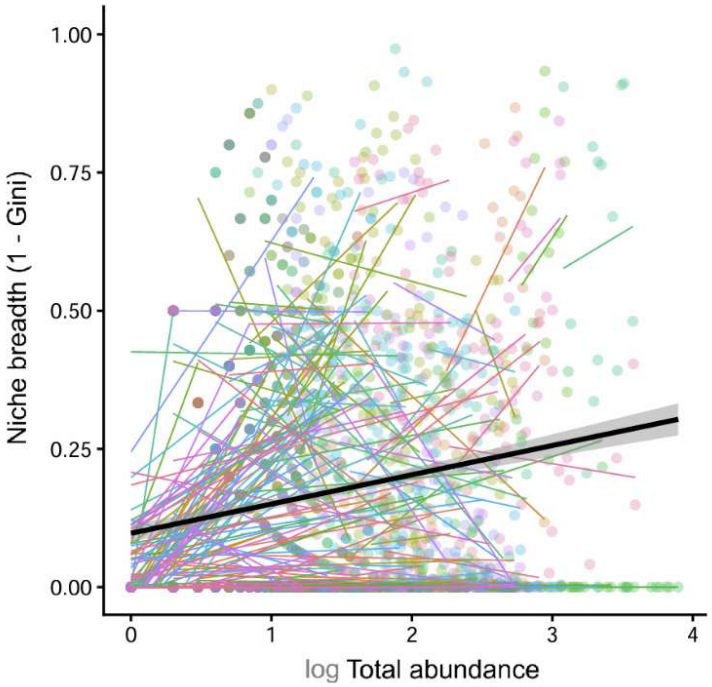


Figure 3. Analysis (zero-inflated beta GLMM) of abundance data for 223 fish species from Moorea shows a positive correlation between total abundance and the perceived niche breadth. Each of the 2457 points is for one species at a single site (5-13 sites for each species). Points and species-specific regression lines are colored by species. The black line is for all species together. As predicted in the simulations, real-life niche breadth is positively correlated with abundance.

2. Methods

While isodars have been used here to demonstrate the problem arising from density-dependent habitat selection, they can also be used as a solution. Both the intercept and the slope of the isodars can be treated as direct niche breadth estimates, as they measure the relative preferences between two habitats. The intercept points at habitat preference independently of density, while the slope represents habitat preferences at high densities when density-dependent habitat selection operates. The intercept and slope estimates can then be combined across habitats to calculate niche breadth measures. Practically, we offer an approach for doing so (implemented in the 'isoniche' package in R; Dubiner *et al.*, 2026), by first fitting isodars and then calculating the adjusted niche breadth prediction to obtain the **density-independent** and **density-dependent niche breadth** indices. While it

is useful to retain the separate information retained within the isodar intercepts and slopes, in practice it is necessary to produce a standardized niche breadth value from these data. After obtaining the isodars for each species (see details in sections 2.2 and 2.3 below), classic niche breadth indices can be applied to a standardized abundance value. This is done by theoretically distributing individuals across habitats according to the isodar slopes and intercepts, for any specified value of total abundance across all sites.

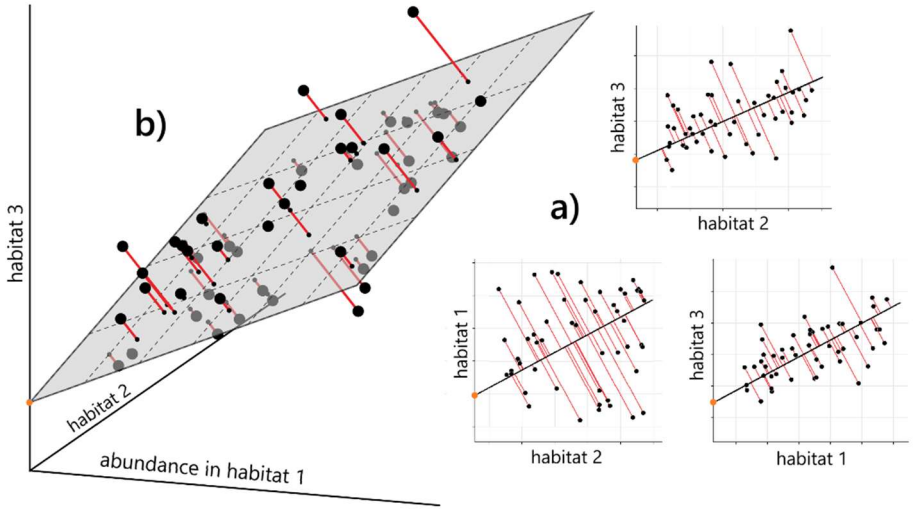
2.1. Correcting niche breadth indices for abundance: Isodar-adjusted inequality

There are several ways to distribute abundance across habitats using the isodars. Here, for a set of pairwise isodars (**figure 4a**, see methodological details in section 2.2), a constrained solver is used to iteratively search possible abundances in each habitat, and the combination of abundances that minimizes the total squared deviation from all isodars is selected as the prediction. For a single *n*-dimensional isodar (**figure 4b**, details in section 2.3), all solutions must correspond to the calculated isodar hyperplane, and the closest to having equal allocation across all habitats is chosen as the prediction. In both cases, solutions must not only satisfy the isodar constraints, but must sum up to the specified total abundance, and contain no negative values (**figure 4c**). The final step is to calculate the niche breadth using the classic Gini index using the predicted habitat abundances above. If expanded to a set or range of abundance values, this process will produce a curve of **isodar-adjusted inequality** (IAI) values relating niche breadth to abundance (analogous to a rarefaction curve, e.g. Cayuela *et al*., 2015; **figure 4d**). Now a specific abundance value can be used to compare across species, as when using rarefaction to compare richness across communities with different numbers of individuals.

Naturally, species differ in many characteristics, such as body size and home range, meaning that a fixed abundance level at which to calculate niche breadth is not attainable. To avoid a choice of abundance value for analysis that is arbitrary, we determined two objective points of reference that nevertheless remain species-specific and context-specific. These will enable both a reliable comparison of isodar-adjusted inequality and have distinct ecological meanings. The first value, termed the **density-independent niche breadth**, is set at the minimum abundance that allows for the presence of individuals within all habitats according to the above prediction method. Low abundances emphasize

the intercept components (habitat preference at low density), The second value, termed the **density-dependent niche breadth**, is set at the highest total abundance present in the data (or, if only low-density data is present, plot the curve and choose the value where it plateaus). Resulting niche breadth values can then be scaled from 0 to 1, where 1 represents a perfect habitat generalist and 0 represents a specialist.

This index can be calculated from using the 'iai' function in the R package 'isoniche' (using the same option for "dim=" as when generating the isodars, and setting "abundances=" to a chosen integer or sequence of integers. Set "abundances=NULL" for the density-independent niche). Alternatively, if only the endpoint value (niche breadth) is desired, the original raw abundance table can be input directly into the 'isoderr' function, which also uses bootstrapping to estimate the niche breadth uncertainty at each density.



c)

total abundance	predicted abundabce habitat 1	habitat 2	habitat 3
1	0	0	1
2	0	0	2
3	0.398	0	2.602
4	0.452	0.816	2.732
5	0.779	1.234	2.986
6	1.107	1.652	3.241
7	1.434	2.070	3.496
8	1.761	2.489	3.750
9	2.089	2.907	4.005
10	2.416	3.325	4.259
11	2.743	3.743	4.514
12	3.070	4.161	4.769
13	3.397	4.579	5.023
14	3.725	4.997	5.278
15	4.052	5.416	5.532

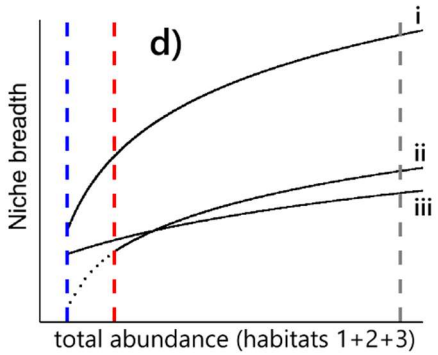


Figure 4. Schematic visualization of abundances in three habitats used to fit pairwise **(a)** or *n*-dimensional **(b)** isodars, wherein TLS minimizes the squared orthogonal distances to the data (red

lines). Whichever approach is taken (a or b), the fit is used to simulate abundances partitioning among the habitats for every value of total abundance **(c)**. A single niche breadth (IAI) value can then be calculated at any abundance, according to the predictions. **(d)** Schematic comparison of IAI along the axis of abundance for three hypothetical species (i-iii). Since comparing niche breadths under different abundances would yield different results, we offer two objective, complementary approaches. To emphasize the **density-independent** niche, choose the lowest total abundance allowing for presence of individuals in all habitats (in c, this value would be 4). This minimum is represented by the blue dashed line for species i & iii, and the red dashed line for ii, resulting in niche breadths i>ii=iii. Choosing lower values than this minimum (dotted extrapolation for ii) is theoretically unjustified and may skew the results. To emphasize the **density-dependent** niche, choose a value in the data (e.g. highest total abundance value in data) where curves approach a plateau. Here, this is represented by the grey dashed line and results in niche breadths i≫ii>iii.

2.2. Fitting the pairwise isodars

In practice, an isodar is simply a Model II regression between the abundance in two habitats, which means that when comparing n habitats we would end up with n (n–1) / 2 isodars, and the regression parameters from each. A perfect generalist would, as explained in the Introduction, have regression intercepts of 0 and slopes of 1 between all habitat pairs. For the regression method, we used **total least squares** (which minimizes the sum of squared orthogonal distances) which permits error in both axes. This method is implemented in the function 'fit_isodars' in the 'isoniche' package (using the option dim="pairwise"). The uncertainty around each isodar is summarized by the standard deviation (SD) of the least squares, which can optionally be used in later stages for inverse variance weighting (weights="1/var" in the 'iai' function, see section 2.3).

2.3. Generalizing the isodar to more than two habitats

If multiple habitat types are represented in each site, an ***n*-dimensional isodar** may be produced. In that case, instead of generating all possible sets of two-dimensional isodars and combining them to compute niche breadth, a single isodar represents the predicted distribution of individuals across all habitats at different abundances. Each observation is a point in an n-dimensional space corresponding to the n habitats, and a generalized total least squares regression identifies the hyperplane (with n–1 dimensions) that minimizes

the orthogonal distance between observations and the fitted hyperplane (thus, the classic isodar is simply a private case of this method, where $n = 2$). The resulting model has one coefficient for each habitat (analogous to the isodar slope) and an intercept. This is implemented in the function 'fit_isodars' in 'isoniche' (using the option dim="ndim").

3. Results

3.1. Applying the proposed index: Simulated populations

In order to test our proposed indices, we used the 'isoniche' package (Dubiner *et al*., 2026) to simulate abundance partitioning across habitat types A, B, and C in a set of 600 simulated populations, using the 'simulate_isodars' function. We ran 15 loops, each generating 40 populations with 10 sites in each population. For each site, we randomly generated abundance values in the three habitats to match predetermined isodar structures (with added Gaussian noise, SD = 0.25; see **figure S1** for a sensitivity analysis of different noise values). The 600 simulations were repeated for three isodar structures: neutral slopes (1) with neutral intercepts (0), positive slopes (of 1.5 between A-B and 1.5 between B-C) with neutral intercepts, and neutral slopes with positive intercepts (of 1.5 between A-B and 1.5 between B-C). Total abundance in the simulated populations ranged from an average of 4 per site to an average of 87 per site (**table S3**). For each simulated population we calculated isodar-adjusted inequality as described in the Methods, plus the 1–Gini inequality of relative abundances as a classic index for comparison (**figure 5**). Isodars were fitted using the 'fit_isodars' function (dim="pairwise" for pairwise isodars; dim="ndim" for *n*-dimensional isodars). Isodar-adjusted inequality indices were subsequently computed using the 'iai' function (abundances=NULL for the density-independent niche; abundances = 100 for the density-dependent niche).

The first notable difference between the classic and isodar-based niche breadth indices is that isodar-adjusted inequality is not dependent on abundance. Crucially, in the classic index it is impossible to distinguish the generalists from the specialists, if they have a non-zero isodar intercept, and if niche breadth is measured at different total abundances (which are both the probable cases under natural circumstances). At low abundances, the

positive-intercept simulations behave like the positive-slope ones, but increase until they are indistinguishable from the generalist simulations (**figure 5a**). This is due to the inability of the Gini index to account for density-dependence, and while this effect gradually attenuates with (see **figure 2**), it is still strongly evident at all tested abundances. In contrast, the isodar-adjusted indices are not affected by density and display a flat line (**figure 5b**; remaining deviations are due to the introduced noise, see **figure S1**). The pairwise method proved more precise and provided much better discrimination between generalists and specialists, while the *n*-dimensional method was less sensitive to noise (more consistent along different values of abundance, see also **figure S1**).

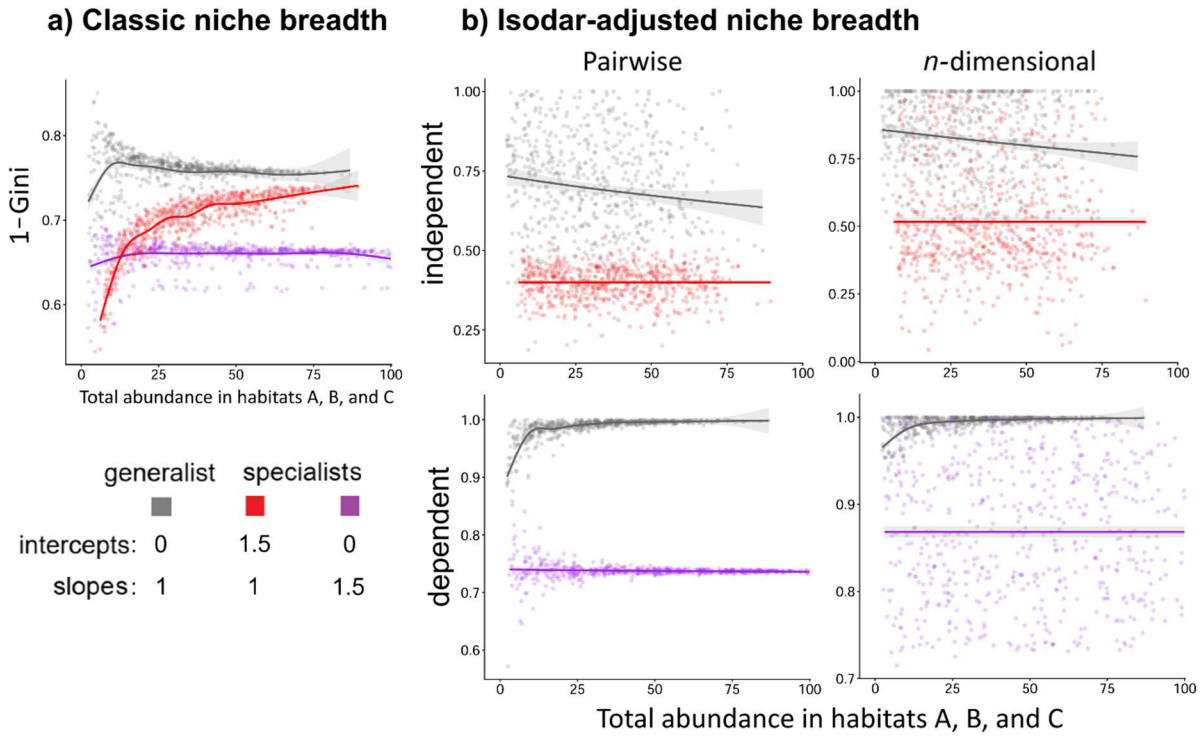


Figure 5. Comparing the classic and proposed niche breadth indices in relation to total abundance (summed across the three habitats, averaged across all sites), in simulated data. We tested the indices using 200 simulated populations with 10 sites each, created using three isodar structures: a perfect generalist with all isodars slopes=1 and intercepts=0 (**grey**), a specialist where we only changed the intercepts (=1.5 between both habitats A-B and B-C, **red**) and a specialist where we only changed the slopes (=1.5 between both habitats A-B and B-C, **purple**). All indices range from 0 indicating the narrowest niche, to 1 indicating broadest niche. The classic index **(a)** clearly

exhibits density-dependence given a non-zero (albeit low) isodar intercept, and therefore doesn't adequately discriminate between generalists and specialists. The isodar-adjusted indices **(b)** do not suffer from this problem. Of these, the top row shows the density-independent (intercept-based) component, based on predicted abundances at the lowest total abundance of individuals, whereas the bottom row emphasizes the density-dependent (slope-based) component, based on highest abundances (n=100; outliers with values >100 were excluded for clarity).

3.2. Applying the proposed index: Empirical data

Returning to the coral reef fishes data from Moorea (see section 1.2.3), we chose three species representing different abundance patterns: *Acanthurus nigrofuscus*, *Scarus schlegeli*, and *Siganus argenteus* (**figure 6a**), and calculated their classic and isodar-adjusted inequality indices. Individual isodar slope, intercept, and SD values were computed for each species across three habitats (barrier reef, fringing reef, and outer slope) using the 'fit_isodars' function in the 'isoniche' package (dim = "pairwise"). The *n*-dimensional isodar parameters were computed for each species across the three habitats using the 'fit_isodars' function (dim = "ndim"). Isodar-adjusted inequality was subsequently computed using the 'iai' function, as described in section 3.1 above. Pairwise isodars were weighted by their inverse variance (weights = "1/var").

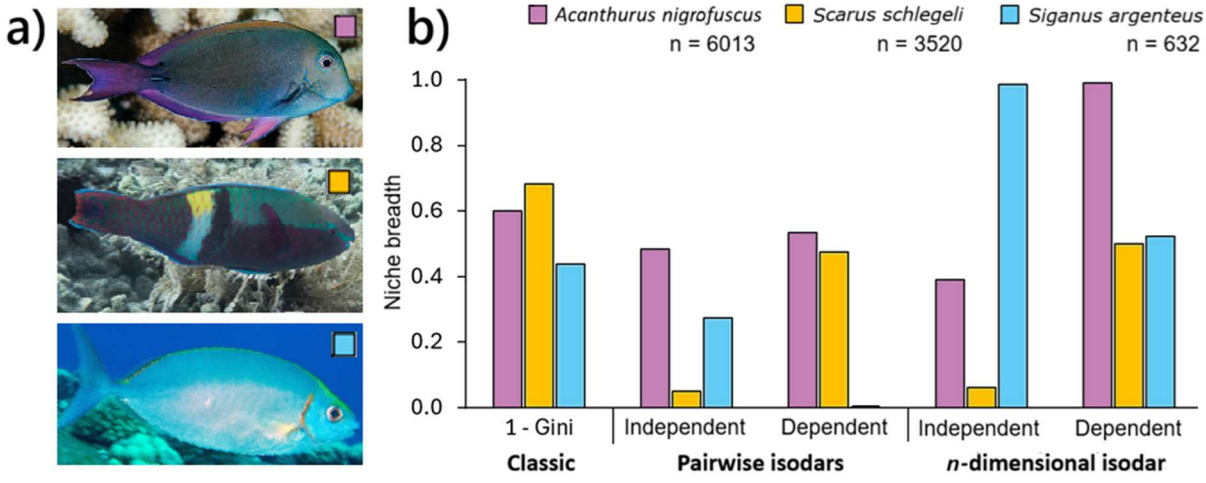


Figure 6. Niche breadth calculated using the abundances of three species of fish from Moorea, across three habitats and 13 sites (Dornelas *et al*., 2025). **a)** The three species, representing different

abundance patterns: *Acanthurus nigrofuscus*, *Scarus schlegeli*, and *Siganus argenteus* (images from FishBase). **b)** Each species' niche breadth estimated using one classical index and the indices proposed in this paper. Note that at low abundances (independent niche breadth) *S. schlegeli* is the has the narrowest niche, despite having the widest niche in the classic index. See **figure S2** for IAI curves and underlying data.

Given all that has been described so far in this paper, it is unsurprising that the Gini index produced a broad niche for the more abundant species, *A. nigrofuscus* (0.6, n=6013) and *S. schlegeli* (0.682, n=3520), but a narrow niche for the least abundant species *S. argenteus* (0.438, n=632). The isodar-based index painted a different picture (**figure 6b**, **table S4**). While the relative generalism of *A. nigrofuscus* was maintained across variations of the index, that of *S. schlegeli* was evidently driven by density-dependent niche breadth. In terms of density-independent (low-abundance) niche breadth, it appears drastically more specialized than the less abundant *S. argenteus*, regardless of isodar calculation approach. The narrow niche of *S. argenteus* in the classic index is heavily skewed by several sites with extreme abundances in the fringing reef (**table S2**), whereas at low abundances (which is the more common state for this species) there is no distinction between the fringing reef and outer slope.

The isodar-based indices differ from the classic index that merely focuses on "where is relative abundance higher". As detailed earlier, Gini is less biased at high densities, which is why the density-dependent (n=1000) niche breadth is more similar to the Gini. However, isodar-adjusting does take all isodars into account, so we consider its resulting density-dependent niche breadth estimates (*A. nigrofuscus* > *S. schlegeli*) to be more reliable than the unadjusted Gini (*S. schlegeli* > *A. nigrofuscus*). The different isodar-generation approaches (pairwise and *n*-dimensional) present differences in value owing not to bias (they both adequately address density-dependence), but to how they deal with variance, which can increase regression dilution. Data with less noise and well-defined habitat relationships accommodate pairwise isodars (**figure 5**), whereas high variance data (like that of *S. argenteus*, see **table S2**) are more consistent under the *n*-dimensional isodar (**figure S1**). The choice between methods should therefore be in accordance with the requirements of the specific data and the research question. However, it seems from these

preliminary analyses that our indices can be applied with ease to real ecological data, and improve and expand the inferences that can be made from them.

4. Discussion

Niche breadth estimates inherently encompass two distinct components: habitat selection in the absence of conspecifics, and changes to this habitat selection as conspecific density increases. Most current niche breadth estimates based on relative abundances or occurrences ignore these two distinct components and calculate a single niche breadth estimate, which leads to them being highly biased by abundance. All subsequent uses of biased niche metrics (see section 1.2.2) are therefore also implicated by this correlation with abundance. For example, studies describing an effect of niche breadth on abundance (or abundance-related metrics, e.g., Castaño-Quintero *et al.,* 2024; Granot *et al.,* 2025; Hernandez *et al.,* 2023; Izabel-Shen *et al.,* 2021; Rocha *et al*., 2018; Song *et al.,* 2022; Stuart-Smith *et. al.,* 2021) carry the risk of containing an inherently circular argument.

In this paper, using simulations and long-term reef fish survey data, we clearly demonstrated that current niche breadth indices are (biologically, and not just statistically) density-dependent. We developed a family of different indices, based on isodar theory, that help reduce bias and improve characterization of the niche concept. We wish to stress that while we focus here on the habitat niche axis, the arguments are relevant to many other niche axes as well. For instance, dietary niche breadth may be strongly affected by abundance (Kie & Bowyer, 1999; Redfearn & Pimm, 1988), and even niche axes that theoretically are non-consumable, like the climatic niche, may be utilized in a density-dependent manner (Ralston *et al.*, 2016).

The isodar-adjusted inequality (IAI) methods presented here are applicable for a wide range of data, but not all. Chiefly, they require several discrete repetitions (e.g., points in space or time) to enable total least-squares, on which all indices are fundamentally based, to be fitted. Accordingly, the 'isoniche' package (Dubiner *et al*., 2026), which implements all the methods described here, requires a table of abundance data with one column for each of the ≥2 habitats and one row for each of the ≥3 sites ("habitat" can stand

in for an equivalent component of niche such as diet item, host, or environment, and "site" can stand in for any relevant repetition in space or time). Beyond the necessary minimum, more repetitions will obviously ensure more accurate isodars, and improve confidence in the downstream indices. The *n*-dimensional isodar is, as we demonstrated, less susceptible to habitats with small sample sizes, weak pairwise relationships, and noisy or zero-inflated datasets. However, the reduction in the number of isodars also means the loss of some information that may be accounted for by the pairwise isodars, namely more precise discrimination among habitats, the absolute values of the isodar slopes and intercepts, and relations between specific habitats of interest. The choice between methods should therefore be in accordance with the specific data and research question.

The suggested index is based on the assumption of density-dependent habitat selection, which is probably true for many species (see section 1.2.3) under most circumstances (Haugen *et al.*, 2006; Kie & Bowyer, 1999; Planque *et al.*, 2011; Rosenzweig, 1991; Schilling, 2005; van Beest *et al.*, 2016). However, inverse density-dependence, where individuals aggregate in space is also possible (Sandin & Pacala, 2005; Stamps, 1988), and may explain why some slopes in real data may be negative. Although this may seem a caveat for isodar based indices, we point that inverse density-dependence and any other divergence from ideal free distribution will also impact classic niche breadth measures (although this issue is usually ignored). Another assumption is that isodars are linear, while in reality density-dependent habitat selection may be more complex. As a solution, it is possible to produce non-linear isodars and use them as the basis for the niche breadth calculations. Thus, the suggested indices may work with any kind of density-dependence model, and we encourage future studies to explore this. Nevertheless, we argue that even if the linear assumption is a simplification, it is still superior to ignoring density-dependence, and thus the abundance dependence, of many contemporary indices.

The argument that niche breadth may be biased by abundance has already been suggested. However, this was mainly raised in regard to detectability: rare species are less detectable, and therefore may appear to have narrower niche breadths (Redfearn & Pimm, 1988; Blüthgen *et al.*, 2008, Herrera-Lopera *et al.,* 2022). Mathematical methods to correct for sampling bias often treat low density as leading to statistical error only (e.g., Herrera-

Lopera *et al.,* 2022; Peguero *et al.,* 2017; Stuart-Smith *et al.,* 2021), yet both the detectability issue and the more inherent density-dependence of niche breadth can affect its estimation and cause it to correlate with total abundance. Some niche hypervolume approaches have incorporated density measures (Blonder, 2018), but for reasons other than those in the present paper. The main difference is that, while n-dimensional hypervolumes estimate niche breadth by examining the extent and shape of niche space occupancy, where density can inform the probability of niche space filling, they do not consider how this shape may change with species density or sampling effort. However, we show that density-dependence is a real problem, and both 2- and *n*-dimensional isodars examine how niche components' relative use changes based on density, addressing this issue directly. Thus, rather than asking how much multidimensional niche space is occupied (or even correcting it for density), our isodar-based approach tests how niche breadth itself changes with overall density. We emphasize that density-dependence is true beyond cases of ideal free distribution; it may be relevant in any system where the total number of individuals can affect an individual's choice, performance, or survival faced with a given habitat, host, diet, or environmental condition. Therefore, we highly encourage the implementation of isodar-adjustment to other niche breadth indices, beyond the relatively straightforward case presented here.

4.1. Conclusion

In summary, we present a set of alternative methods to calculate niche breadth indices based on isodars, which (in contrast to the current methods) are unbiased by total abundance and reflect both the density **dependent** and **independent** components of habitat selection, and are thus more reliable and informative. The **isodar-adjusted inequality** index may shed new light on many patterns in ecological niches, such as the relationship between breadth and richness or latitude (Granot & Belmaker, 2020; Granot *et al*., 2025), range size (Slatyer *et al.,* 2013; Stuart-Smith *et al.,* 2021), vulnerability to climate change (Colles *et al.,* 2009; Gaüzère *et al.*, 2015; Laidre *et al.*, 2008; Weaver & Mallinger, 2022), risk of extinction (Ceretta *et al.*, 2020; Clavel *et al.*, 2011; Davies *et al.*, 2004; Munday, 2004) and invasion probability (Vazquez, 2006; Granot *et al.,* 2017; Hui *et al.,* 2023). It is

possible that, as a consequence, our understanding of at least some of these patterns will change or expand.

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Supplementary files

Table S1: Review of niche breadth metrics in ten leading ecology journals (2015-2025).

Table S2: Fish abundance data from Moorea island.

Table S3: Abundance and niche breadth indices for each site in the simulated data.

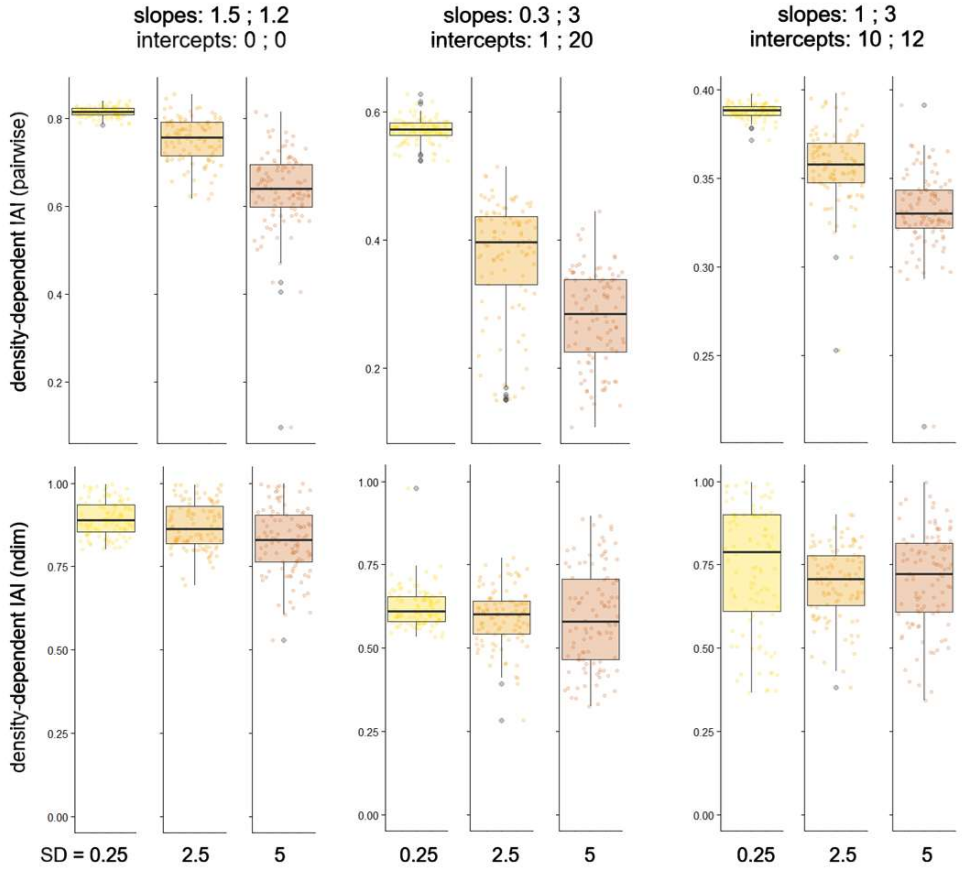
Table S4: Abundance and niche breadth indices for the three fish species used.

Code: R script to achieve all figures, tables, and statistical analyses presented here. The code for the isodar-adjustment method itself is available through the 'isoniche' package (Dubiner *et al*., 2026).

Figure S1: Density-dependent isodar-adjusted inequality (IAI) for 100 simulated populations all with the same isodars structure (see parameters). The only difference was the variance of the data (SD of the Gaussian noise). Both the pairwise and *n*-dimensional methods remain uncorrelated with total abundance. However, while the pairwise method (**top row**) is more precise, the simulations show that it is strongly influenced by variance, presumably due to regression dilution. In contrast, the *n*-dimensional method (**bottom row**) is constant, even under high values of noise or slope. SD values were 0.25 (yellow), 2.5 (orange), and 5 (brown).

Figure S2: a) Each species' niche breadth estimated using one classical index and the indices proposed in this paper. **b)** Raw survey data for the three species (higher values in red). **c)** Rarefaction-like curves of isodar-adjusted inequality against total abundance, used to obtain the values of density-independent breadth (inequality at the **minimum** abundance in the curve) and density-dependent breadth (inequality at the **maximum** abundance in the curve: n = 1000). Curves begin at the lowest value predicted by the isodars to contain individuals in all three habitats (from left to right: n = 127 and 35 for *A. nigrofuscus*, 48 and 2 for *S. schlegeli*, and 10 and 1 for *S. argenteus*. **P**: pairwise, **N**: n-dimensional

709 Figure S1



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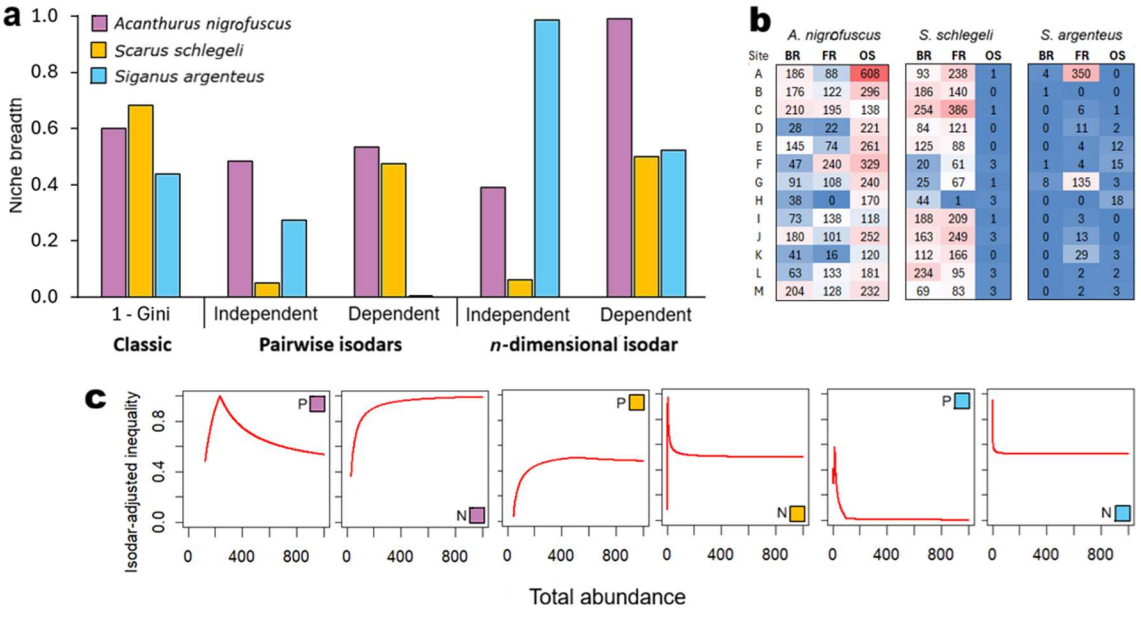
712 Figure S2



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