



REVIEW ARTICLE

Measuring insect rarity: practical issues, pragmatic approaches

Simone Fattorini^{1,2} Andrea Di Giulio³ Leonardo Dapporto⁴

¹*Azorean Biodiversity Group (GBA, CITA-A) and Platform for Enhancing Ecological Research & Sustainability (PEERS), University of the Azores, Rua Capitão João d'Ávila, Pico da Urze, 9700-042, Angra do Heroísmo, Terceira, Azores, Portugal.*

²*Water Ecology Team, Department of Biotechnology and Biosciences, University of Milano Bicocca, Piazza della Scienza 2, 20126, Milan, Italy. E-mail: simone.fattorini@virgilio.it*

³*Department of Sciences, University of Roma Tre, Viale G. Marconi 446, 00146, Rome, Italy.*

⁴*Centre for Ecology, Environment and Conservation, Department of Biological and Medical Sciences, Oxford Brookes University, Headington, Oxford, OX3 0BP, UK.*

Abstract: Rarity is often considered an indication of species extinction risk, and rarity measures are used as important tools to predict species vulnerability and hence to establish conservation priorities. For these reasons, rarity is among the most important issues involved in conservation programs. A number of studies have attempted to investigate relationships between rarity and extinction risk in plants and vertebrates, whereas only few papers have investigated similar issues in invertebrate taxa. This has limited the use of standardized rarity measures in invertebrate conservation studies. Assessing rarity is especially important when other pieces of information are difficult, or even definitively impossible, to obtain, as commonly found for most insects. Four broad categories of rarity are commonly recognized: geographical, ecological, population and phylogenetic rarity. On the basis of this framework, we present here a short review of the rarity forms most frequently investigated in insect studies, and their relationships with the main species traits related to extinction risk (such as body size, mobility, trophic level, host specificity, larval and adult behaviours, etc.). We discuss what they mean, how they can be measured, which type of data (field collections, museum data, literature information) are needed and how to avoid the most common pitfalls associated with rarity studies, with indications for pragmatic approaches in data analysis.

Key words: Extinction risk, conservation biology, vulnerability, distribution, threat, invertebrates, arthropods.

Introduction

We value rare things like diamonds, gold or antiquities because they are difficult to obtain. We value rare species because they are difficult to preserve. Rare species are considered to be intrinsically more prone to extinction than non-rare species because of various reasons. For example: (1) species with smaller populations can decline below the minimum viable population more easily than larger populations, because of demographic, genetic and environmental stochasticity; (2) species with smaller geographical distributions have fewer alternatives for surviving catastrophic events (such as fires, pollution, habitat destruction or alteration, etc.) than more widespread species, which can survive in unaffected areas of their larger ranges; (3) ecologically specialized species have fewer chances of coping with environmental changes than less specialized species, which may remain unaffected by changes in the availability or quality of certain resources or may respond to such changes by using other resources (Pullin 2002). For these reasons, rarity is often considered an indication of species extinction risk (Davies *et al.* 2000) and rare species are considered to be particularly vulnerable and of highest conservation concern (Lawler *et al.* 2003).

However, a higher level of rarity should not be confounded with true extinction risk. Cave dwelling arthropods are extremely rare because they are confined to a very particular biotope (the cave), have a restricted range (the total cave area or only a portion, for example the innermost part) and small populations (because of the limited space and resources available in caves) (Samways 1994). Thus, they are theoretically highly vulnerable and they are proven to be really threatened in some cases (see Samways 2007). Yet, if the caves are difficult to reach and are placed in well preserved, remote areas (as they do in many cases), then such species would be less likely to be threatened in practice (see Pullin 2002). By contrast, even extremely common species can be threatened (Gaston 2010), for example if they are persecuted. The most impressive examples are probably the North American bison *Bison bison* (probably with a population of 60-70 million individuals at its maximum, few hundreds in the 1890s and now some tens of thousands; Isenberg 2000) and the passenger pigeon *Ectopistes migratorius* (which had populations of 3 to 5 billions birds and became extinct in the wild in 1899; Peterson 1980; Blockstein 2002). Thus, we are faced with three different, albeit interrelated concepts: rarity, vulnerability and extinction risk. We define these three concepts as follows:

1) A species is more or less rare than others, for one or more traits that can be quantified, such as its distribution area, population consistence or habitat use, when these measures have particularly smaller values than those found in the other species.

2) A species is more vulnerable than others if its biological traits may predispose it to a higher probability of being extinct, other things being equal.

3) Finally, a species is more imperilled than others (i.e. it has a higher extinction risk) if it has a higher probability of being extinct as a result of the interrelationships between its rarity, ecology and enviromental changes with particular reference to human activity (Pullin 2002).

A rare species (because of its reduced range) is more vulnerable than more widespread species (because it has a higher probability of being extinct for stochastic events or local environmental changes in its reduced range), but it is not necessarily imperilled (as long as no change occurs). Therefore, rarity does not imply necessarily a higher threat and a need for urgent conservation (Rodrigues & Gaston 2002; Maina & Howe 2000). That said, if a species is more vulnerable than others, this will tend to enhance its extinction risk, and if rarer species are more vulnerable, they will tend to have higher extinction risk, albeit not necessarily. This makes rarity a good proxy for extinction risk.

When there is sufficient information about the biology of a species (including its rarity) and the kinds of threats that can affect it, extinction risk can be evaluated in a comprehensive way using some standardized procedures (e.g. IUCN 2001, 2003). However, for most arthropod species this is (and will remain) impossible because of a number of impediments (Cardoso *et al.* 2011). The conservation status of arthropods, which constitute the vast majority of all living organisms, has been strictly evaluated only for an insignificant number of species, yet they need urgent conservation actions (Cardoso *et al.* 2011; Dunn 2005). Thus, recent works have repeatedly proposed using vulnerability indexes based on rarity measures to define conservation priorities (Fattorini 2008, 2010ab, 2011, 2013; Fattorini *et al.* 2012, 2013). Recent publications have also provided evidence that the species that were highly vulnerable on the basis of their rarity were also those that went extinct locally (Fattorini 2011).

Measuring rarity in arthropods poses a number of challenges that can be grouped into three main categories:

- 1) Which form(s) of rarity should be measured
- 2) Which kind(s) of measure should be used
- 3) Which kind(s) of data should be considered

The aim of this short review is to present brief insights on these practical issues with indications for pragmatic approaches.

Pitfalls of rarity

A well known outcome of most insect samples is that there are a few species represented by many individuals and many species represented by a few, or only one, individuals. In general, only after several repeated sampling sessions the number of singleton species become less numerous than species observed as two individuals (e.g. Pielou 1975). This simple example suggests that rare species can be identified only after intensive field research. Even assuming that all species have been finally sampled, defining which species are really "rare" remains problematic. In most cases, rarity is assessed on a relative basis among a set of species belonging to a given species assemblage, which can be defined on a taxonomic, ecological or biogeographical basis (e.g. species within genera, families, or orders; species within a guild; species of various taxa within a certain area, etc.). Defining the set of species for analysis is thus the first complex decision in any assessment of species rarity. Indeed, because of the well known ecological pyramid it is impossible to directly compare, in terms of rarity, the occurrence of say two eagles, one hundred lizards and one thousand butterflies at a given site. However, even if a coherent group is selected, differences in natural history traits among species can determine biased measures of relative rarity. For example, when holometabolous insects are under study, only winged adults are usually sampled. Nevertheless, some species are univoltine with adults restricted to short flying periods and other polyvoltine with flying adults occurring for longer periods. Even if the number of living individuals of a univoltine species is similar to a polyvoltine species, the first species can appear rarer just because it passes a longer time as undetected in immature stages.

Contactability is another great problem in assessing rarity. There are indeed species even with very similar phenology that are less difficult to encounter (contacted) than others. For example, if light traps are used to sample moths, counts for species having wingless females can be halved compared with those having winged females even if they are equally abundant; this bias occurs also in winged species since traps tend to accumulate more male than female moths.

Differences in methods of data collection are also important in the final outcome. To objectively measure rarity we need some standardized method that can include field collection techniques, examination of literature and/or museum data. Any standardized field collection method is prone to undersample some species and to oversample other species. It is well known that biases in sampling methods have plagued butterfly recording in the UK, both for atlas collected data and transect records (Dennis *et al.* 1999; Isaac *et al.* 2011). Sources of biases are various. For example, not all moths are equally attracted by light traps. Similarly, not all beetle species, even within the same family, are equally attracted by the same substances used to bait pitfall traps (Adis 1979; Spence & Niemelä 1994; Delabie *et al.* 2000). Even samples from unbaited traps are biased by species mobility, the most mobile species being more easily caught. Museum collections are also often biased by the tendency of collectors to prefer rare, larger or more attractive species (*viz.*, aberrations) with respect to common and unapparent ones. Finally, faunistic studies often concentrate on particular elect areas where many species can be found and where rare species are known to occur more frequently; this may lead to overestimating the abundance of scarce species. These arguments suggest that any dataset for the assessment of rarity should initially be analyzed with care and the following main questions answered:

- 1) Is the sample comprehensive and extensive enough to obtain reliable information about (relative) frequency of species in terms of detected individuals, studied area, investigated environmental units?
- 2) Is the species set used for the relative assessment an ecologically coherent group?
- 3) Can the relative frequency of the species belonging to the studied group be biased by different contactability or, in the case of literature and museum data, can the relative presence of such species be considered as biased by collectors' decisions?

Answering these questions is far from being trivial. In most practical circumstances, it is difficult for a researcher to be certain that he/she has eliminated any source of bias. Yet, we believe that, even if biases cannot be eliminated, they can be reduced and that reliable, (largely) unbiased estimates of species rarity can be obtained. In the next paragraphs we describe different definitions of rarity and methods to measure them; we also provide pragmatic solutions for obtaining rarity measures that could be useful in practical contexts such as those associated with conservation decisions.

Forms of rarity

Species rarity has many facets. In Table 1 we report a selection of forms of rarity, with emphasis on those that have been most frequently investigated in, or which might be more important for, insects. After Rabinowitz's (1981) seminal work, there is now a certain tendency to distinguish three forms of rarity: range, ecology and population. These three aspects of rarity are in fact broad categories and Table 1 is also an attempt to rubricate our selection of rarity forms into these three categories.

On the basis of this framework, we present here a short review of insect rarity forms by discussing what they mean, how they can be measured and which type of data are needed.

Geographical distribution

Geographical rarity can be estimated using measures of area of occupancy (AOO) and extent of occurrence (EOO) (Gaston & Fuller 2009).

The EOO can be thought of as the area included within the shortest imaginary boundary linking continuous records that can be drawn to encompass all the known, inferred sites of present occurrence of a taxon. In general, occurrences due to recent introductions or

vagant individuals are excluded. Thus, EOO tends to coincide with the idea of species range. A common way to describe the EOO is that of a minimum convex polygon (i.e. the smallest polygon in which no internal angle exceeds 180 degrees) encompassing all known normal occurrences of a particular species. This is obviously a practical solution, but other techniques can be used to trace species ranges.

Table 1. Factors that can enhance extinction risk and associated forms of rarity.

Factors that can enhance extinction risk	Associated rarity
Restricted range	Extent of occurrence, area of occupancy
Fragmented range	Extent of occurrence, area of occupancy
Small ecological niche, habitat specialization	Ecological rarity
Small population(s)	Population rarity
Few populations	Population rarity
Declining population(s)	Population rarity
Low population density	Population rarity
Reduced genetic variability	Population rarity, measures of heterozygosity
Reduced mobility (reduced ability of habitat exploitation; reduced ability to escape habitat destruction/alteration)	Ecological rarity
Seasonal migrations (use of different biotopes at particular times)	Ecological rarity
Association with stable/well preserved biotopes (e.g. mature forests)	Ecological rarity
Association with biotopes of reduced size	Ecological rarity
Restricted phenology (reduced ability of habitat exploitation)	Ecological rarity
Collection/persecution/eradication	(via small population)
Large home range	(via small population)
Large body mass	(via small population)
Long life/r-strategy	(via small population)

Within the EOO, not all places will be really occupied by the species. The area encompassing only places where the species actually occurs is the AOO. A fundamental relationship between AOO and EOO of a species is that AOO, being the space within the distributional limits of the species where its populations actually occur, should always be smaller than EOO (Gaston & Fuller 2009).

A common way to describe the AOO of a species is to divide the study region into a matrix of equally sized cells (grid cells) and record if the species is present in or absent from each cell. The size of the area of occupancy will be a function of the scale at which it is measured (e.g. IUCN 2001, 2003). The scale of analysis, and hence grid size, should be appropriate to relevant biological aspects of the taxon and kind of available data.

Consider the following caveats and examples:

1) EOOs can be usually estimated more confidently than AOOs, which are more sensitive to differences in sampling intensity. A species less sampled than another might appear to have a smaller AOO than another one only because of this sampling bias. Consider the example in Figure 1. The two species have identical EOO and AOO. On the basis of known locations, the EOO of the two species can be correctly traced. However, although the two species co-occur exactly at the same locations, species A was not recorded from certain locations (where it actually occurs) because of inadequate sampling. Thus species A seems to have a smaller AOO (11 cells) than species B (14 cells).

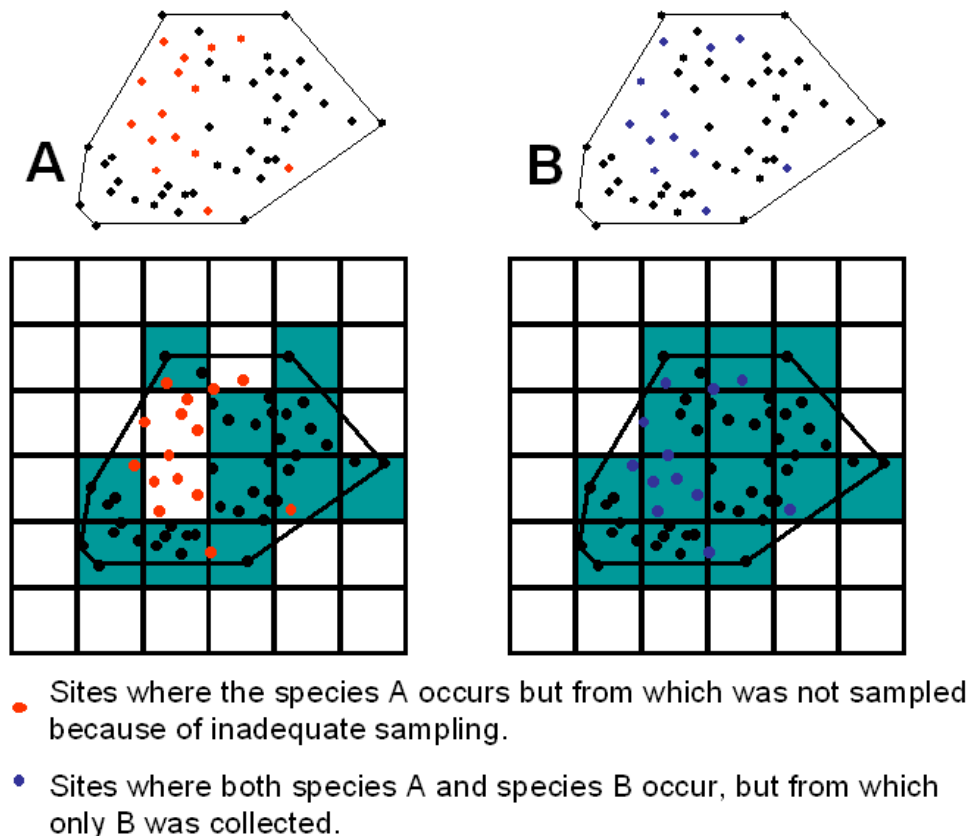


Figure 1. Effect of different sampling intensity on estimates of Extent Of Occurrence and Area Of Occupancy. Dots indicate species records.

2) Grid size influences the estimate of AOOs. As the resolution of mapping increases, the AOO declines markedly because fine-scale mapping inevitably uncovers unoccupied space within “occupied” coarse cells (Hartley & Kunin 2003). At the grid size of Figure 2a, the two species A and B have the same number of occupied cells. But, if a finer resolution is used Figure 2b, species B will reveal a larger AOO (10 cells) than species A (5 cells). The finer the grid, the greater should be the sampling effort.

3) Consider again the case of the two species of the example above. If species A has been undersampled, it might be unrecorded from sites where it in fact occurs. This is illustrated in Figure 3, where the species A and B should have identical AOOs, but species A have fewer cells because of a lack of sampling. Thus, grid size should be selected according to sampling effort; larger grids may obscure differences among species, but might be more appropriate if sampling effort was uneven among species.

Both EOO and AOO can be used to measure geographical rarity, depending on the aim of the research and type of available data. In general, EOO can be traced more easily and more confidently than AOO, but the EOO can be highly influenced by the presence of a single outlying population or individual (Gaston 1994). Moreover, species that can have very similar EOO may differ profoundly for AOO. For example, two species of aquatic insects may have similar ranges, but may differ in the number of ponds that are actually inhabited within the respective range.

To reduce the effect of the uncertainty in the EOO, a broad categorisation can be made according to the species' presence/absence in biogeographically distinct areas. This way, the EOO of a species can be quantified as the number of regions it occupies (Fattorini 2011). It is reasonable to assume that (1) dispersion across regions is less frequent than dispersion within a region (where metapopulation dynamics tends to be dominant), and (2) faunistic knowledge is generally more adequate to decide if a species is present or not in a region than to trace species' ranges. Thus, measuring EOOs as number of inhabited regions may be a practical solution when distributional information cannot allow an accurate reconstruction of species ranges. An important drawback of using regions is that they may be very different in their surface area. Thus, a species that is distributed in three small regions receives the same rarity score as one occurring in three larger regions.

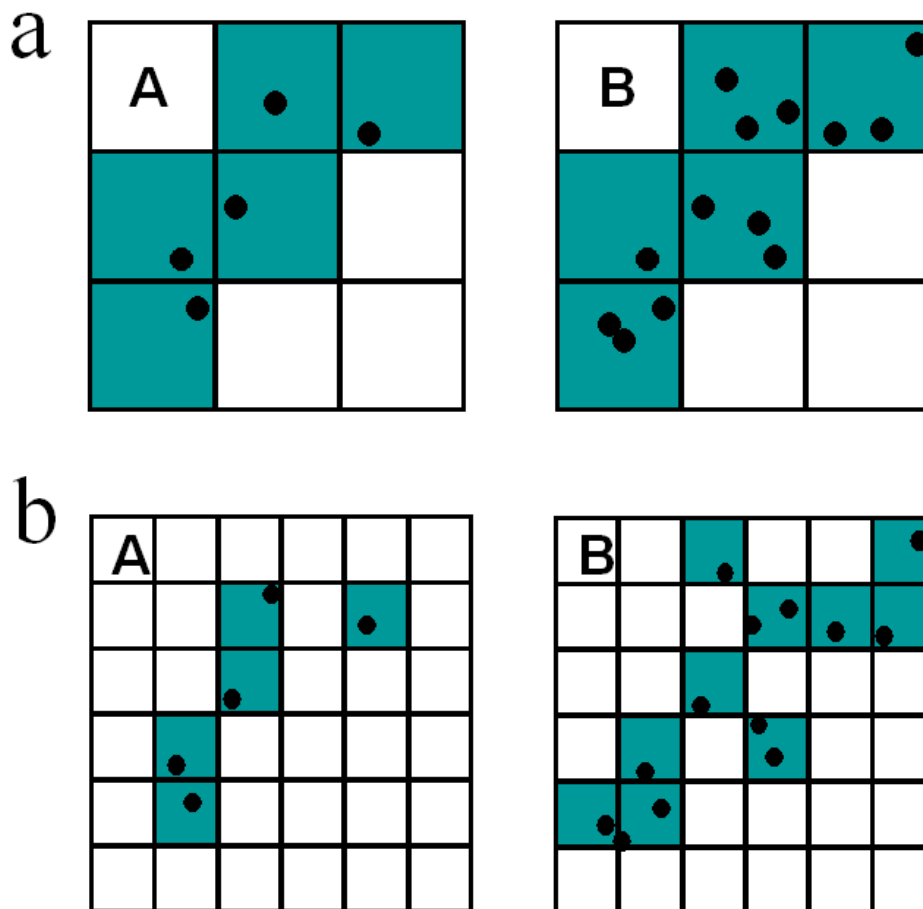


Figure 2. Effect of grid size (a larger, b smaller) on estimates of Area Of Occupancy for two species A and B.

AOOs is usually measured by dividing the study area into a number of equally sized sampling units, but in practice the spatial referencing of records may be based on geopolitical units of unequal size, such as counties or countries. Relatively large sample units may produce an AOO value that may approximate or even exceed the EOO defined range size (Hartley & Kunin 2003), hence the importance of using the finest resolution compatible with data “resolution” (sampling intensity; see above).

When AOO is measured using grid cells, the number of occupied cells depends to some extent on the arbitrary location of the grid boundaries relative to the recorded points of the species' distribution. To minimize the possibility of recording atypical values, Hartley & Kulin (2003) suggest two modifications to the measurement procedure: (1) find the grid registration that, for each scale, minimizes the number of cells required to encompass all the recorded points or (2) calculate an average AOO from a series of different grid registration schemes.

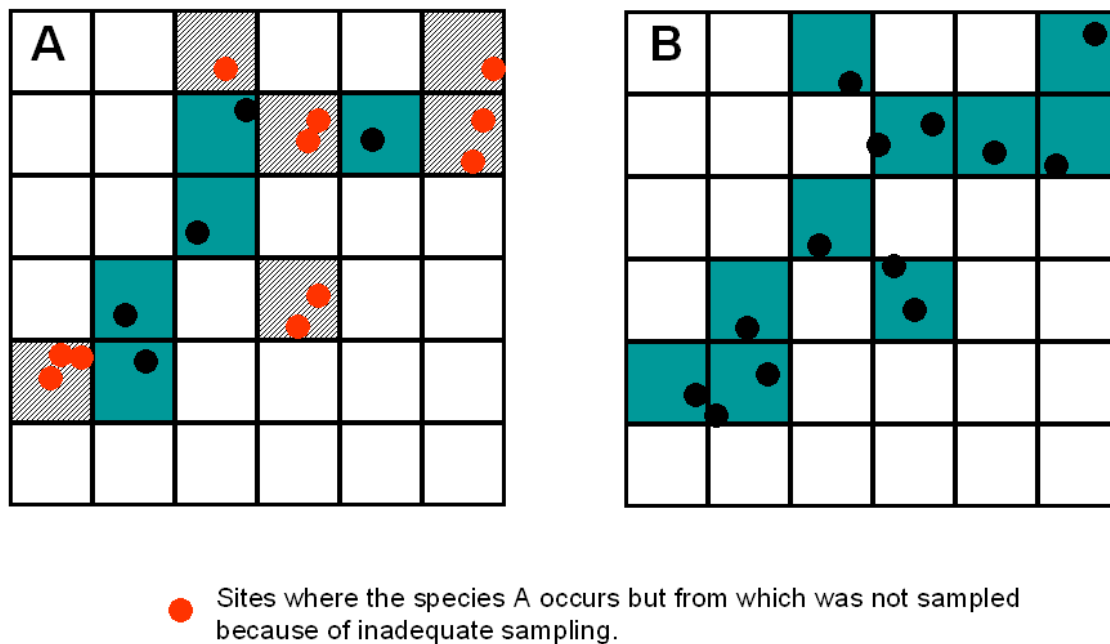


Figure 3. Effect of undersampling on estimates of Area Of Occupancy for two species A and B.

Theoretically, any grid registration scheme may be used to record species occurrences, but the most frequently used are those based on the the Universal Transverse Mercator (UTM) geographic coordinate system or the Military Grid Reference System (MGRS), which is derived from the UTM system. The UTM grid consists of squares of scaleable side size, e.g. 1 km, 10 km, 50 km or 100 km. Because the Earth is spherical, compensating triangles are necessary to counterbalance the squares, which leads to the presence of trapezoidal cells in certain zones. Problems with interposed compensation triangles are in general negligible. In national or regional maps small 'squares' are necessary to express species distributions. Such squares are typically of 10×10 km or smaller (see, for example, papers presented in Reemer *et al.* 2003), but when geographic coverage on this scale is poor, a wider grid size (e.g. 50×50 km) is used (Romo *et al.* 2006).

Other frequently used recording schemes are based on graticules (degrees of latitude and longitude). However, 'squares' determined by the same number of grades, minutes and seconds (for example, $30' \times 60'$) are not of the same size. Whereas the latitude remains constant ($30'$ measures about 55 km) on the European scale, the longitude of $60'$ varies according to the latitude: it measures about 85 km in southern Europe (e.g. Sicily), about 72 km in central Europe (e.g. Germany) and 52 km in northern Europe (e.g. Sweden).

A further, completely different approach is that of using geographical units of very different size such as administrative regions. For example, to express tenebrionid rarity in

Latium, Fattorini *et al.* (2013) counted the number of communes from which a species was known. Communes are small administrative units, of varying size but typically smaller than 10 km², whose boundaries typically reflect major topographic changes, and which might encompass an environmentally relatively uniform area. Rarity scores based on communes were strictly correlated with those obtained using UTM cells. In general, recent large scale works demonstrated that country-based analyses of species distributions tend to produce results analogous to those achieved using finer grid systems (Keil & Hawkins 2009), which suggest that use of large political units such as countries may be an acceptable way to quantify species geographical rarity. In general, species records/incidence for irregular spatial units which differ in size can be corrected for using regression techniques (Dennis *et al.* 1991; Dennis *et al.* 2002).

In studies dealing with islands, each island can be considered a unit (albeit of different size), geographical rarity can be expressed as the proportion of islands from which the species is known on the total number of islands (e.g. Dennis *et al.* 2000; Fattorini 2008; Dapporto & Dennis 2008a).

Species frequencies on islands tend to be correlated with frequencies on mainlands, but there are many cases of species showing high discrepancies (Dapporto & Dennis; 2008b, 2009) since species that are very common on mainlands may occur with low frequencies on islands (and vice versa). In this view, these procedures lead to an estimation of rarity on the basis of the geographic distribution within the studied islands. For species that are endemic to the study area, these measures express a good measure of species' rarity, but for species that are widely distributed outside of the study area, these estimates should be considered as a local assessment strictly relative to the insular environments.

Estimating the geographical rarity of a species depends on the spatial scale of analysis (Gaston 1994; Gaston & Blackburn 2000); so Fattorini *et al.* (2012), in a study on the arthropods of the Azorean Islands, suggested a two-level (global vs. regional) approach. At a global level, they considered as geographically rare the species which are endemic to the Azorean Islands, even if distributed in more than one island. At a regional level, they considered as geographically rare the species which are endemic to single Azorean Islands (single island endemics). Endemics are typically considered as taxa of conservation concern (Myers & De Grave 2000; Cook & MacDonald 2001), and this approach also ensured that endemic taxa are scored as important, at least in terms of geographical rarity, from a global and a regional perspective. These alternative measures of geographical rarity produced different outcomes and no particular choice can be recommended in general, because both may be useful depending on the aim of the study. For example, the use of single island endemics may be more appropriate to prioritise forest fragments among islands because it enhances the total number of species included in the final set of prioritised areas (Fattorini *et al.* 2012).

Ecology

Ecological rarity is the most elusive form of rarity. Several concepts, including those of habitat specialization, ecological specialization or niche breadth, may be evoked to define species ecological rarity. In principle, ecological rarity should express the diversity and extent of either the resources used or the environmental conditions tolerated by a species. The wider the resources used/ environmental condition tolerated, the lower the species' rarity.

Because any dimension of species' ecological niche may be used as form of ecological rarity, we have a virtually immense set of ecological characteristics and the hypervolume of the convex hull encompassing the ecological niche can be considered as a

measure to quantify ecological rarity, either individually or simultaneously. However, for most insect species, direct ecological information is limited or completely absent. This may discourage any attempt to quantify ecological rarity. Yet, we may use a great deal of 'indirect' ecological information. In general, we know species' distributions as locality records. These locality records can be profitably used to deduce species' ecology. GIS facilities make it possible to project point records on environmental maps showing, for example, elevational, geological, climatic, land use, biotope and vegetational characteristics of the area under study. From the overlap between point records and an environmental map, we can confidently estimate an hypervolume of environmental characteristics of occupied areas, thus a species' ecological rarity. This measure can be also more suitable to measure rarity than the direct evaluation of resources needed. Indeed, it is not certain that species using a restricted number of resources are less common than more generalist ones, although this tends to be the case. Conversely, if a species is restricted to a few areas, the probability that they encompass a smaller number of environmental characteristics is high. For example, a species that has been found in many land use categories should be considered less rare than one found in few categories regardless of the number of resources reported as necessary for its survivorship.

Quantifying ecological rarity implies the use of an index of diversity. As the environmental continuum is necessarily divided into discrete units, the most obvious solution is simply counting the number of units occupied by a species: the lower the number, the higher the rarity. As reference units, one can count the number of biotopes, plant associations, elevational belts, land use types, soil type etc. in which a species has been found. For example, Fattorini (2010ab) counted the number of biotopes (defined as a modified version of CORINE Land Cover classification) occupied by tenebrionid beetles and butterflies in the Central Apennines of Italy.

Because a species distribution across environmental categories is obviously uneven, simply counting the number of categories occupied can be excessively simplistic. For example, consider the case of a species A that is found in three biotopes, with five records in biotope 1, six in biotope 2, and four in biotope 3; and a species B that is also found in three biotopes, but with 10 records in biotope 1, 2 in biotope 2, and 1 in biotope 3. Both species have the same number of biotopes, yet the second one is strongly concentrated in one biotope, thus it should be considered more rare. This problem is analogous to that widely discussed in community ecology for the choice of diversity indices that does not express only "richness", but also the proportional contribution of abundances (evenness). We do not discuss the properties of these indices because they are widely discussed in many reviews, but prefer to briefly illustrate how they can be applied to express ecological rarity. For this we will refer to just few indices as examples, because they have been widely used or seem to be particularly appealing for such purposes.

1) Counts. Fattorini *et al.* (2013) evaluated "habitat specificity" (Hughes *et al.* 2000) of tenebrionid beetles living in Latium (Central Italy) by assessing species distribution across the 15 main phytoclimatic units occurring in this region and defined on the basis of climatic indices and vegetational settings (Blasi 1994). The assumption was that the larger the number of phytoclimatic units occupied by a species, the wider the species ecological tolerance. Elevational range can be considered as a habitat envelope in which a species is able to survive (see Brändle *et al.* 2002) and may be used to express ecological rarity. Because a number of environmental (notably climatic) parameters vary with altitude, Fattorini *et al.* (2013) also suggested using measures of elevational range to express ecological rarity. For this, they first divided the study area into 24 elevational belts of 100 m (0-100 m, 101-200 m,

201-300 m, etc). Then, they calculated for each species the number of occupied belts, assuming that a smaller elevational range reflects higher ecological specialization.

Phytoclimatic units are a categorization that encompasses two main sets of environmental variables, vegetation and climate, and vegetation is in turn affected by soil characteristics, topography, past climate, relationships among plants, etc. (Blasi 1994). Elevational gradients reflect both current and past climatic history as well as geological factors (Lomolino *et al.* 2010). Phytoclimatic units may not be readily available in other areas, but high-resolution maps of bioclimatic units and of bioclimatic variables (which have a broader meaning than strictly phytoclimatic units) are available for the whole globe (see Hugget 2004 for examples). Species elevational ranges are even easier to obtain, because they can be always deduced from locality records. Because of the difficulties in obtaining other measures of species ecology (Cardoso *et al.* 2011), elevational gradients could be adopted as a sort of standard measure for ecological rarity.

2) Proportional abundance. As a measure of habitat specificity based on proportional abundances, Fattorini *et al.* (2013) calculated for each species of tenebrionid beetles living in Latium a Shannon H' index (Devictor *et al.* 2010) using species abundances across phytoclimatic units. Decreasing values indicate increasing habitat specificity of the species. A similar approach was applied using species abundances across the elevation belts (Fattorini *et al.* 2013).

Shannon measures reflect both diversity and evenness of distribution of cases across any multivariate space, in our case number of records of a given species in different environments. Conversely, simple counts of the number of occupied phytoclimatic units or elevational belts measures the extent of such a dimension. Thus, Shannon measure and counts express different meanings, although they may produce strongly correlated results (Fattorini *et al.* 2013). In calculating indices that use proportional abundances, various approaches can be adopted. In the aforementioned examples, species abundance per environmental unit (such as phytoclimatic unit or elevational belt) has been used. However, if species abundance data are not available, surrogates can be used. For example, one can use number of records per unit or the number of collection localities per unit. It is important to note that, if the ecological units used in the study have very different surface, this may imply that a species associated with a unit that covers a large surface will tend to be sampled more frequently, and hence have a higher abundance (or a larger number of records or collection localities). Thus, before using abundance data to calculate ecological rarity, it might be important to standardize them according to the extent of each ecological category.

It is usually postulated that specialist species are more prone to extinction than generalist ones. Compared with specialists, generalists are hypothesized to contend better with environmental changes, primarily because they can shift among resources that are affected by environmental changes (e.g. Habel & Schmitt 2012; Dennis *et al.* 2012 for insects). Nevertheless, most species are specialized in using particular resources and only a minor fraction of generalist organisms exist, most prominently in insects (Loxdale *et al.* 2011). Actually, generalists incur extra costs associated with exploiting multiple resources and depend on the evolution of costly tolerances to variable environmental conditions (Richmond *et al.* 2005). Therefore, there is an evolutionary trade off between costs associated with generalism and extinction probabilities. It is clear that in different environmental conditions the fitness associated with the two strategies (generalism vs. specialism) can change. However, hypothesizing that generalists are always favoured in disturbed regions is exposed as too simplistic a point of view (Thomas 2000; Habel & Schmitt 2012; Dapporto & Dennis 2013). Indeed, specialist species might be considered to be more capable of exploiting reduced resources available in small habitat patches and to be less affected by

genetic isolation (Habel & Schmitt 2011). This hypothesis has been directly tested by Dapporto & Dennis (2013) on the British butterflies. Actually, among the British butterflies, mid-generalists were revealed to be most affected by population decline, while many specialists benefitted from population increases due to rapid exploitation of new habitats available as a consequence of management (Dapporto & Dennis 2013). Similarly, limited distribution is not always a direct indication of extinction risk. This can be evident even in insular endemics, which represent the most extreme case of distributional rarity. Indeed, insular endemics can be considered as extreme cases of specialism and, actually in some cases, they have been shown to be among the most common species on their islands.

Population

Population size (or density) is probably the most obvious type of rarity to define, because it is simply the number of individuals (recorded or living in a given area). In fact, it is generally impossible to really count how many individuals of a given species live in a certain area (or globally). But, as rarity is a relative concept, we are not interested here in knowing how many individuals of a certain species live in a given area, but if they are more or fewer than those of another species in the same area. In other words, we want to have measures of relative (proportional) abundance (population size). This usually implies the use of sampling techniques to obtain standardised quantitative data. These techniques vary according to the ecological characteristics of the animals of concern (a collection of techniques is described in Samways *et al.* 2010). In general, insect groups tend to include species that have very different ecological characteristics, and hence require different techniques. For example, pitfall traps may be appropriate to sample ground-dwelling species, whereas light traps can be used to collect night-flying species. Considering simultaneously organisms collected with different techniques is a difficult matter; actually, the overall efficiency of different methods can be different, resulting in the impossibility of directly comparing results.

Standardised sampling methods can be easily used to assess species abundance at small spatial and temporal scales, but can be hardly applicable to wide areas and long times. Measuring rarity at a large temporal and spatial scales would be however an important achievement for most conservation studies, because we are usually interested in establishing species rarity at regional or global scale and in detecting population trends. A possible solution is to use museum collections as source of data. The basic idea is that species that are more abundant in collections are those that are more frequently encountered (contacted) by collectors. Because encounter rates are proportional to population density (Strayer 1999), species contactability may be considered a proxy for population size (or density). This may be acceptable if collections are not biased towards particular species (in general, rare species attract collectors more than common ones). In general, data obtained from examination of museum collections can be considered as much as long as:

- 1) they are abundant;
- 2) arise from a larger number of sources (collections);
- 3) occur in a larger number of collections (or obtained by a larger number of collectors);
- 4) the more diversified are the collectors' interests;
- 5) the larger is the number of collecting techniques;
- 6) the wider and denser is the geographical coverage of place records;
- 7) the longer is the temporal extent of collections

The very large sampling effort made over a long time by a number of collectors interested in different groups and who have used different collecting methods will “ensure”

that the data will collectively form a 'random' sample, not affected by biases due to collector preferences for certain biotopes, sites or species. In general, large museum collection will tend to satisfy these characteristics and may be profitably used to assess species abundance in rarity analyses.

Fattorini *et al.* (2013), in a study on tenebrionid beetle rarity in Latium (Central Italy) found that abundance data obtained from pitfall traps were strongly correlated with total number of specimens found in museum collections, which indicates that using total number of specimens is a good measure for population size, at least analogous to what can be obtained by standardized techniques.

Scoring rarity values

As rarity is a relative, rather than an absolute, concept, it is quite common to see rare species defined on the basis of some quantile of the frequency distribution of a certain rarity measure (Gaston 1994). Gaston (1994) recommended using the 25th quantile for sampling reasons. However, defining cutpoints is always subjective decision.

The quantile is a fixed proportion of the species pool. Thus, while the identity of species delineated as rare may change, the number of rare species remains unchanged, and we will always find a certain proportion (e.g. 25%) of rare species in any assemblage. To address this limitation, it has been proposed to adopt some absolute criteria (e.g., insect species recorded from ≤ 15 10 km survey quadrats from a possible 2862 [Hopkins *et al.* 2002]).

Both the relative and the absolute definitions of rarity can be criticized for the lack of an objective ecological justification, yet any rarity threshold has the merit of setting a standard against which to judge whether the degree of rarity is trending toward or away from that expected under the reference (spatial or temporal) conditions.

Instead of using a 25% criterion, many authors dichotomize species into two groups (common and rare) according to whether they were above or below the median of rarity measures (cf. Arita *et al.* 1990; Isaac *et al.* 2009), especially when different measures have to be combined to obtain vulnerability scores. Using a median-based dichotomization for three measures of rarity (range, ecology and population), the following rarity categories are obtained (Figure 4): 1: species that are not rare for any dimension (measure); 2: species rare only for abundance; 3: species rare only for habitat; 4: species rare only for range; 5: species rare for both habitat breadth and abundance; 6: species rare for both geographical range and abundance; 7: species rare for both habitat breadth and geographical distribution; 8: species rare for geographical distribution, habitat breadth and abundance. A multidimensional characterization of species rarity has been introduced by Rabinowitz (1981) and applied to bryophytes (Gabriel *et al.* 2011), vertebrates (e.g. Kattan 1992; Manne & Pimm 2001; Isaac *et al.* 2009) and arthropods (e.g. Dapporto & Dennis, 2008a; Fattorini 2008, 2010ab, 2011, 2013; Fattorini *et al.* 2012).

Previous studies using Rabinowitz's forms of rarity (Rabinowitz 1981; Rabinowitz *et al.* 1986) found that while a high proportion of species have relatively small geographical ranges, only few species are widespread and abundant, and the condition of 'abundant and localized' is extremely rare since locally abundant populations tend to rapidly occupy new sites (Gaston 1994; Brown 1995; Gaston & Blackburn 2000;). However, it is noteworthy to consider the scale of analysis, and hence the way geographical rarity is assessed.

Moreover, comparisons of multiple taxa within the same geographical context revealed that proportions of different categories of rarity tend to change considerably among taxa (Fattorini 2010b). Thus, no generalization seems possible and rarity measures always

have a relative value, depending on the particular assemblage of species under study (cf. also Kattan 1992; Dobson & Yu 1993; Manne & Pimm 2001).

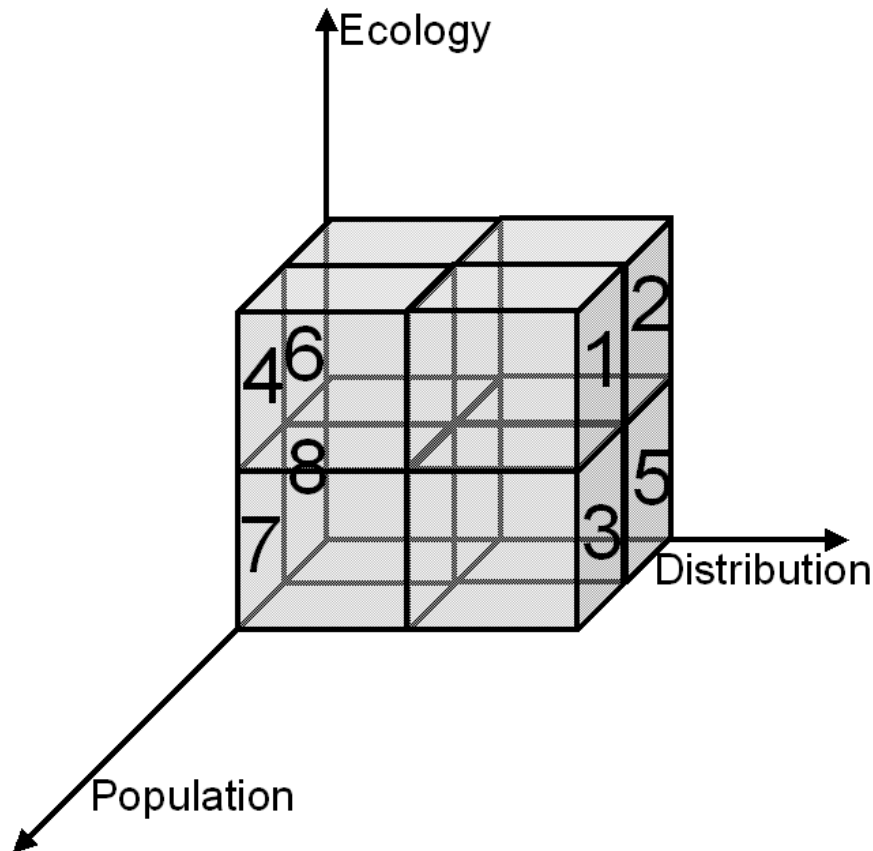


Figure 4. Space defined by three rarity dimensions: distribution, ecology and population. Median values for each axis divides this rarity cube into eight cubes representing various forms of rarity: 1: species that are not rare for any dimension; 2: species rare only for abundance; 3: species rare only for ecology; 4: species rare only for distribution; 5: species rare for both ecology and population; 6: species rare for both distribution and population; 7: species rare for both ecology and distribution; 8: species rare for distribution, ecology and population.

Use of median values to dichotomise species into the categories common/rare may seem to recognize an excessively large number of species as rare, because for any range of rarity scores always 50% of the analysed species will be classified as rare. However, some macroecological considerations support this choice. Analyses of the frequency distribution of range size revealed a virtually ubiquitous highly right skewed distribution: most species have small ranges, few are widespread (see Lomolino *et al.* 2010 for examples, and Gaston 1990 for exceptions). Moreover, widespread species tend to be more abundant than localised ones (Gaston 1990). Species abundance distribution analyses typically indicate that most species that form a community are present with few individuals, and only few species are really abundant (Pielou 1975). Similarly, only few species in a given community are ecologically generalists, most species being ecologically specialised (e.g. Dapporto & Dennis 2013).

Influence of body mass

Theoretical argumentations suggest that larger species should have larger ranges, which is a commonly observed pattern, but theoretical reasons exist for a reverse pattern, which is also frequently found (Gaston 1990).

Dobson & Yu (1993) argued that the influence of body size should be statistically removed before the degree of rarity of species is examined. For example, many small mammals should be able to live in the range of one large mammal, simply because small species use fewer resources per individual. Thus, a small mammal with the same local population density as a large mammal, should be considered rare for population size, because large mammals need much larger areas and more environmental resources than small species per individual. Similarly, larger species would be expected to use larger ranges than smaller species per individual. Thus, according to Dobson & Yu (1993), it is not population density or range area per se that indicate rarity, but rather it is the effect of these variables after the adjustment for body size that needs to be considered. By the same token, also ecological rarity should be corrected for body size.

Although the idea of adjusting rarity measures for body size appears reasonable, and may change species ranking considerably (see Dobson & Yu 1993 for the Neotropical mammals), implications for conservation biology are not so obvious.

First, potential for extinction may be more correctly expressed by rarity measures that are not corrected for body size. For example, small populations are intrinsically prone to extinction (for example, because the effects of genetic loss and higher exposure to stochastic environmental changes; Pullin 2002), irrespectively of the body size of the species concerned (for example, a population below 250 individuals in conjunction with certain threats is always considered Critically Endangered according to the IUCN criteria; IUCN 2001).

Second, although rarity is often considered an indication of species extinction risk (Davies *et al.* 2000), and various aspects of rarity may correlate with body size, this does not imply necessarily that rarity measures corrected for body size are better proxies of man-induced extinction risk, which is the product of the interrelationships between species ecology and human activity (Pullin 2002).

Third, the method proposed by Dobson & Yu (1993) relies on the assumption that there is a linear relationship between body size and rarity measures. In fact, the relationship between body size and rarity has been investigated with a certain extent only for range size of vertebrates, where in fact only weak correlations are usually detected (Gaston & Blackburn 1996).

For the tenebrionid beetles of Latium, Fattorini & Di Giulio (2013) found out that range trends were correlated with vulnerability index independently of body size correction, the species with the highest vulnerability being those that experienced the strongest range contraction for both corrected and uncorrected measures. Also, they found that correcting for body size may be problematic because of the weak correlations between body size and geographical and ecological rarity (notably, abundance was not correlated). On the other hand, Dennis *et al.* (2012) found that butterfly species showing larger wingspan tend to occur more frequently on islands, mainly in northernmost and most isolated ones, because they are able to travel for longer distances. These findings indicate that correcting rarity for body size can be sometimes theoretically questionable, and its usefulness for conservation purposes must be assessed by preliminary analyses.

Phylogenetic rarity

Phylogenetic relationships are usually treated more as a “problem” that should be controlled for due to the non independence of data because of phylogenetic autocorrelation (Felsenstein 1985; Strona *et al.* 2012) than a possible source of rarity in itself (Vane-Wright *et al.* 1991; Posadas *et al.* 2001). However, Cotgreave & Pagel (1997) argued that rare species are typically found among lineages that split from basal nodes and the role of phylogeny as a driving factor of macroecological patterns has recently come into focus (Harcourt *et al.* 2005).

To express phylogenetic rarity, some indices have been proposed that are based on taxon relationships expressed by phylogenetic reconstructions (cladograms) (Vane-Wright *et al.* 1991; Posadas *et al.* 2001). The index I measures the amount of information contained in cladograms based on values of taxonomic distinctiveness between taxa. To calculate I , a value of 1 is assigned to each terminal taxon that belongs to a pair of terminal sister taxa. The taxon that constitutes the sister group of this pair receives a value of 2 (equal to the sum of its sister group), and so on for each taxon in the cladogram. I scores increase with the basal position of the node from which the taxon arose, whereas taxa at the end of intense bifurcation processes receive low scores and equal values are assigned to sister taxa. However, according to Posadas *et al.* (2001), this index tends to produce results affected by the over-weighting of lineages that split from more basal nodes. The index W , which is calculated as the number of phylogenetically informative statements that can be made for each taxon, is not affected by this problem. Calculation of W requires some steps. First, an index i is used to express the number of phylogenetic steps involved in the diversification pattern of each taxon. This index is calculated as the number of groups (nodes) to which each taxon belongs. Then, the basic phylogenetic weight Q is calculated for each terminal taxon as $Q_j = \sum i_{ij}$, where j is each specified taxon (tribe). Individual Q values reflect the proportion of the total diversity of the group contributed by each taxon. W scores are obtained for each Q value as $W = Q_j / Q_{min}$. In spite of the fact that W index gives the highest values to lineages that split from the most basal nodes, it does not over-weight these taxa (Posadas *et al.* 2001). Lower values indicate higher cladistic “isolation”, whereas species at the end of an intense process of diversification will receive higher scores. Although these indices express “cladistic” relationships, they may be used as a simple way to express phylogenetic rarity.

Conclusion

Coming back to the initial metaphor, measuring rarity should be not seen as the search for the Holy Grail, but much more likely working with precious stones. There are different kinds of stones (geographic, ecologic, population and phylogenetic rarity) and each one has its collection risks (pitfalls), can be found in different places (field collections, museum data, literature information) and requires specific cuts (data analysis). Assessing rarity is among the most important issues evaluated by conservation agencies like the IUCN. Actually, when methodological problems are correctly addressed, rarity provides fundamental information for conservation biology. However, there are important exceptions breaking the apparent link between rarity and extinction risk (see Thomas 2000; Gaston 2010; Habel & Schmitt 2012, Dapporto & Dennis 2013). Such exceptions seem to be mostly linked to counterintuitive relationships involving the degree of specialization (a form of rarity in itself), the ability to exploit small habitat patches and different effects of limited gene flow among species (Habel & Schmitt 2011; Dapporto & Dennis 2013). To further complicate a complicated story, the relationship between extinction risk and ecological rarity strongly interacts with environmental conditions and can be modeled by very different analytical approaches, so that

different studies can result in completely different results (compare Thomas 2000; Polus *et al.* 2007; Habel & Schmitt 2011; Dapporto & Dennis 2013 for studies on European butterflies). Yet, rarity measures are an important tool to predict species vulnerability and hence to establish conservation priorities, especially when other pieces of information are difficult, or even definitively impossible to obtain, as commonly found for most insects. A number of studies have attempted to investigate which species traits influence species proneness to extinction in vertebrates. By contrast, researches involving insects are scarce, because of difficulties in obtaining complex assessments of species extinction risk and measures of species traits (see Dennis *et al.* 2000; Dennis *et al.* 2004 for examples). Predicting the fate of species on the basis of their biological traits and hence correctly managing those which appear to be particularly prone to extinction are among the most ambitious tasks of conservation biology. A number of studies have attempted to investigate which species traits influence species proneness to extinction in plants (e.g. Mills & Schwartz 2005) and vertebrates (e.g. Laurance 1990; Kattan 1992; Dobson & Yu 1993; Angermeier 1995; Manne & Pimm 2001), whereas only few papers have investigated species ecological correlates of extinction risk in invertebrate taxa (e.g. Thomas 1994; Koh *et al.* 2004; Shahabuddin & Ponte 2005; Driscoll & Weir 2005). These studies have typically involved particular measures of species traits, such as body size, mobility, trophic level, host specificity, larval and adult behaviours, etc. (Koh *et al.* 2004; Driscoll & Weir 2005; Shahabuddin & Ponte 2005). In general, these measures are difficult to obtain for most insect species for several reasons (including modern scarce attention to natural history and ecological studies based on broad sampling programs), which typically prevented their use in conservation studies (see Cardoso *et al.* 2011). Although rarity measures may correlated with a number of species traits and may be practical surrogates for extinction risk (Fattorini 2013), recognizing the relationships between species rarity and conservation trends with their life traits, environmental conditions and conservation strategies in a comprehensive framework will be among the most important challenges of conservation biology in the coming years.

Acknowledgements

We are very grateful to R. L. H. Dennis for his many comments on and revision of a previous version of this paper.

References

- Adis J. 1979.** Problems of interpreting arthropod sampling with pitfall traps. *Zoologischer Anzeiger* 202:177–84.
- Angermeier P. L. 1995.** Ecological attributes of extinction-prone species: loss of freshwater fishes of Virginia. *Conservation Biology* 9: 143–158.
- Arita H. T., Robinson J. G. & Redford K. H. 1990.** Rarity in Neotropical forest mammals and its ecological correlates. *Conservation Biology* 4: 181–192.
- Blasi C. 1994.** *Carta del fitoclima del Lazio*. Regione Lazio and Università di Roma “La Sapienza”, Rome, Italy.
- Blockstein D. E. 2002.** Passenger Pigeon (*Ectopistes migratorius*). In: *The Birds of North America Online* (A. Poole, editor). Cornell Lab of Ornithology, Ithaca. <http://bna.birds.cornell.edu/bna/species/611>.
- Brändle M., Öhlschläger S. & Brandl R. 2002.** Range sizes in butterflies: correlation across scales. *Evolutionary and Ecology Research* 4: 993–1004.
- Brown J. H. 1995.** *Macroecology*. University of Chicago Press, Chicago, 269 pp.

- Cardoso P., Erwin T. L., Borges P. A. V. & New T. R. 2011.** The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* 144: 2647–2655.
- Cook J. A. & MacDonald S. O. 2001.** Should endemism be a focus of conservation efforts along the North Pacific Coast of North America? *Biological Conservation* 97: 207–213
- Cotgreave P. & Pagel M. 1997.** Predicting and understanding rarity: the comparative approach, pp. 237–261. In: *The Biology of Rarity: the causes and consequences of rare-common differences*. (W. Kunin and K. Gaston, editors). Chapman and Hall, London, 294 pp.
- Dapporto L. & Dennis R. L. H. 2008a.** Island size is not the only consideration. Ranking priorities for the conservation of butterflies on Italian offshore islands. *Journal of Insect Conservation* 12: 237–249.
- Dapporto L. & Dennis R. L. H. 2008b.** Species' richness, rarity and endemism of Italian offshore islands: complementary signals from island-focused and species-focused analyses. *Journal of Biogeography* 35: 664–674.
- Dapporto L. & Dennis R. L. H. 2009.** Conservation biogeography of large Mediterranean islands. Butterfly impoverishment, conservation priorities and inferences for an ecological “island paradigm”. *Ecography* 32: 169–179.
- Dapporto L. & Dennis R. L. H. 2013.** The generalist-specialist continuum: Testing predictions for distribution and trends in British butterflies. *Biological Conservation* 157: 229–236.
- Davies K. F., Margules C. R. & Lawrence J. F. 2000.** Which traits of species predict population declines in experimental forest fragments? *Ecology* 81: 1450–1461.
- Delabie J. H. C., Fisher B. L., Majer J. D. & Wright I. W. 2000.** Sampling effort and choice of methods, pp. 145–154. In: *Ants: Standard Methods for Measuring and Monitoring Biodiversity*. (D. Agosti, J. Majer, E. Alonso and T. Schultz, editors). Biological Diversity Handbook Series. Smithsonian Institution Press. Washington D.C., 280 pp.
- Dennis R. L. H., Williams W. R. & Shreeve T. G. 1991.** A multivariate approach to the determination of faunal units among European butterfly species (Lepidoptera: Papilionoidea, Hesperioidea). *Zoological Journal of the Linnean Society* 101: 1–49.
- Dennis R. L. H., Sparks T. H. & Hardy P. B. 1999.** Bias in butterfly distribution maps: the effects of sampling effort. *Journal of Insect Conservation* 3: 33–42.
- Dennis R. L. H., Donato B., Sparks T. H. & Pollard E. 2000.** Ecological correlates of island incidence and geographical range among British butterflies. *Biodiversity and Conservation* 9: 343–359.
- Dennis R. L. H., Shreeve T. G., Olivier A. & Coutsis J. G. 2000.** Contemporary geography dominates butterfly diversity gradients within the Aegean archipelago (Lepidoptera: Papilionoidea, Hesperioidea). *Journal of Biogeography* 27: 1365–1383.
- Dennis R. L. H., Shreeve T. G., Sparks T. H. & Lhonore J. E. 2002.** A comparison of geographical and neighbourhood models for improving atlas databases. The case of the French butterfly atlas. *Biological Conservation* 108: 143–159.
- Dennis R. L. H., Hodgson J. G., Grenyer R., Shreeve T. G. & Roy D. B. 2004.** Host plants and butterfly biology. Do host plant strategies drive butterfly status? *Ecological Entomology* 29: 12–26.
- Dennis R. L. H., Dapporto L. & Hardy P. B. 2012.** Nestedness in island faunas: novel insights into island biogeography through butterfly community profiles of colonization ability and migration capacity. *Journal of Biogeography* 39: 1412–1426.

- Devictor V., Clavel J., Julliard R., Lavergne S., Mouillot D., Thuiller W., Venail P., Villéger S. & Mouquet N. 2010.** Defining and measuring ecological specialization. *Journal of Applied Ecology* 47: 15–25.
- Dobson F. S. & Yu J. 1993.** Rarity in Neotropical forest mammals revised. *Conservation Biology* 7: 586–591.
- Driscoll D. A. & Weir T. 2005.** Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. *Conservation Biology* 19: 182–194.
- Dunn R. R. 2005.** Modern insect extinctions, the neglected majority. *Conservation Biology* 19: 1030–1036.
- Fattorini S. 2008.** A multidimensional characterization of rarity applied to the Aegean tenebrionid beetles (Coleoptera Tenebrionidae). *Journal of Insect Conservation* 12: 251–263.
- Fattorini S. 2010a.** Use of insect rarity for biotope prioritisation: the tenebrionid beetles of the Central Apennines (Italy). *Journal of Insect Conservation* 14: 367–378.
- Fattorini S. 2010b.** Biotope prioritisation in the Central Apennines (Italy): species rarity and cross-taxon congruence. *Biodiversity and Conservation* 19: 3413–3429.
- Fattorini S. 2011.** Insect rarity, extinction and conservation in urban Rome (Italy): a 120-year-long study of tenebrionid beetles. *Insect Conservation and Diversity* 4: 307–315.
- Fattorini S. 2013** Species ecological preferences predict extinction risk in urban tenebrionid beetle guilds. *Animal Biology* 63: 93–106.
- Fattorini S. & Di Giulio A. 2013.** Should we correct rarity measures for body size to evaluate arthropod vulnerability? Insights from Mediterranean tenebrionid beetles. *Biodiversity and Conservation* DOI: 10.1007/s10531-013-0556-7.
- Fattorini S., Cardoso P., Rigal F. & Borges P. V. A. 2012.** Use of arthropod rarity for area prioritisation: insights from the Azorean Islands. *PLoS ONE* 7:e333995, doi:10.1371/journal.pone.0033995.
- Fattorini S., Sciotti A., Tratzi P. & Di Giulio A. 2013.** Species distribution, ecology, abundance, body size and phylogeny originate interrelated rarity patterns at regional scale. *Journal of Zoological Systematics and Evolutionary Research* DOI:10.1111/jzs.12026.
- Felsenstein J. 1985.** Phylogenies and the comparative method. *American Naturalist* 125: 1–15.
- Gabriel R., Homem N., Couto A., Calvo Aranda S. & Borges P. A. V. 2011.** Azorean bryophytes: a preliminary review of rarity patterns. *Açoreana* Suplemento 7: 149–206.
- Gaston K. J. 1990.** Patterns in the geographical ranges of species. *Biological Review* 65: 105–129.
- Gaston K. J. 1994.** *Rarity*. Chapman & Hall, London, 201 pp.
- Gaston K. J. 2010.** Valuing common species. *Science* 327: 154–155.
- Gaston K. J. & Blackburn T. M. 1996.** Conservation implications of geographic range size-body size relationships. *Conservation Biology* 10: 638–646.
- Gaston K. J. & Blackburn T. M. 2000.** *Patterns and processes in macroecology*. Blackwell Science Ltd, Oxford, UK, 377 pp.
- Gaston K. J. & Fuller R. A. 2009.** The sizes of species geographic ranges. *Journal of Applied Ecology* 46: 1–9.
- Habel J. C. & Schmitt T. 2012.** The burden of genetic diversity. *Biological Conservation* 147: 270–274.

- Harcourt A. H., Coppeto S. A. & Parks S. A. 2005.** The distribution-abundance (density) relationship: its form and causes in a tropical mammal order, Primates. *Journal of Biogeography* 32: 565–579.
- Hartley S. & Kunin W. E. 2003.** Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology* 17: 1559–1570.
- Hopkins G. W., Thacker J. I., Dixon A. E. G., Waring P. & Telfer M. G. 2002.** Identifying rarity in insects: The importance of host plant range. *Biological Conservation* 105: 293–307.
- Huggett, R. J. 2004.** *Fundamentals of biogeography*. Second Edition. Routledge. Abingdon, UK, 439 pp.
- Hughes J. B., Gretchen C. & Ehrlich P. R. 2000.** Conservation of insect diversity: a habitat approach. *Conservation Biology* 14: 1788–1797.
- Isaac N. J. B., Cruickshanks K. L., Weddle A. M., Rowcliffe J. M., Brereton T. M., Dennis R. L. H., Shuker D. M. & Thomas C. D. 2011.** Distance sampling and the challenge of monitoring butterfly populations. *Methods in Ecology and Evolution* 2: 585–594.
- Isaac J. L., Vanderwal J., Johnson C. N. & Williams S. E. 2009.** Resistance and resilience: quantifying relative extinction risk in a diverse assemblage of Australian tropical rainforest vertebrates. *Diversity and Distributions* 15: 280–288.
- Isenberg A. C. 2000.** *The destruction of the Bison: An environmental history, 1750–1920*. Cambridge University Press, Cambridge, 206 pp.
- IUCN. 2001.** *IUCN Red list categories and criteria. Version 3.1. IUCN Species survival commission*. IUCN, Gland, Switzerland and Cambridge, UK, 30 pp.
- IUCN. 2003.** *Guidelines for application of IUCN Red list criteria at regional levels. Version 3.0*. IUCN species survival commission. IUCN, Gland, Switzerland and Cambridge, UK, 41 pp.
- Kattan G. 1992.** Rarity and vulnerability: the birds of the Cordillera Central of Colombia. *Conservation Biology* 6: 64–70.
- Keil P. & Hawkins B. A. 2009.** Grids versus regional species lists: are broad-scale patterns of species richness robust to the violation of constant grain size? *Biodiversity and Conservation* 18: 3127–3137.
- Koh L. P., Sodhi N. S. & Brook B. W. 2004.** Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology* 18: 1571–1578.
- Laurance, W.F. 1990.** Comparative responses of five arboreal marsupials to tropical forest fragmentation. *Journal of Mammalogy* 71: 641–653.
- Lawler J. J., White D., Sifneos J. C. & Master L. L. 2003.** Rare species and the use of indicator groups for conservation planning. *Conservation Biology* 17: 875–882.
- Lomolino M. V., Riddle B. R., Whittaker R. J. & Brown J. H. 2010.** *Biogeography*. Fourth Edition. Sinauer Associates, Sunderland, 560 pp.
- Loxdale H. D., Lushai G. & Harvey J. A. 2011.** The evolutionary improbability of ‘generalism’ in nature, with special reference to insects. *Biological Journal of the Linnean Society* 103: 1–18.
- Maina G. G. & Howe H. F. 2000.** Inherent rarity in community restoration. *Conservation Biology* 14: 1335–1340.
- Manne L. L. & Pimm S. L. 2001.** Beyond eight forms of rarity: which species are threatened and which will be next. *Animal Conservation* 4: 221–229.
- Mills M. H. & Schwartz M. W. 2005.** Rare plants at the extreme of distribution: broadly and narrowly distributed rare species. *Biodiversity and Conservation* 14: 1401–1420.
- Myers A. A. & De Grave S. 2000.** Endemism: origins and implications *Vie et Milieu* 50: 195–204.

- Peterson R. T. 1980.** *A field guide to the birds of Eastern and Central North America.* Houghton Mifflin, Boston, 384 pp.
- Pielou E. C. 1975.** *Ecological Diversity.* John Wiley and Sons, NY, 165 pp.
- Polus E., Vandewoestijne S., Choutt J. & Baguette M. 2007.** Tracking the effects of one century of habitat loss and fragmentation on calcareous grassland butterfly communities. *Biodiversity and Conservation* 16: 3423–3436.
- Posadas P., Miranda Esquivel D. R. & Crisci J. V. 2001.** Using phylogenetic diversity measures to set priorities in conservation: an example from southern South America. *Biological Conservation* 15: 1325–1334.
- Pullin A. S. 2002.** *Conservation Biology.* Cambridge University Press, Cambridge, 345 pp.
- Rabinowitz D. S. 1981.** Seven forms of rarity, pp. 205–217. *In: The Biological aspects of rare plant conservation.* (H. Synge editor) Wiley, Chichester, United Kingdom.
- Rabinowitz D., Cairns S. & Dillon T. 1986.** Seven forms of rarity and their frequency in the flora of the British Isles, pp. 182-204. *In: Conservation biology: the science of scarcity and diversity.* (M. E. Soulé editor).. Sinauer Associates, Sunderland, 598 pp.
- Reemer M., van Helsdingen P. J., Kleukers R. M. J. C. (Editors) 2003.** Changes in ranges: invertebrates on the move. *In: Proceedings of the 13th International Colloquium of the European Invertebrate Survey, Leiden, 2-5 September 2001.* European Invertebrate Survey – The Netherlands, Leiden, 137 pp.
- Richmond C. E., Breitburg D. L. & Rose K. A. 2005.** The role of environmental generalist species in ecosystem function. *Ecological Modelling* 188: 279–295.
- Rodrigues A. S. L. & Gaston K. J. 2002.** Rarity and Conservation Planning across Geopolitical Units. *Conservation Biology* 16: 674–682.
- Romo H., Garcia-Barros E. & Lobo J. M. 2006.** Identifying recorder-induced geographic bias in an Iberian butterfly database. *Ecography* 29: 873–885.
- Samways M. J. 1994.** *Insect conservation biology.* Chapman & Hall, London, UK, 374 pp.
- Samways M. J. 2007.** Insect conservation: A synthetic management approach. *Annual Review of Entomology* 52: 465–487.
- Samways M. J., McGeoch M. & New T. R. 2010.** *Insect conservation.* A handbook of approaches and methods. Oxford University Press, Oxford, 441 pp.
- Shahabuddin G. & Ponte C. A. 2005.** Frugivorous butterfly species in tropical forest fragments: correlates of vulnerability to extinction. *Biodiversity and Conservation* 14: 1137–1152.
- Spence J. R. & Niemelä J. K. 1994.** Sampling carabid assemblages with pitfall traps: the madness and the method. *The Canadian Entomologist* 126: 881–894.
- Strayer D. L. 1999.** Statistical power of presence–absence data to detect population declines. *Conservation Biology* 13: 1034–1038.
- Strona G., Galli P., Montano S., Seveso D. & Fattorini S. 2012.** Global-scale relationships between colonization ability and range size in marine and freshwater fish. *PLoS ONE* 7(3): e33995. doi:10.1371/journal.pone.0033995.
- Thomas C. D. 2000.** Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society B* 267: 139–145.
- Thomas J. A. 1994.** Why small cold-blooded insects pose different conservation problems to birds in modern landscapes. *Ibis* 137: 112–119.
- Vane-Wright R. I., Humphries C. J. & Williams P. H. 1991.** What to protect? Systematics and the agon of choice. *Biological Conservation* 55: 235–254.

Correspondence: Simone Fattorini, e-mail: simone.fattorini@virgilio.it

Received: 09.08.2013 Accepted: 18.09.2013 Published: 26.09.2013

Cite paper: Fattorini S., Di Giulio A. & Dapporto L. 2013. Measuring insect rarity: practical issues, pragmatic approaches. *Journal of Insect Biodiversity* 1(10): 1–21.

<http://dx.doi.org/10.12976/jib/2013.1.10>

<http://www.insectbiodiversity.org>