METHODS AND TOOLS

The role of ecological specialization in shaping patterns of insular communities

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Abstract

Aim: Research on the response of species richness to area and environmental heterogeneity so far has not addressed possible effects of species' differences in ecological specialization. Herein we provide a new metric, 'ecorichness', in an attempt to fill this gap.

Location: Aegean islands (Greece).

Taxon: Terrestrial isopods.

Methods: 'Ecorichness' estimates an island's biodiversity by integrating species richness and the specialists-generalists spectrum. We calculated 'ecorichness' for terrestrial isopods from 43 Aegean islands based on the habitats they exploit. 'Ecorichness' then was regressed on area, habitat diversity and the K-parameter of the Choros model using linear and quadratic models, compared based on AIC_c. A reduced data set, without halophilous species and coastal habitats, as well as an alternative description of habitat diversity, also was explored. The small island effect (SIE) thresholds identified using both a path analysis approach and piecewise continuous linear models were compared to the area of maximum 'ecorichness'.

Results: 'Ecorichness' response to area and habitat heterogeneity was best fitted by quadratic models with peaks located at an area similar to the SIE threshold identified by path analysis. Different measures of habitat diversity produced similar patterns. Exclusion of coastal species and habitats shows that the response of 'ecorichness' to area is mostly shaped by the increasing contribution of specialists in the assemblages of larger islands.

Main conclusions: 'Ecorichness' facilitates exploration of the role of ecological specialization in shaping community patterns. It can be applied to different community data sets, whenever habitat range exploitation can be quantified. Results from the case study accord with previous suggestions that the relative contribution of generalists and specialists differs between small and large island communities.

KEYWORDS
Aegean islands, generalist species, habitat diversity, habitat range, island biogeography, small island effect, specialist species

1 | INTRODUCTION

Habitat diversity, a measure of environmental heterogeneity, has been considered one of the main factors that shapes patterns of diversity in insular communities (Hortal et al., 2009, 2013; Ricklefs & Lovette, 1999; Stein et al., 2014; Triantis et al., 2003), even though its definition and measurement has not yet found a consensus among researchers. MacArthur and Wilson (1967, p. 8) in the first pages of their seminal book, explicitly stated their view on what an ultimate theory of species diversity should be based: "Our ultimate theory of species diversity may not mention area, because area seldom exerts a direct effect on a species' presence. More often area allows a large enough sample of habitats, which in turn control species occurrence. However, in the absence of good information on diversity of habitats, we first turn to island areas". We still lack "good information" on habitat diversity for most insular systems, so area remains the most common predictor of species richness, either as a proxy of environmental heterogeneity or as a factor acting 'per se' (e.g. Triantis et al., 2012). Attempts to incorporate an estimate of habitat diversity sometimes use elevation or some general typology of 'habitats' that has been formalized for conservation and other purposes, like the classification of habitat types in the Habitat Directive (92/43/EEC), the European Nature Information System (EUNIS, Davies et al., 2004) and IUCN's habitat classification scheme (http://www.iucnredlist.org/technical-documents/classification-schemes). There has been some controversy on how to best describe habitats and/or what habitat diversity actually is, and we still need a robust definition of relevant terms (see Dengler, 2010; Hall et al., 1997; Mitchell, 2005; Sfenthourakis & Triantis, 2017). Nevertheless, the diversity of habitats envisioned by MacArthur and Wilson (1967) as a critical component of an ultimate theory of island biogeography, is crucial for any global comparison and synthesis of factors shaping species richness for a wide range of study systems.

An important component in the interactions among species and their habitats, is the range covered by each species within the continuum of habitat specialization, from narrow specialists to wide generalists (e.g., see Holt, 2010). In the classical theory of island biogeography (MacArthur & Wilson, 1967) all species are usually considered as ecologically equivalent, an assumption that is at odds with established ecological niche theory. This was one of the drawbacks of the equilibrium model that according to Lomolino (1999) dictates the need for a new, species-based, paradigm in island biogeography. At the same time, the neutral theory of biodiversity and biogeography (Hubbell, 2001) was also based on the assumption of ecological equivalence among species, a contentious issue that was among the major targets of the theory's criticism (Matthews & Whittaker, 2014; Ricklefs, 2006; Tilman, 2004). Despite this much discussed problem, though, most island biogeography models are still based on simple counts of species without reference to their ecological variability.

Habitat specialization, in addition to its extensive use in population and conservation genetics, has received considerable attention in community ecology and metacommunity dynamics frameworks (e.g., Granot & Belmaker, 2020; Levins, 1968; Pandit et al., 2009), but less so in island biogeography. Gravel et al. (2011) proposed the 'trophic theory of island biogeography' using a food-web approach based on species interactions to evaluate the probabilities of species occurrences, but not directly address specialization. Some authors working on habitat fragmentation, however, have addressed specialization more directly by grouping species as either habitat generalists or specialists (e.g. Krauss et al., 2004; Rondinini et al., 2011; Soga and Koike, 2013; Matthews et al., 2014; Freeman et al., 2018). In island biogeography, these two categories are analysed separately or the distinction is exploited to explain phenomena such as the small island effect (SIE) (see Sfenthourakis & Triantis, 2009). However, this binary classification does not locate individual species along what is effectively a continuum across the generalist-specialist range thus ignores the diversity of ecological roles that might have important consequences for patterns at the community level; more so when different approaches to specialization are considered (see Bolnick et al., 2002; Devictor et al., 2010). The diversity of positions within the generalist-specialist continuum could be expressed quantitatively (e.g., see Julliard et al., 2006), and then be used in island biogeography models, instead of simple species richness measurements. Such an approach, though, assumes a detailed knowledge of each species' habitat preferences, as well as a meaningful classification of habitats occurring in the respective study area, but most studies do not report such data. At the same time, there is some dispute over the proper description of habitats. Some authors prefer a generalized description that fits all taxa whereas others support a taxon-based description that may vary according to the ecology of the organisms studied (for example, see debate between Dengler, 2010 and Triantis & Sfenthourakis, 2012). Here, we adopt the latter approach but our approach is compatible with both.

A related approach is to use 'functional diversity' as an estimate of species roles in island biogeography models (e.g. see Whittaker et al., 2014). Although functional diversity is a broad term aiming to evaluate species and organismal traits that influence ecosystem functioning (Tilman, 2001), most studies in the field address use of 'ecological space' on the basis of species' characters (Butler et al., 2000; Petchey & Gaston, 2002; Tilman, 2001). Functional diversity is usually assessed with multiple traits, and measures species' interactions with their environment indirectly, assuming that traits are related to meaningful ecological dimensions. Furthermore, no direct or generalized relationship between species traits and their place in the specialist-generalist continuum has been shown. Therefore, the effects of ecological specialization can be explored in a more direct way by a method that quantifies specialization range per se, instead of an indirect approximation via species' traits.

Here, we attempt a first tentative exploration of the effects of area and environmental heterogeneity on a modified metric of species richness that incorporates the varying ecological specialization of different species. The approach to specialization we follow herein could be seen as corresponding to the 'fundamental Grinnelian specialization' sensu Devictor et al. (2010, see methods for further details). In effect, we replace the occurrence of each species in the presence/absence matrix with the number

of habitat types it exploits in the study system and then we estimate an index of 'ecorichness' for each island by adding these values for all its species and standardizing for species richness, thus elucidating the interactions among species richness, habitat diversity and area in an informative way. Further, we evaluate the performance of the 'ecorichness' metric by applying it to a data set on terrestrial isopods from the Aegean islands (Greece), for which a detailed description of species' habitat ranges is available (Sfenthourakis, 1994).

2 | MATERIALS AND METHODS

2.1 | The metric

With prior knowledge on the habitat types exploited by the species included in the focal data set, we can assign each species a value equal to the actual number of habitats it exploits at the island group or archipelago level. These values range from 1 for the most strict specialists to the maximum number of habitats exploited by the most generalist species (evidently, a number that is either equal to or lower from the total number of habitats identified in the studied system), but the expected distribution of these values remains unknown. This is an important issue for future research in ecological niche theory, but for now it dictates the use of a 'null model' approach in evaluations of statistical significance of forthcoming results.

As already mentioned, this is a resource-oriented or fundamental Grinnellian metric of specialization, sensu Devictor et al. (2010), and uses a unique value for each species in all its occurrences, regardless of the actual habitat range present on each island. This means that a generalist species that might exploit 15 habitat types, is assigned the original value of 15 even on islands that host, for example, only five habitat types.

After assigning each species a habitat range value, we sum these values for all species occurring on each island (or community if the method is to be applied in other systems), substituting species richness with a 'habitat-range sum'. This value systematically increases with species richness at a rate depending on the relevant position of each constituent species in the specialist-generalist continuum. Therefore, to facilitate comparisons and explore further properties of this sum, we standardized the values. One approach would be to standardize with species richness, so that each island's sum is divided with its respective species richness, leading to a comparable set of species habitat specialization metrics per island, i.e. low values indicating islands with a dominance of habitat specialists and vice versa.

Another approach is to divide each sum with the average sum of randomized 'habitat ranges' for each island given by a null model. We assigned a random value of habitat range to each species, drawn from the whole range of values recorded in the studied system. Then we calculated the sum of these randomized values for each island, and repeated this for a computationally reasonable number of times and estimate the average sum. Of course, the number of nulls was

constrained by the number of available habitat types, in order to avoid redundancy. It should be noted, though, that both standardization approaches are identical, in the sense that the resulting values are linear functions of each other. This is so because the value assigned to each species in each random run is drawn from the full set of habitat range values, therefore, after a number of tries, each species should have been assigned all such values, and this happens for all species. In effect, the final randomized set of values for each island is a linear function of each species richness. So, elegance notwithstanding, a simple division of habitat range sums with species richness is a much easier and quick method, leading to the simpler metric presented herein:

$$\text{Ecorichness} = \frac{\sum_{i=1}^{S} \text{HR}_i}{S} \qquad (1)$$

where HR is the habitat range value of a species i and S is the species richness of the island.

'Ecorichness' can be used as an alternative and complementary metric in biogeographical and ecological analyses that traditionally use species richness. We do not suggest that 'ecorichness' should substitute for species richness, only that it may offer a new and different insight into community structure compared to the use of simple species richness. More specifically, it can reveal possible differences in community composition among islands, systems or taxa, focusing particularly on the relative contribution of specialist and generalist species. Furthermore, the metric avoids a simplistic binary assignment of species as specialists or generalists, as it is based on each species' range within the respective continuum.

2.2 | Predictions

In our previous work (Sfenthourakis & Triantis, 2009), based also on theoretical considerations (see also Holt, 2010), we suggested that small island communities consist mainly of generalists while specialists are added with increasing area. This is in accordance with the predictions of the equilibrium theory of island biogeography (ETIB) regarding turnover rates, which should be higher for smaller islands, allowing the occurrence of species with good dispersal abilities and, on average, of those that are more opportunistic, which are more often also generalists. If this assumption is valid, we would expect a decreasing or a unimodal 'ecorichness'—area curve. Whatever the pattern at the left part of the curve, though, the right part (larger islands) should always show a decreasing trend. This is due to the following effects:

a. 'Ecorichness' of very small islands should be strongly affected by the actual values of the generalists they host since the denominator of the formula (see Equation 1) will be a very small number. This means that they are not expected to show a consistent pattern, especially in cases where there is a strong SIE, i.e. when effects of area on species richness are decoupled from those of

habitat diversity on small islands, and they are not the same as those on larger islands, if any effects remain at all.

b. When the SIE is not particularly strong, 'ecorichness' should increase with area due to a disproportionate mixture of more generalists and less specialists, whose habitat range values' sum would be divided by a small species richness value.

c. 'Ecorichness' should peak at an area threshold where the contribution of generalists is maximized, and then

d. Should decrease above this threshold, due to the lower increase of nominator values (see Equation 1) as the specialists' contribution increases, leading to smaller 'ecorichness' values.

2.3 | Case study

In order to provide an empirical example of our proposed method and predictions, we use data on terrestrial isopods (Oniscidea) from central Aegean islands (see Appendix S1), for which we do have the necessary information (see Sfenthourakis, 1994, 1996). The 43 islands included in this case study range in area from 0.025 to 477.94 km^2 and have a variable topography, geological structure and isolation history (see also the papers in Sfenthourakis et al. 2018 for additional ecological and palaeogeographical data on Aegean islands).

Isopod species richness on these islands ranges from five to 38 species, with a grand total of 69 species across all the islands. On each island, the whole range of habitats exploited by terrestrial isopods has been sampled, and a detailed description of the habitats in each sampling site has been recorded. A total of 20 habitat types that are relevant to Oniscidea were identified (see Appendix S2), with the smallest islets having three and all 20 types present on larger islands (in particular, Samos, the largest island in the data set, and Ikaria, the fifth largest, but ecologically very variable island).

In order to test for possible effects of the specific habitat type description, we also ran the same analysis with a more inclusive habitat classification using only 11 habitat types, after merging similar types of the more detailed classification. The corresponding changes in species' habitat ranges should not be trivial (i.e. a directly analogous reduction of values), though, since some species may exploit similar habitats only, while others exploit a more variable set. The reduced set of habitat types is shown in the Appendix S2.

Terrestrial isopod assemblages on insular regions always include a few halophilous species that are restricted to coastal habitats, two of which at least are widespread on the islands. These species are 'specialists' according to the definition used herein, as they exploit up to two habitat types, but in fact they occur in all coastal areas that have their general category (e.g. *Ligia italica* lives on rocky shores, which are present on all islands, regardless of other characteristics, such as substrate type). Thus these species may introduce some bias in the estimation of the metric, so we also checked the effect of area on 'ecorichness' after their exclusion (following also Sfenthourakis & Triantis, 2009). The eight excluded halophilous species are shown in Appendix S1.

2.4 | Data analysis

All the following statistical analyses were implemented within the R programming environment (R Core Team, 2019). We explored the relationship between the isopod 'ecorichness' metric and log_{10}-transformed island area (hereafter Area) but all the following analyses were also conducted using alternative predictor variables: log_{10}-transformed habitat diversity (HD), and Area × HD (=K) as implemented in the 'Choros' model (Triantis et al., 2003). In order to test how 'ecorichness' varies along the area gradient, we first fitted a simple linear model with Area as a unique predictor and a second model including the quadratic term $Area^2$ to identify any potential hump-shaped patterns. The significance of both models was assessed using the F-statistic, with the goodness of fit compared using R^2 and we further compared these two models using the small sample size-corrected AIC_c. The quadratic model was preferred to the linear model if three criteria were met: (a) the difference in AIC_c (ΔAIC_c) between the linear and the quadratic model, in favour of the quadratic model, was > 2, (b) the two slopes of the quadratic model were significant, and (c) the first slope was positive and the second negative. Residuals of the best models were inspected in order to detect deviations from normality and homoscedasticity and to identify outliers. When the quadratic model was preferred, we estimated the area at which 'ecorichness' is expected to be maximum (E_{max}), which corresponds to the vertex of the quadratic model and is calculated as:

$$E_{max} = -\frac{z_1}{2z_2} \tag{2}$$

where z_1 is the slope estimated for Area and z_2 is the slope estimated for $Area^2$.

Since the quadratic model provided better fit, we further checked whether such a model could be the product of the specific combinations of 'ecorichness' values used in this specific analysis. To do this, we implemented a null model approach that consisted of 10,000 runs on a randomized data set produced by shuffling the observed habitat range values among species and re-calculating 'ecorichness', keeping species richness and incidences of the original presence–absence matrix constant. At each run, we recalculated 'ecorichness' for each island, we refitted a linear and quadratic model, and counted how many runs met the three aforementioned criteria.

In a next step, we checked for the presence of a SIE in our log_{10} transformed species richness in order to compare the threshold(s) with the Areas of slope change in the quadratic model estimated for 'ecorichness'. To do so, we used two approaches. First, we identified the SIE area threshold, if present, with the path-analysis approach of Triantis et al. (2006). The path-analysis approach uses partial correlations among area, habitat diversity and species richness, to identify a SIE threshold at the point where (and if) the direct effects of Area on species richness become statistically not significant, even though indirect effects may still occur via HD, which is most often strongly correlated with Area. The test is implemented through the exclusion

of islands sequentially from the largest to the smallest, and meanwhile estimating the standardized partial coefficients b_A and b_{HD} of Area and HD, respectively. When b_A reaches zero or becomes negative, the corresponding area is considered as the upper limit of the SIE (Triantis et al., 2006). A more detailed description of the method can be found in Triantis et al. (2006). Second, we implemented the four piecewise continuous models of Yu et al. (2020), namely the continuous one-threshold and the left-horizontal one-threshold models and the continuous and the left-horizontal continuous two-threshold models. To test whether the relationships between species richness and Area exhibited a SIE, we also compared the aforementioned piecewise models with a simple linear model. Models were compared using Akaike's information criterion (AIC_c) corrected for small sample size (Burnham & Anderson, 2002).

All analyses were done using R (R Core Team, 2019) and the package 'sars' (version 1.3.0; Matthews et al., 2019). The new functions for the piecewise models will be published on CRAN, but are currently available on GitHub and can be installed in R using the command: devtools::install_github("txm676/sars", ref ="thresholds_2"). See also for Matthews et al. (2020) for further details on the fitting procedure).

3 | RESULTS

For the total data set, the relationship between 'ecorichness' and Area was best fitted by the quadratic model ($R^2 = 0.27$, $p = 0.001$, Figure 1a and Table 1). In the null model analysis, only 3.7% of the 10,000 null model iterations reproduce a pattern similar to the one observed, a finding that supports the statistical significance of the model.

The alternative habitat type description when applied to the total data set gave very similar results (Appendix S3), with the fit of the quadratic relationship between 'ecorichness' and Area being even better (quadratic: $R^2 = 0.35$, $p = 0.001$, $AIC_c = 24.22$; linear: $R^2 = 0.14$, $p < 0.013$, $AIC_c = 34.11$). Therefore, our results are not biased by the habitat type description used.

A linear model fits the data better ($R^2 = 0.45$, $p < 0.001$) after the exclusion of halophilous species (Figure 1b and Table 1). The quadratic model becomes better again ($R^2 = 0.49$, $p < 0.001$; Figure 1c) after the exclusion of three outliers, i.e. islands with very few non-halophilous species (two or three). The denominator in the 'ecorichness' formula for these islands becomes disproportionately small after the exclusion of halophilous species, possibly biasing patterns. The slope of the left part of the curve for the reduced data set is not statistically significant, meaning that very small islands do not produce a consistent pattern (Table 1). Since Area, HD and K were all highly correlated with each other (Area−HD: $r = 0.97$; Area−K: $r = 0.99$; HD−K: $r = 0.98$), all the aforementioned statistical analyses produced very similar results when performed with HD and K instead of Area as the predictor (Appendix S4).

A significant SIE threshold was identified at an area of 4.58 km^2 using the method of Triantis et al. (2006) (Figure 2a) and at 0.31 km^2 according to the left-horizontal one-threshold model ($AIC_c = -91.35$), that fitted better the data than a continuous one-threshold ($AIC_c = -90.04$), a left-horizontal and a continuous two-thresholds models ($AIC_c = -90.62$ and -87.76, respectively), or a simple linear model ($AIC_c = -84.91$) (Fig. 2b, $R^2 = 0.92$, $p < 0.001$). Accordingly, the E_{max} for the quadratic model of 'ecorichness' and area for the total data set was estimated at 13.33 km^2. After the exclusion of halophilous species, it was estimated at 0.96 km^2, but without statistical support (Table 1).

4 | DISCUSSION

Species–area and species–habitat diversity relationships are well-known patterns in biogeography. Nevertheless, the ways these two
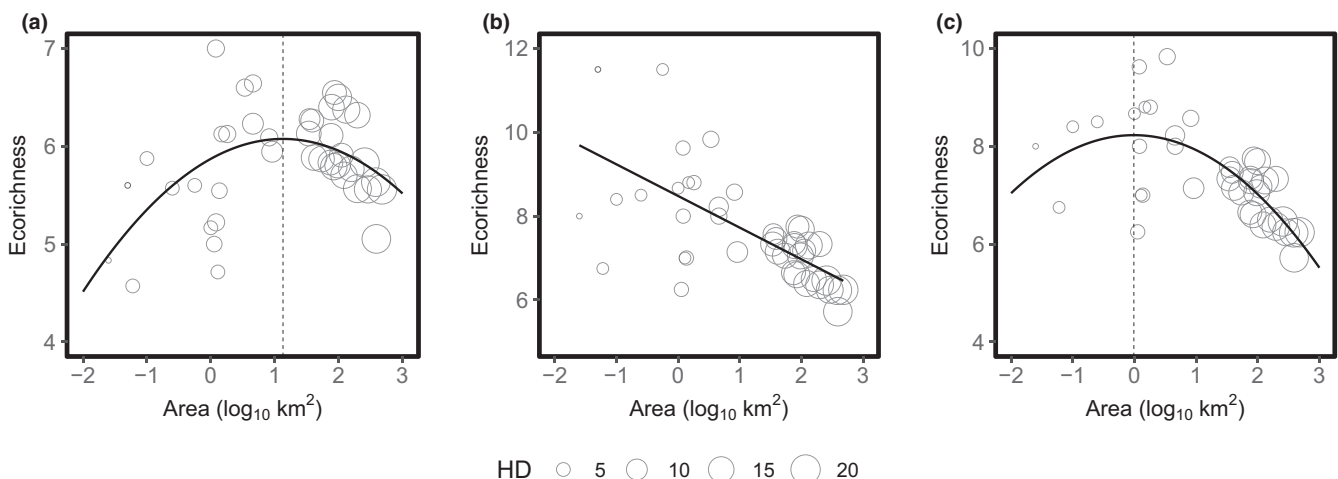

FIGURE 1 The response of 'ecorichness' to log$_{10}$area for the total data set (a), after the exclusion of halophilous species and coastal habitats (b), and after the further exclusion of three outliers (c), as explained in the text. Dots indicate islands. To illustrate the strong correlation between area and habitat diversity (HD), the size of dots was made proportional to the number of habitats on each island. The dashed vertical lines represent the E_{max} of the quadratic model

TABLE 1 Results of the different models fitting to the relationship between 'ecorichness' and $\log_{10}$area. Asterisks denote statistical significance (***<0.001, **<0.01). The slopes z_1 (first-order) and z_2 (second order), the R^2, the AIC_c as well as the value of E_{max} for the quadratic model are given.

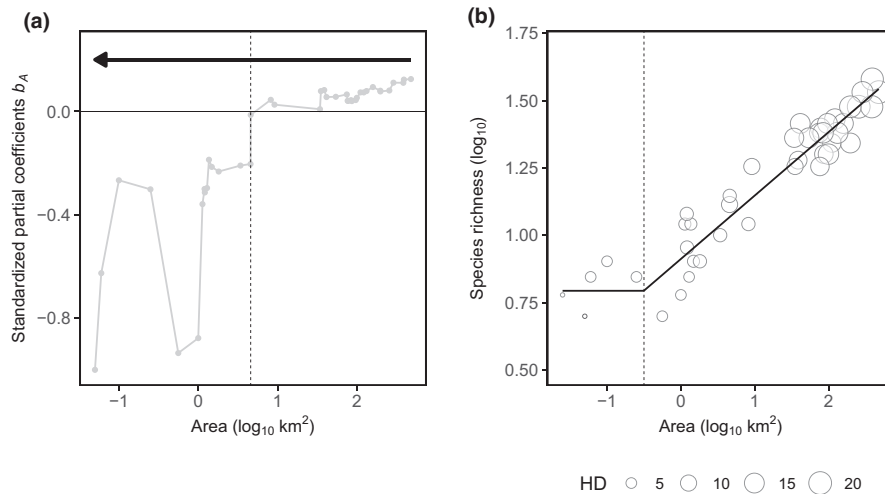| Model	Parameters	Complete data set	Without halophilous species	Without halophilous and outliers
Linear	z_1	0.14 ± 0.06***	-0.76 ± 0.13***	-0.48 ± 0.11***
	R^2	0.11	0.45	0.33
	AIC_c	68.73	131.29	100.31
Quadratic	z_1	0.36 ± 0.09***	-0.61 ± 0.210**	-0.01 ± 0.17
	z_2	-0.16 ± 0.05**	-0.11 ± 0.118	-0.30 ± 0.09**
	E_{max} (km^2)	13.33	0.002	0.96
	R^2	0.28	0.46	0.49
	AIC_c	62.16	132.84	91.77

FIGURE 2 Results of two analyses conducted to seek for the presence of a small island effect (SIE) in $\log_{10}$ transformed species richness. (a) Variations of standardized partial coefficients of $\log_{10}$area b_A with the sequential exclusion of islands from the largest to the smallest (arrow). When the coefficient b_A reached a zero or negative value, the corresponding area was considered as the upper limit of the SIE and was indicated with the dashed vertical line. (b) The species–area relationship for terrestrial isopods on the Aegean islands. The thick solid lines represent the predicted values of the left-horizontal one-threshold model which was found to best fit the data. The best model was selected using AIC_c-based model selection. To illustrate the strong correlation between area and habitat diversity (HD), the size of dots was made proportional to the number of habitats of each island. The dashed vertical line represents the SIE threshold of the model

factors interact to determine biota remain elusive. Triantis et al. (2003) proposed the Choros model to depict the ecological space experienced by species on each island, and found that it provides a better prediction of species richness than the predictions made by using area or habitat diversity alone, in most of the cases studied (see also Pereira & Daily, 2006; Tjorve, 2002). Herein, we attempted a more elaborate description of the 'ecological potential' of each island in terms of the habitat range that species actually exploit, using a metric that also reflects the degree of habitat overlap among species.

We adopt a taxon-specific definition of habitats (see also Manning et al. 2004 for a similar approach in habitat fragmentation studies), but the method should work also for other habitat descriptions that capture the variability in the habitat range exploited by different species. Nevertheless, we do believe that environmental heterogeneity is perceived differently by different taxa, so a good knowledge on the ecology of the organisms studied is imperative for a meaningful estimation of habitat diversity (Triantis & Sfenthourakis, 2012). It should be noted also that our method is not

based on the actual values of the proposed metric but on the pattern of its response to area (or other factors). As such, we expect that any measurement of habitat diversity should produce patterns that can prove useful, not only in the exploration of the specific study system, but also in the comparison between different systems and taxa. The effect of the relative contribution of specialists and generalists on area, for example, should be retrieved regardless of the exact mode of habitat classification.

A possible drawback of the method is that it implicitly uses all habitat types as equivalent. Of course, habitats do not cover the same area and habitats do not host equal numbers of species. The effect of habitat area on species richness exploiting them (Ricklefs & Lovette, 1999) might be an interesting topic for the future development of the 'ecorichness' approach. Nevertheless, until such data become available, our method is an improvement of the simplistic binary specialist/generalist assignment of species.

The metric we established has the potential to provide insights into the relative contribution of specialists and generalists in the

insular biotic assemblages studied. It can be implemented in island biogeography studies, in addition to traditional species-area and/or species-habitats approaches, as a complementary tool that expands our view on biotic processes. It can be useful also in other kinds of data sets, such as those from habitat islands and other biotic communities. A variant of the metric described herein could be applied also on habitat fragments, where the relative contribution of specialists and generalists is of particular interest (Ewers & Didham, 2006; Tischendorf et al., 2003). Since, by definition, fragments comprise the same habitat, the quantification of each species' habitat range in this case should be based on data stemming from their total distributional range. In addition, if the taxon-specific habitat view is adopted, even fragments can be seen as comprising different sets of special habitats and/or micro-habitats of their constituent species, so that 'ecorichness' can be calculated using the formula described herein.

In addition to area, it would be informative to explore the relationships between 'ecorichness' and other factors, such as habitat diversity and isolation. For example, we might expect isolated archipelagos to host a higher percentage of more generalist species, given that they are characterized by a higher dispersal ability and a stronger potential to establish populations in new environments compared to specialists. On the other hand, systems with higher habitat diversity might be expected to host a higher percentage of specialists as a result of niche partitioning. In a similar line of reasoning, 'ecorichness' might prove useful in exploring different responses of different taxa to the environmental heterogeneity of the same system.

'Ecorichness', thus, should be seen as an exploratory tool that is not expected to show consistent patterns among all systems and taxa. Such consistent patterns would be found only if some generalized distribution of 'habitat ranges' underlie patterns of most communities, as it seems to be the case with species-area effects. At the moment, though, we have no such theory, given also that even

niche theory (see Hirzel & Le Lay, 2008; Miller & Holloway, 2017; Vandermeer, 1972) does not predict any such general distribution of species by niche breadth at the community level. When a sufficiently large amount of data from a variety of case studies will have been accumulated we might be able to detect possible general trends.

Most island biogeography studies do not record or, at least, report data on population abundance per habitat type, so the use of a metric such as the one proposed by Levins (1968), is not possible in most cases. Of course, we are aware of the scarcity of published data on habitat range per species for most island systems, which is an obstacle to the application of the proposed method. Nevertheless, we expect this work to provide a catalyst for collecting and publishing more such data in the future. Thus, the case study presented herein should be seen as a preliminary test of the new metric, highlighting its potential in the exploration of interesting community patterns.

In agreement with our prediction, the relationship of 'ecorichness' with logArea is expressed as a hump-shaped curve for the total data set, ascending for small values of area and descending for areas larger than the SIE threshold. The widely distributed halophilous species in the studied taxon seem to affect the shape of the curve, as they lower 'ecorichness' values on very small islands. Thus, the exclusion of these halophilous species and the corresponding coastal habitats leads to a 'heightening' of the left part of the curve, i.e., an increase in 'ecorichness' values for smaller islands, strongly affected by outliers. All these responses are in accordance to the original predictions, based on Sfenthourakis and Triantis (2009), supporting the observation that communities of small islands consist mostly, but not exclusively, of generalist species, while the contribution of specialists becomes important above the SIE threshold.

Therefore, our findings reveal different responses of small and large islands (that is, islands with low and islands with high habitat richness, since area and habitat richness exhibit an almost perfectly linear relationship), documenting an increased role of ecological specialization with area. Given that habitat diversity of the studied
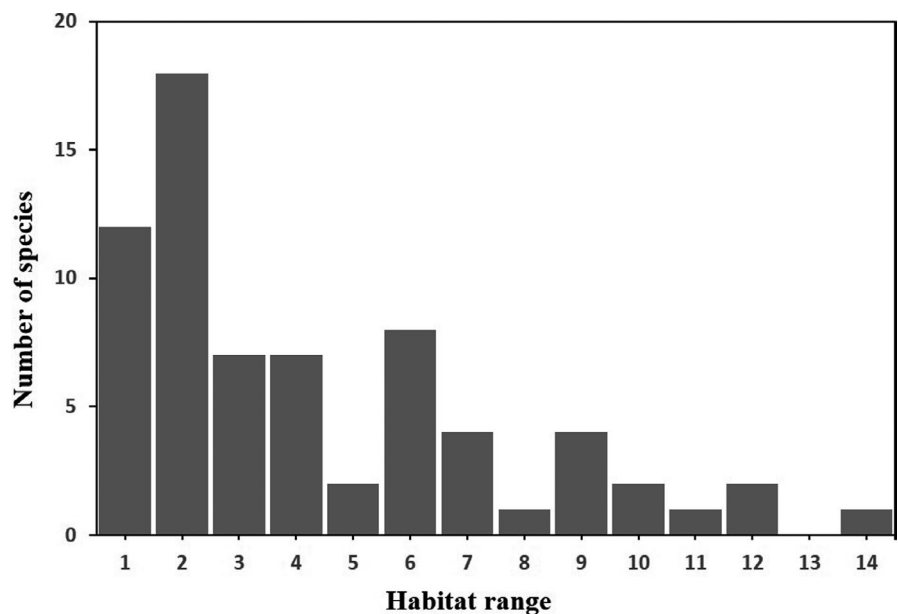
FIGURE 3 The frequency distribution of species' habitat ranges

system does not show 'saturation' with area, our results can be explained only by the increasing contribution of specialists in the island faunas. Sfenthourakis and Triantis (2009) attributed this pattern, at least partly, to the gradual occurrence of more keystone habitats (see Tews et al., 2004) with increasing area, such as permanent freshwater that is crucial for the occurrence of certain isopod species and in the Aegean is absent from very small islands. Similar effects of other 'key' habitats and habitat features can be expected to affect other taxa, such as the occurrence of tree stands, a more rugged topography, or a more variable vegetation. Furthermore, our findings corroborate the results of the meta-analysis performed by Granot and Belmaker (2020) on various communities that showed species in richer sites to be more specialized.

The slope change in the quadratic model occurs at an area of 13.33 km^2, which corresponds well to the SIE threshold (4.58 km^2) estimated by the method of Triantis et al. (2006). This result provides further support to the above-mentioned role of key habitats above an area that enables an increased participation of specialists in insular communities, possibly due to topographical reasons (e.g., allowing existence of permanently running streams, tree stands, cultivations, ponds and/or swamps). The one-threshold SIE model gives a much lower threshold but this model completely ignores the indirect effects of habitat diversity on species richness via its collinearity with area, so it does not offer much insight into 'ecorichness' patterns.

The implications of the approach followed herein may also shed light on the debate about effects of increasing habitat diversity on species richness (see Hortal et al., 2009; Allouche et al., 2012; Hortal et al., 2013; Kadmon and Allouche, 2007). According to Allouche et al. (2012), species richness should decrease with increasing habitat diversity above some threshold, due to the high fragmentation of available habitats that would not allow persistence of some species. The increasing contribution of specialists with increasing habitat richness might superficially seem to be in line with such a prediction. Nevertheless, we should note (see Figure 3) that almost half of the species in this system exploit between 3 and 9 habitats (or 15%–45% of all habitats), and another 26% of the species exploit 2 habitats (or 10% of total), meaning that the vast majority of species are not the strict specialists, sensitive to the extreme fragmentation, assumed by the model of Allouche et al. (2012). Real species exploit the whole range of a generalist-to-specialist spectrum. Our findings here only underline the importance of more habitats being available with increasing area, allowing larger communities that consist of more and more species towards the specialist side of the spectrum. As Hortal et al. (2013) have shown, a more realistic incorporation of this variation in species habitat range (and of other biological parameters as well) leads to a constant increase or, at least, a plateau of species richness with increasing habitat diversity.

We believe that the 'ecorichness' approach can offer useful insights into the processes lying behind the relationships among area, species richness and habitat diversity, in general, through a quantification of the 'ecological resource space' used by species in each case. This approach falls within the general framework of a species-based

theory of island biogeography envisioned by Lomolino (1999), and addresses an aspect of community structuring implicit in 'assembly rules' (see Weiher & Keddy, 1999). Furthermore, the concept of a quantitative evaluation of individual species' habitat ranges, despite its strong affinities, remains distinct from the concept of niche breadth, for which we have a prolific literature, as it focuses on local habitat exploitation for which published data are very scarce. This scarcity of data on a species-by-species habitat range does not allow for a generalization of the present results, but we hope that our approach will trigger further studies producing such data in the near future, so that the model can be tested in a variety of taxa and systems, not necessarily restricted to islands. Of course, the study of functional diversity has its own merits in terms of species' adaptations and trait divergence, which the approach via specialization range cannot tackle. A synthesis of both approaches, then, might offer important insights into processes shaping island communities.

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SUPPORTING INFORMATION

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