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BIODIVERSITY RESEARCH

Integrating multiple scales in rarity assessments of invertebrate taxa

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ABSTRACT

Aim To provide a procedure for measuring the rarity of both invertebrate species and assemblages of species from multiple scales without the need for fine-resolution datasets over broad areas.

Location The western Palearctic (WP) and western France.

Methods On the basis of different datasets from different geographical extents, we applied a multiscale rarity weight to species occurrence from multiple scales. Multiscale rarity weights were then averaged at an assemblage level in a multiscale index of relative rarity (I_{RR}). These rarity weights were calculated using a flexible, scale-dependent method that ensures equitable contributions of each scale to the final index. We provided a simple two-scale example of the application, on spiders of western France, for which we obtained occurrence information from a regional-extent dataset (regional scale) and a western Palearctic-extent dataset (WP scale). Thus, we showed the necessity of a two-scale approach by successively analysing species occurrence, multiscale rarity weights of species and multiscale indices of species assemblage. Finally, we presented a case study within a nature reserve.

Results Species occurrences are not predictable from one scale to another, and rarity indices of assemblages are poorly congruent among scales, which supports the necessity of a two-scale approach. Multiscale rarity weights accurately showed information on species rarity from both scales. Multiscale indices of assemblages were congruent but with additional information over each one-scale index.

Main conclusions The novelty of the multiscale method developed here is to accurately combine different datasets of varying extents and resolutions to provide multiscale rarity weights for species and indices for assemblages. Given the increasing availability of datasets for invertebrate taxa, this method represents a significant improvement for rarity and conservation studies on invertebrates.

Keywords

Management monitoring, occurrence data, rare species, rarity hotspots, spiders, western Palearctic.

INTRODUCTION

Ecology is scale dependent; hence, the scale with which we assess ecological systems affects our perspective of the system (Schneider, 2001). This is valid for rarity studies: a species may be considered rare on a local scale, yet common at a regional or global scale (Flather & Sieg, 2007). Indeed, processes controlling the distribution of species have relative importance that change with scale (McGill, 2010). Thus, rarity is also scale dependent, and growing awareness of this consideration has led ecologists to quantify rarity across multiple scales (Rabinowitz, 1981; Hartley & Kunin, 2003; Fagan *et al.*, 2005; He & Condit, 2007).

Rabinowitz (1981) developed a typology of rarity based on three axes of species distribution, each relating to a different scale of analysis: geographical range size, habitat specificity and local density. This typology has been widely applied in conservation studies (e.g. Kattan, 1992; Abellán *et al.*, 2005; Broennimann *et al.*, 2005; Isaac *et al.*, 2009); however, apart from few rare examples (Fattorini, 2010; Fattorini *et al.*, 2012), its application on lesser-known taxa, such as invertebrates, is often problematic because of lack of data on the

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abundance and habitat specificity or difficulties in obtaining such data. In contrast, data on geographical range size (e.g. occurrence data) are more readily available, and thus, most multiscale approaches are specifically developed for this. The most frequent multiscale methods based on range size are the scale–area or occupancy–area curves (Fagan *et al.*, 2002; Hartley & Kunin, 2003; Fagan *et al.*, 2005; He & Condit, 2007; Azaele *et al.*, 2012). Scale–area curves consist of plotting the area occupied by a species as a function of scale (defined as a grid-cell area); these curves were used for measuring the extinction risk (Fagan *et al.*, 2002; Hartley & Kunin, 2003; Fagan *et al.*, 2005). A shared conclusion of multiscale studies is the necessity of using and combining information from multiple scales when investigating species rarity (e.g. Warman *et al.*, 2004), especially when making a link between rarity and extinction risk (Hartley & Kunin, 2003; Fagan *et al.*, 2005). Thus, for a given study, different conservation priorities might have been chosen had a different arbitrary scale been chosen as a standard (Pearman, 1996 in Hartley & Kunin, 2003). However, although published conservation studies based on multiscale analyses can be found for vertebrates (e.g. Fagan *et al.*, 2002, 2005) and plants (Pärtel *et al.*, 2005), the task is much more difficult for invertebrates. An interesting two-scale (regional and European) method for assessing butterflies was proposed by Fattorini (2009). However, this method uses the Red List statuses of species, which are lacking for most invertebrates (Rands *et al.*, 2010; Zamin *et al.*, 2010; but see Cardoso *et al.*, 2011a). In fact, the majority of rarity studies on invertebrates are single-scale studies, irrespective of their aim of biodiversity conservation (e.g. Samu *et al.*, 2008; Dapporto & Dennis, 2008) or others (e.g. McCreadie & Adler, 2008). Therefore, integration of multiple scales when investigating invertebrate rarity for conservation studies is required to improve reliability and reduce biases.

Although scale–area curves are a promising multiscale approach for invertebrates, we identified two major issues precluding their application in invertebrate conservation studies. First, the lack of broad-scale distributional data for most invertebrate taxa (Cardoso *et al.*, 2011b) is restrictive. Indeed, to be meaningful, scale–area curves require several different scales, that is, they require a broad area dataset at a fine resolution. However, distribution data for invertebrates are either at fine resolutions but on restricted scales (e.g. a region or a small country) or at broad scales but with coarse resolutions (e.g. Fauna Europaea, 2011). Hence, for invertebrates, scale–area curves will most often be applied using a restricted number of scales. Second, the diversity of most invertebrate taxa implies conservation at the assemblage level, whereas multiscale methods were designed at the species level. Consequently, most conservation studies on invertebrate taxa focus on either surrogate species for assemblages or habitats (Cardoso *et al.*, 2011b), or assemblage-level assessments such as scoring procedures (e.g. Dapporto & Dennis, 2008; Simaika & Samways, 2009; Fattorini, 2010; Leroy *et al.*, 2012). Therefore, a multiscale rarity metric at the assemblage level would be a valuable improvement to invertebrate conservation studies. The aim of this study is to provide a procedure to measure the rarity of both invertebrate species and assemblages from multiple scales, without the need for fine-resolution datasets over broad areas.

To generalize this procedure, it has to be based on the most available data regardless of the taxa: occurrence data. The basic assumption is that because we lack a broad-extent fine-scale database, we can combine multiple datasets to obtain a multiscale procedure. Indeed, this is possible because of the increasing availability of datasets (see Jetz *et al.*, 2012), irrespective of whether local, regional, or national scales (e.g. atlas data or regional surveys such as Harvey *et al.*, 2002), or even larger scales (e.g. datasets combining occurrence data from different sources such as Global Biodiversity Information Facility (GBIF, 2012) or species lists from different countries such as Fauna Europaea, 2011). Thus, scale is here defined as the extent of the considered dataset. We apply the method introduced by Leroy *et al.* (2012) to calculate a multiscale rarity weight for species from species occurrences at different scales. Multiscale rarity weights are then integrated at the assemblage level with the Index of Relative Rarity; the advantages were discussed in Leroy *et al.* (2012).

We describe the multiscale weighting method and index of relative rarity (I_{RR}) and provide a two-scale example of analysis on spiders of western France. At a regional scale, spider occurrences are obtained from a fine-resolution database for western France (Pétillon *et al.*, 2007a). At a biogeographical scale, spider occurrences are obtained from a coarse resolution database for western Palearctic (WP) (Canard, 2005, updated in 2011). We first analyse the relationship between regional and WP occurrence of the species and then apply the multiscale index on a case study in a national nature reserve. On the basis of these examples, we discuss the improvements provided by a multiscale rarity measure over single-scale rarity measures.

METHODS

Multiscale weights of rarity

Rarity weights are calculated on the basis of species occurrence at each scale with a weighting method that can be adjusted according to a user-chosen rarity cut-off point (Leroy *et al.*, 2012). Rare species receive rarity weights that increase exponentially when their occurrence falls below a rarity cut-off point. Thus, weights of rare species (with occurrence lower than the cut-off) are amplified, whereas weights of common species (with occurrence higher than the rarity cut-off) tend to be zero. This method has been proven to be less biased than the other existing methods, mainly because of its flexibility (Leroy *et al.*, 2012). Here, we applied an improved and easier version of weighting function from Leroy *et al.* (2012) (see Appendix S1 in Supporting Information). Adjusting the function to the selected rarity cut-off

point formerly required a numerical approximation that made it difficult to implement; therefore, we fitted a weighting function with the same properties as in Leroy *et al.* (2012), but where the rarity cut-off point is a direct parameter of the function (Eqn. 1). The function is adjusted such that, at the rarity cut-off point, species weight is always equal to 5% of the maximum weight. Below the rarity cut-off, weights increase exponentially; above the rarity cut-off, weights tend to be zero.

First, each species received as many rarity weights (w_{ij}) as there were scales according to the following formula:

$$w_{ij} = \exp\left(-\left(\frac{Q_{ij} - Q_{j\min}}{r_j \times Q_{j\max} - Q_{j\min}} \times 0.97 + 1.05\right)^2\right) \quad (1)$$

where all parameters are defined at the considered scale j: Q_{ij}, occurrence of species i; $Q_{j\ \min}$ and $Q_{j\ \max}$, minimum and maximum occurrences, respectively; and r_j, chosen rarity cut-off point (as a percentage of maximum occurrence). The maximum occurrence is defined as the highest occurrence found among species at scale j.

Second, the multiscale weight (w_{Mi}) of each species was calculated by taking the sum of each one-scale rarity weight:

$$w_{Mi} = \sum w_{ij} \quad (2)$$

Scale dependency of rarity cut-off points

The rarity cut-off point is typically defined in relation to the frequency distribution of species occurrence (Gaston, 1994; Flather & Sieg, 2007). As these distributions often differ among scales, rarity cut-off points are likely to be different among scales (Fig. 1a,b). If an arbitrary cut-off is chosen, a scale might be promoted because more species will be classified as rare (Fig. 1c) for this particular scale; consequently, the results of the community index might be biased towards this particular scale. Conversely, if a scale-dependent cut-off is chosen (according to Gaston's quartile definition) (Fig. 1d), equal proportions of species will be classified as rare at all scales. Hence, contributions of each scale to the community index should be roughly equal. Here, we provide evidence for this 'equitability' property of multiscale I_{RR} on simulated datasets (see Appendix S2).

Spider occurrence data

We provide a two-scale example of the described method on spiders of western France. At a regional scale, spider occurrences, defined as the number of grid cells (16 × 16 cells grid, approximately 683 km² per cell) in which the species were found, were obtained from the western France spider database (Pétillon *et al.*, 2007a). At a biogeographical scale, spider occurrences were obtained from the Catalogue of Spider Species from Europe and the Mediterranean Basin (Canard, 2005; taxonomy and occurrence of species updated in 2011). This coarse-resolution database references the occurrences of 5692 spider species totalling to 33,932 records across 75 units. Spatial referencing of records was based on biogeopolitical units, and therefore, of unequal size. Because island faunas often differ from country fauna, islands or groups of islands were considered as separate units (Ysnel *et al.*, 2008; see Appendix S3). Therefore, the WP occurrence of a species was defined as the number of units in which the species was found. Here, only the 705 spider species occurring in western France were considered. Thus, each species had both regional and WP occurrence.

Relevance of a two-scale approach

Because a two-scale analysis is relevant only if no strong linear relationship is observed between the scales, we analysed the relationship between regional and WP occurrences of the species and fitted linear and polynomial regression models to determine the type and strength of the relationship between regional and WP occurrence of spider species.

Choice of rarity cut-off points

As emphasized previously, the selection of rarity cut-off points should ensure scale-dependent cut-offs. We recommend defining cut-offs on the basis of either Gaston's quartile definition (rare species are the 25% species with lowest occurrence) or guidelines by Leroy *et al.* (2012) (rarity cut-off point is the occurrence at which the average proportion of rare species in local assemblages is 25%). The latter ensures that the chosen cut-off will be sufficient to distinguish among assemblages of species (see Discussion in Leroy *et al.*, 2012) but is calculated from a set of comparable assemblages. As our regional database had 166 assemblages of spiders on the basis of standardized samplings, we used the guidelines by Leroy *et al.* to calculate the cut-offs.

Two-scale weights of rarity of western France spider species

On the basis of the calculated cut-offs at each scale, we calculated two-scale weights of the 705 spider species occurring in western France. We analysed the distribution parameters of the two-scale weights (minimum, maximum, median and mean [± standard deviation (SD)]) according to four rarity categories that can be expected from a two-scale approach: (1) species rare at both regional and WP scales, (2) species rare for only regional scale, (3) species rare for only WP scale and (4) species not rare.

Index of relative rarity

The I_{RR} of an assemblage is calculated as the average weight of rarity of all the species of the assemblage. The I_{RR} is subsequently normalized between 0 and 1: $I_{RR} = ([\Sigma(w_i)/S] - w_{\min})/(w_{\max} - w_{\min})$ where w_i is the weight of the ith species

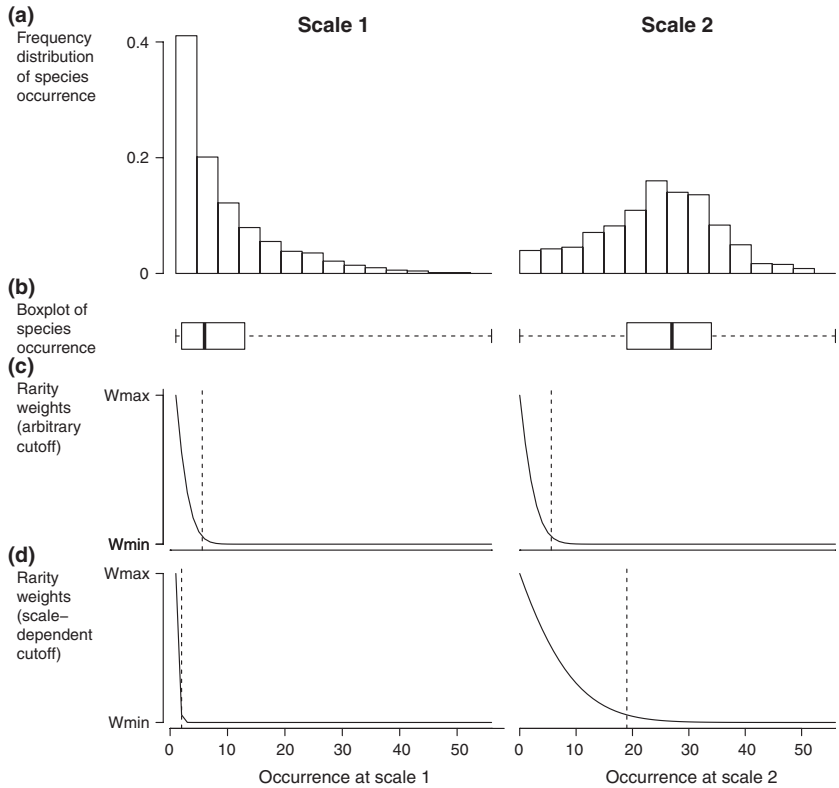

Figure 1 Theoretical illustration of the scale dependency of rarity cut-off points on the basis of our spider species datasets. (a) Histogram of frequency distributions of species occurrences for both scales. (b) Box plots of frequency distributions of species occurrences for both scales. (c) Rarity weighting function (w_{ij}) with an arbitrary cut-off (10% of the maximum, dashed lines). (d) Rarity weighting function with a scale-dependent cut-off based on Gaston's quartile definition; dashed lines: rarity cut-offs of each scale.

of the assemblage; S, species richness; and $w_{\min}$ and $w_{\max}$, minimum and maximum possible weights, respectively.

Congruencies between one-scale and two-scale indices

For each of the 166 assemblages of spiders in our regional database, we calculated three indices: (1) a regional-scale I_{RR} based only on regional rarity weights, (2) a WP I_{RR} based only on WP weights and (3) a multiscale I_{RR} based on multiscale rarity weights.

To assess the relevance of the multiscale index, we analysed the congruence between regional and WP scale I_{RR}. We assumed that if both regional and WP I_{RR} were strongly congruent, then there is no need for a two-scale index because one scale would be sufficient to capture the information provided by both scales. Then, we analysed the congruence between the two-scale I_{RR} and each one-scale I_{RR} (regional and WP). Our second assumption was that if the two-scale index did not show any congruence with one-scale indices, then it has failed to capture information from these scales. Congruencies were assessed using Spearman rank correlation coefficient.

Case study in a nature reserve

To provide an example, we applied the two-scale I_{RR} on a case study of 15 sampled assemblages of 225 spider species of the National Nature Reserve of Séné (France, 47.61°N, 2.71°W), which we extracted from the database. We chose these case study assemblages because they were sampled from contrasting habitats: wet grasslands, salt marshes, salt meadows, several disturbed and undisturbed meadows, open lawn, heathlands and hedgerows. Salt marshes and sub-halophytic meadows are known to host stenotopic, halophilous species (Pétillon *et al.*, 2008), which is not the case with the other sampled habitats. Because salt marshes are common in western France but extremely restricted at the WP scale (Pétillon *et al.*, 2007b), we expected their rarity value to be influenced by the presence of species rare at the WP scale. Ten of the presented assemblages had already been compared with the I_{RR} single-scale version (Leroy *et al.*, 2012). We calculated and analysed the single- and two-scale I_{RR} values and ranks of all 15 spider assemblages.

Data analyses

All data analyses were performed using R (R Development Core, 2012). Single and multiscale rarity weights and I_{RR} were calculated using the new package 'Rarity' published on the Comprehensive R Archive Network along with this article.

RESULTS

Relationship between regional and WP occurrence of spiders

The relationship between regional and WP occurrences of spider species is best described by a second-degree polynomial model ($R^2 = 0.401$, $P < 0.0001$, $n = 705$) (Fig. 2). Nearly all spiders having low WP occurrence also had low

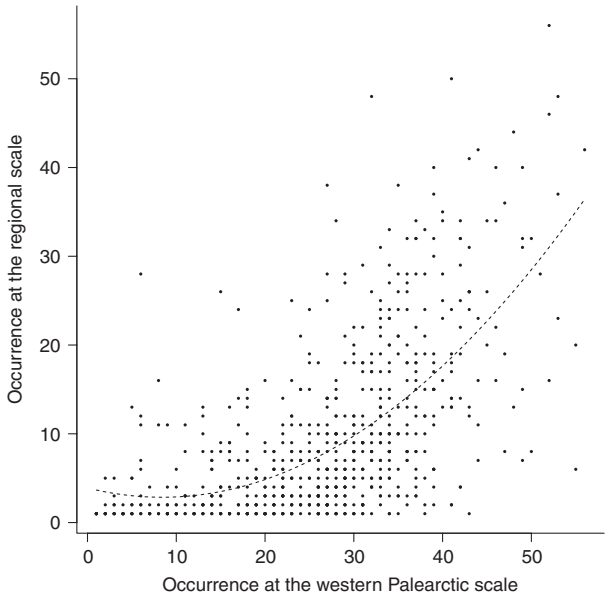

Figure 2 Occurrence of spider species at the regional scale as a function of their occurrence at the western Palearctic (WP) scale. The regional-scale occurrence is the number of cells in which species have been found from a regional-extent dataset (16 × 16 cells grid, ca. 683 km² per cell). The WP scale occurrence is the number of biogeopolitical units in which species have been found from a WP extent dataset (see Appendix S3). Dashed line: second-degree polynomial model ($R^2 = 0.401$, $P < 0.0001$, $n = 705$) best describing the relationship between regional and WP occurrence of spider species.

regional occurrence. In contrast, spiders having low regional occurrence could have had low, moderate or high WP occurrence. Spider species with the highest WP occurrences also had the highest regional occurrences.

Two-scale rarity weights of western France spiders

The regional rarity cut-off was 23.2% of the maximum occurrence (i.e. for species occurring in less than 13 grid cells). The WP rarity cut-off was 50.5% of the maximum occurrence (i.e. for species occurring in < 29 areas). We compared species weights (see Appendix S4) according to the four categories of rarity that we can expect from a two-scale approach (Table 1):

1. 350 species (49.7%) were defined as rare at both scales. Their weights were, on average, higher than those of the other categories.

2. 165 species (23.4%) were classified as rare at the regional scale but not at the WP scale. Their weights were, on average, half the weights of species rare at both scales.

3. 37 species (5.2%) were classified as rare at the WP scale but not at the regional scale. Their weights were, on average, half the weights of species regionally rare.

4. 153 species (21.7%) were not classified as rare. Their weights were, on average, very low (0.02 ± 0.02). Intriguingly, some species could have had weights higher than those of the regionally or WP-rare species (0.09 vs. 0.07 or 0.05, respectively). The occurrence of these species was extremely close to the rarity cut-off point at both scales. For example, *Dendryphantes rudis*, whose regional and WP occurrences were 13 and 29, respectively, had a two-scale weight of 0.09.

Two-scale indices of relative rarity vs. one-scale I_{RR} of western France spider assemblages

There was a significant but mediocre congruence between regional and WP indices of the 166 spider assemblages in our database (Spearman's $\rho = 0.37$, $P < 0.0001$, $n = 166$). In contrast, the two-scale indices of the 166 assemblages were strongly correlated with those of the regional (Spearman's $\rho = 0.87$, $P < 0.0001$, $n = 166$) and WP indices (Spearman's $\rho = 0.74$, $P < 0.0001$, $n = 166$). Nevertheless, there were marked differences between one-scale and two-scale I_{RR}, and the majority of sites received a high (i.e. worse) rank with the two-scale I_{RR} (see Appendix S5). The number of sites receiving a higher or lower rank was similar regardless of the scale. Very few sites received identical ranks between one-scale and two-scale I_{RR}.

Case study in a nature reserve

Indices of the assemblages of the nature reserve differed and, on average, regional I_{RR} were higher and more dispersed than WP I_{RR} (Table 2). Two-scale I_{RR} corresponded to the arithmetic mean between regional and WP I_{RR}. This is a mathematical consequence of the formulas, because one-scale weights are summed into two-scale weights and then averaged in the assemblage index. The following different patterns were distinguished: (1) six assemblages had similar rankings among indices because of either low (wet grassland S2, open lawn S8), intermediate (grazed salt marsh S5, post-cultural meadow S9) or high I_{RR} (Atlantic salt scrub S7,

Table 1 Different categories of species rarity that can be expected from a two-scale approach. For each category: number of western France spider species falling in that category and two-scale weights of rarity (minimum, maximum, median and mean (± standard deviation [SD])).

Regional scale	West-Palearctic scale	Number of species	Minimum weight	Maximum weight	Median weight	Mean weight (SD)
Rare	Rare	350	0.11	2.00	0.90	0.93 (0.47)
Rare	Not rare	165	0.07	1.05	0.36	0.43 (0.30)
Not rare	Rare	37	0.05	0.76	0.11	0.19 (0.17)
Not rare	Not rare	153	< 0.01	0.09	0.02	0.02 (0.02)

Table 2 Regional scale, western Palearctic scale and two-scale Indices of Relative Rarity (I_{RR}) of spider assemblages from the Séné National Nature Reserve of and corresponding rankings.

			I_{RR}			Ranking			
Label	Habitat	Management mode	Regional	Western Palearctic	Two-scale	Regional	Western Palearctic	Two-scale	Species richness
S1	Wet grassland	Grazed	0.041	0.075	0.058	14	7	13	43
S2	Wet grassland	–	0.061	0.055	0.058	12	12	13	41
S3	Atlantic salt meadow	Grazed	0.081	0.069	0.075	9	10	8	56
S4	Atlantic salt meadow	–	0.090	0.067	0.078	8	11	6	34
S5	Atlantic salt marsh	Grazed	0.077	0.070	0.074	10	9	9	55
S6	Atlantic salt marsh	–	0.092	0.136	0.114	5	1	1	19
S7	Atlantic salt scrub	–	0.121	0.093	0.107	2	2	2	49
S8	Open lawn	Mowed	0.033	0.033	0.033	15	15	15	34
S9	Post-cultural meadow	Mowed	0.104	0.081	0.093	4	6	4	40
S10	Tallgrass meadow	–	0.059	0.086	0.072	13	4	11	43
S11	Fallow land	–	0.092	0.072	0.082	5	8	5	72
S12	Gorse thickets	–	0.092	0.035	0.064	5	14	12	40
S13	Heathlands	–	0.123	0.087	0.105	1	3	3	46
S14	Monospecific hedgerows	–	0.063	0.082	0.073	11	5	10	37
S15	Deciduous hedgerows	–	0.105	0.051	0.078	3	13	6	54

heathlands S13); (2) two assemblages had marked differences between regional and WP I_{RR} and ranks, which resulted in intermediate two-scale I_{RR} and rankings (tallgrass meadow S10, deciduous hedgerows S15); (3) five assemblages had marked differences between regional and WP I_{RR} and ranks, but the resulting two-scale ranks were very close to either the regional (grazed wet grasslands S1, fallow land S11, monospecific hedgerows S14) or WP (ungrazed salt marsh S6, gorse thickets S12) ranks; (4) surprisingly, two assemblages had better two-scale ranks than both their one-scale ranks (grazed and ungrazed salt meadows S3 and S4, respectively).

Among these different patterns, the most striking results were the top three assemblages according to the two-scale I_{RR}. Most importantly, the ungrazed salt marsh S6 was ranked first, although only fifth with the regional I_{RR}. This assemblage had a very high WP I_{RR}. Salt scrub (S7) I_{RR} were clearly congruent between scales and thus were ranked second, and heathlands (S13) were ranked third.

DISCUSSION

In this study, we addressed the lack of inclusion of multiple scales in conservation studies of invertebrate taxa using an innovative approach based on datasets of different extents. We provided an example carried out on spiders for which we calculated species occurrence using two different datasets, corresponding to two different scales: a regional-scale dataset (western France) and a biogeographical scale dataset (western Palearctic). We demonstrated that a multiscale approach is necessary because of the lack of predictability of species occurrence between scales, and the poor congruence of rarity indices of assemblages among scales. Therefore, we integrated species occurrence from both scales into multiscale rarity weights for species and multiscale rarity indices for assemblages of species, using a new multiscale method. The major improvement of the multiscale method developed here is that it overcomes the gap between datasets of different extents, regardless of the resolution. In other words, the difference between our multiscale method and the classical scale–area curves is that the former is based on different datasets of varying extents, whereas the latter is designed for a single, high-resolution dataset with a fixed extent. Ideally, a dataset with a biogeographical extent (large enough to encompass complete species ranges) and fine resolution would allow the application of scale–area curves. In practice, such datasets do not exist for invertebrate taxa, and when broad-extent datasets are available, they often comprise coarse resolutions such as geopolitical units of unequal sizes (e.g. Fauna Europaea, 2011). Hence, our multiscale method is a valuable improvement to conservation studies, allowing any rarity assessment to integrate information on species rarity at different spatial scales. In a regional-scale assessment of rarity of species and assemblages, we demonstrated how we could integrate information on rarity at a larger scale such as the western Palearctic.

The most important part of the design of such a multiscale method is the calculation of species rarity weights; the final I_{RR} of assemblages of species corresponds to the average rarity weight of species of the assemblage. The formula transforming species occurrence into rarity weights is a critical feature. In most single-scale studies (e.g. Ysnel *et al.*, 2008; Kier *et al.*, 2009), rarity weights are calculated as the inverse of occurrence; however, although intuitive, this method was criticized in Leroy *et al.*, (2012) for its lack of flexibility, which could bias the results when comparing different assemblages. Leroy *et al.* (2012) proposed a flexible method to assess species rarity weights that ensure appropriate

calculation according to the considered taxa, spatial scales and geographical areas. As shown in this study, such a flexible weighting method was necessary to avoid bias in the final index towards one of the considered scales. Our basic assumption was that there should initially be neutrality among scales and that neutrality should not be transgressed because of the mathematical characteristics of the method. Nevertheless, if the user chooses to promote a given scale, either a high cut-off can be assigned to that scale such that more number of species receive high weights or a low cut-off can be assigned to the other scales. The cut-off definition applied here was based on the guidelines by Leroy *et al.* (2012). This cut-off definition is more relaxed than that by Gaston because it is applied to assemblages of species rather than to the entire database. This explains the high numbers of species classified as rare at each scale; however, species did not necessarily receive high weights because they were classified as rare, which should mitigate any bias associated with a relaxed definition of rarity, as warned by Grenyer *et al.* (2006).

Given that previous multiscale studies have clearly shown that rarity patterns vary with scales (Hartley & Kunin, 2003), the possibility of integrating multiple scales in rarity studies for invertebrates is a major improvement. Because different scales mean different extinction processes (Hartley & Kunin, 2003), the use of a single scale means that extinction processes acting at other scales are overlooked, which implies partially informed conservation studies. This risk was illustrated by our finding that the regional occurrence of spider species was not linearly correlated to their WP occurrence. Hence, species that were rare at the regional scale could be either rare or common at the WP scale. Therefore, species rare at both scales would have been overlooked in a single-scale study, even though they are the most at-risk species. Conversely, the two-scale rarity weights assigned to species were consistent according to the different categories of rarity resulting from a two-scale approach. Species rare at both scales received, on average, a higher weight than species rare at a single scale, and weights were mitigated according to species occurrence; therefore, the multiscale weighting method proposed here accurately represents species rarity according to the considered scales.

A further illustration of the limitations of a single-scale study is the very weak congruence among single-scale indices of species assemblages. This implies that the arbitrary choice of one scale or the other would have led to very different rankings. Conversely, this also implies that these two scales provide different, and therefore, complementary information on the rarity of species assemblages. Additionally, the two-scale I_{RR} was strongly congruent with both one-scale indices. The two-scale I_{RR}, therefore, combines these two complementary scales to provide additional and consistent information over each one-scale index. The final rankings based on the two-scale I_{RR} are subsequently different from, but related to, each single-scale ranking. A good illustration of the differences between one-scale and multiscale indices is the case study at the Séné Nature Reserve. Rankings appeared to be scarcely identical among indices, which seemed logical given the low congruence between one-scale indices. Nevertheless, some assemblages showed similar patterns among indices, such as the last-ranked spider assemblage of the very disturbed open lawn S8, comprising only ubiquitous species. Another interesting example is the assemblage of the Atlantic salt scrub, comprising high proportions of species rare at both scales, resulting in a constant second rank among indices. Another interesting pattern was that the two-scale rankings were often similar to one of the one-scale rankings. For example, the ungrazed Atlantic salt marsh S6 was ranked first with the WP I_{RR}, fifth with the regional I_{RR}, but first with the two-scale I_{RR}. This final first ranking was obtained because of a very high two-scale I_{RR} that, in turn, was explained by a very high WP value. In other words, the Atlantic salt marsh contained a very high proportion of species very rare at the WP scale, but relatively frequent at the regional scale. Indeed, salt marshes are relatively common in western France but extremely restricted at the WP scale (Pétillon *et al.*, 2007b; Leroy *et al.*, 2012). In contrast, some assemblages had nearly opposite rankings between one-scale indices, such as the deciduous hedgerows S15 characterized by the presence of regionally rare species that were relatively widespread at the WP scale. Unexpectedly, two-scale ranks of assemblages were sometimes worse (S2) or better (S3 and S4) than both one-scale ranks. The former case can occur when the majority of species rare at one scale are very frequent at the other. The latter case can occur when assemblages contain species that are rare at both scales, or at least that are rarer at both scales than the average of the compared assemblages.

The methodological improvements proposed here might represent a significant step in rarity metrics for both species and assemblages; however, some important caveats need to be considered. First, the reliability of the results clearly depends on the chosen occurrence datasets (see Discussion in Leroy *et al.*, 2012). Occurrence datasets often suffer numerous biases, mainly because they were not initially designed for such analyses (see Discussion in Pearman *et al.*, 2006). When applicable, completeness metric should be applied to quantify the quality of the dataset (Soberón *et al.*, 2007) and moderate interpretations. One might also question the reliability of coarse-resolution datasets such as the WP dataset used here. Similar coarse-scale data have previously been utilized in the assessment of species vulnerability for conservation prioritization (Abellán *et al.*, 2005). To be as accurate as possible from a biogeographical point of view, geopolitical units of the WP were subdivided into biogeopolitical units. Accordingly, islands and island groups were separated from mainland areas and split according to the composition of their fauna (Canard, 2005). Areas north of the biogeographical limit of the Sahara Desert were included because their spider fauna is shared with that of areas north of the Mediterranean Sea (e.g. Canard, 1989). Although such a spatial referencing of records allows accurate representation of data within a reasonable amount of time, it implies that the units are of unequal sizes. Such

differences in surfaces among areas introduce a bias in occurrence estimation because species with a large range in a single large area will appear rarer than species with a small range overlapping different areas. Nevertheless, we believe that even with such coarse resolution, a combination of the complementary WP scale with the regional scale provides a benefit by emphasizing the rarest or least known species. Furthermore, from a conservation point of view, the possibility of discriminating species that are regionally rare but common elsewhere from species that are rare at both scales justifies the usefulness of the coarse-scale dataset. Another drawback of coarse-scale datasets is the occurrence of non-native accidental species for a few times in a single region, and therefore, mistakenly receiving a very high rarity weight. Only rigorous checking of species lists, synonymy, and when available, specimens, can avoid such errors. Such rigorous checking was applied to the WP dataset in this study, and non-native species were excluded from rarity analyses.

Another caveat is that when assemblages are ranked, the ranking is relative (i.e. assemblages are ranked in comparison with each other). To have an idea of the rarity value according to the considered region, the regional ranking method proposed by Leroy *et al.* (2012) can be applied with the multiscale I_{RR}. For example, a particular sampled habitat can be compared with all the assemblage sampled in the same habitat of the reference region. Once the limits of such a method are considered, we believe that because it is flexible and robust, it should clearly improve rarity evaluations for various studies (e.g. monitoring management practices, changes in land use, identification of rarity hotspots in a given region). Moreover, because this method is easy to implement, we hope that it will be used to improve the placement of numerous neglected invertebrate taxa in applied conservation. Regarding spiders, the availability of regional or national lists for many European countries (e.g. U.K.: Harvey *et al.*, 2002; CZ: Buchar *et al.*, 2002) and two European-scale databases (Canard, 2005; Fauna Europaea, 2011) should make it easy to implement throughout the continent. As a final consideration, the principle behind our approach, that is, combining different datasets of different extents, can be applied to improve regional applications of the IUCN criteria (i.e. IUCN, 2003) for taxa without evaluations at larger spatial scales.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Modification of the original weighting function by Leroy *et al.* (2012)

Appendix S2 Demonstration of the equitability property of the flexible weighting function.

Appendix S3 Spatial referencing of records at the western Palearctic scale.

Appendix S4 Occurrences and rarity weights of spider species.

Appendix S5 Indices of relative rarity and rankings of spider assemblages.

BIOSKETCHES

Boris Leroy is a PhD student at the Muséum National d'Histoire Naturelle of Paris and has special interests in conservation biogeography and climate change. His thesis focuses on the development and application of robust and general tools (rarity indices and species distribution models) for the conservation of lesser-known taxa such as invertebrates.

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Author contributions: BL and FY designed the study. BL designed the methodology and performed analyses. AC and FY compiled the databases with help from BL. BL wrote the first draft of the manuscript, and all the authors contributed substantially to writing.

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