How and why species are rare: A mechanistic reappraisal of the Rabinowitz rarity framework

Varina Crisfield¹, F. Guillaume Blanchet¹, Dominique Gravel², and Ciara Raudsepp-Hearne³

¹Université de Sherbrooke ²Université de Sherbrooke Département de Biologie ³Wildlife Conservation Society of Canada

November 3, 2022

Abstract

The three-dimensional rarity typology proposed by Rabinowitz in 1981, based on range size, habitat specificity, and local abundance, is perhaps the most widely used framework for describing rarity in ecological and conservation research. While this framework is descriptive and does not explain the causes of rarity, recent advances in ecology may be leveraged to add explanatory power. We propose a modification of Rabinowitz's typology to better distinguish between the dimensions of rarity and the processes that drive them and explore the conservation implications of our modified framework. We suggest replacing habitat specificity, which is arguably a cause of rarity, with occupancy (the proportion of occupied sites within a species' range), yielding a modified classification based on range size, occupancy, and local abundance. Abundant, widespread habitat specialists are no longer considered rare; however, we argue that this modification more accurately identifies truly rare species, as habitat specialists may be common if their habitat is abundant. Finally, we draw on the functional literature to identify the key processes and associated traits that drive each rarity axis. In this respect, we identify four processes (environmental filtering, movement, demography, and interactions), and hypothesise that range size and occupancy are primarily driven by environmental filtering and movement, whereas local abundance is more strongly influenced by demography and interactions. Our work aims at providing a basis for developing hypotheses about the causes of rarity in particular taxa and identifying suitable conservation measures targeting different types of rare species.

Introduction

Rare species have been the focus of considerable attention in ecology and conservation biology. Rare species are more prone to extinction than common species , and are often among the targets of conservation efforts . Rarity is also of interest from a theoretical perspective as it touches on fundamental questions in ecology, particularly those related to the drivers that influence distribution and abundance; though in the case of rare species we are more precisely interested in what *constrains* their distribution and abundance. However, as with other aspects of ecology, the study of rarity is complicated by a sea of contingencies, and identifying generalities has proven difficult.

Numerous ecologists have sought to bring order to the seemingly anarchic phenomenon of rarity. Early work tended to focus on single factors: for example, proposed that rare species were newly evolved taxa which have not yet occupied their full niche, whereas hypothesised that they are relictual species that have decreased in abundance or distribution. emphasised low heterozygosity as a root cause of rarity. While overly simplistic, these early studies began the work of identifying traits associated with rarity, an undertaking that continues today in the form of comparative studies of the traits of rare and common species (e.g., .

More recent work has taken a less monolithic perspective on rarity and has attempted to parse the concept

into a variety of types or causes. The most well-known of these efforts is the framework developed by , which classifies species based on three dimensions of rarity: local abundance, habitat specialisation, and range size. Local abundance refers to a species' typical population size at the local scale; habitat specialisation refers to the range of habitat types in which a species is found, and is roughly analogous to the concept of niche breadth; and range size refers to the geographic extent within which a species occurs. The three dimensions are dichotomised and then combined to form eight possible groups, seven of which represent different types, or forms, of rarity (Table 1). Rabinowitz' seven forms of rarity have been widely used to describe rarity in a variety of assemblages and regions identify conservation priorities , and assess extinction risk .

Other ecologists have taken a mechanistic approach to understanding rarity, and causal theories have been proposed to explain rarity and endemism in plants. based their system on two axes, taxon age and range size, which are dichotomised and combined to form four different rarity types. They then propose a different hierarchy of explanatory causes for each of the four resulting groups. emphasized the need for a synthetic approach to understanding endemism, and proposed a system that incorporates the effects of historical, genetic, and ecological processes.

Though frequently cited, the theories of and have rarely been applied to real species or assemblages (though see). While this is in striking contrast to the popularity of the Rabinowitz framework, the difference may be attributable to the availability of the type of information they require to classify species. Rabinowitz' system requires comparatively basic ecological information on range, abundance, and habitat requirements, which can be obtained with relative ease from expert knowledge and/or survey data. Conversely, the information required to apply the theories of Stebbins or Fiedler & Ahouse, such as taxon age or genetic information, may be less readily available, particularly for very rare species.

As a result, we are left with a widely applied classification system that is well-suited to describing rarity, but not to explaining its causes, and two theories that explain rarity, but which are scarcely used in practice. While the system developed by Rabinowitz is useful as a phenomenological scheme, it does not explain the root causes of rarity (nor was it intended to). asserted that a typology of the causes of rarity "is a distant goal"; however, the four decades since the development of the seven forms of rarity have seen considerable progress in ecology, and linking Rabinowitz' scheme to ecological theory may serve to update the framework and expand its utility from description towards explanation. The fields of functional ecology and macroecology may be of particular value to this quest: the former seeks to identify the processes that influence species' patterns of occurrence based on measurable traits, and has frequently been used to infer mechanistic causes of rarity, whereas the latter provides insight into the fundamental processes that drive broad-scale ecological patterns.

Stebbins' emphasis on synthetic explanations is likely salient, as patterns of abundance and distribution in species are driven by a variety of factors operating across a range of spatial and temporal scales . However, to provide practical value for conservation, such an explanation must also be accessible and usable despite the knowledge gaps that often exist for rare species. Here, we seek to increase the robustness of the conceptual underpinnings of studies of rarity by developing a process-based framework of rarity. To achieve this objective, we revisit the Rabinowitz framework and link it to insights from theoretical and functional ecology. We propose a modification to the Rabinowitz framework that will more clearly distinguish between dimensions of rarity and their underlying causes, use theory and empirical work to explore the common causes of these dimensions, and discuss the implications of our proposed framework for conservation.

Describing and explaining rarity: pattern vs. process

The field of ecology distinguishes between pattern and process: patterns are observable, repeated tendencies , whereas processes are the mechanisms that drive patterns. Historical approaches to understanding rarity can be divided along this pattern–process dichotomy: the causal theories of Stebbins and Fieldler & Ahouse sought to identify the fundamental processes that result in rarity, whereas the Rabinowitz framework took the approach of describing different patterns of rarity.

While patterns are linked to ecological processes, they are also significantly affected by a second class of

causal factors: contingencies, which are external factors that impact ecological patterns . Examples of contingencies include climate change, ecological drift, availability of specific habitats, and human or natural disturbances. Here, we use an expanded definition of contingencies that also accounts for geographic factors (e.g., dispersal barriers) that can influence patterns of occurrence in ways that could not be predicted from a strictly process-based perspective.

Ecological patterns should thus be understood as arising from the interaction between ecological processes and contingencies. Contingencies can complicate and obscure the search for general patterns in ecology ; however, by recognizing the separate, but interrelated roles of both contingency and process, we hope to identify the key processes that lead to rarity despite the vast diversity in patterns of rarity that stem from the influence of contingencies.

Describing rarity: Pattern

There is no universally agreed-upon definition of rarity or what exactly constitutes a rare species. While the term is most commonly used to refer to species characterised by a restricted distribution, low abundance, or both , some authors have incorporated different metrics into their definitions of rarity, including habitat breadth, occupancy, or persistence . As a starting point, we define rarity as being uncommon. While this "uncommonness" can be defined at various scales—e.g., within a particular biotic community, the boundaries of a jurisdiction, or globally—we focus on species that are globally uncommon. Thus, species that are rare only within a certain context, such as a particular jurisdiction or habitat type, are not considered here.

Despite the popularity and evident utility of the Rabinowitz framework, it does have weaknesses. First, the three rarity dimensions (range size, local abundance, and habitat specialisation) represent a combination of pattern and process. Whereas range size and local abundance both describe patterns in species' occurrence, habitat specialisation is arguably a process (environmental filtering) and it can influence both patterns. Creating a process-based framework for rarity requires a clear distinction between patterns of rarity and the processes that drive them. Second, the Rabinowitz framework captures patterns of occurrence either at very broad scales (i.e., range size) or very fine scales (i.e., local abundance), but lacks a measure of regional-scale rarity. As scale can substantially affect patterns of rarity, along with related issues such as population decline , this omission may create an important gap in assessing rarity.

We propose addressing both these issues by removing habitat specialisation from the Rabinowitz framework, and replacing it with a new dimension, namely occupancy. In some contexts, occupancy is a binary variable that indicates whether a species occurs at a particular site (as in occupancy surveys or models, e.g., . It has also been defined as the proportion of cells in a gridded landscape currently occupied by the species . Here, we define occupancy as the proportion of habitat patches (or sites, grid cells, etc.) within a species' range that is occupied by the species. While it is somewhat unconventional to define occupancy specifically in relation to a species' range, by doing so we can capture the density at which the species occurs within the range, which has implications for the persistence of rare species and the type of conservation measures they may require. We discuss these implications in *Conservation implications* (below).

The distinction between occupancy and range size warrants some further precision, as the two are often used interchangeably in the literature, including some studies that have applied the Rabinowitz framework (e.g., . However, as shown in Figure 1, we defined occupancy in a way that is distinct from range size: whereas range size refers to the global limits of the area within which a species occurs (i.e., extent of occurrence), occupancy denotes the density of occurrences within those limits. While occupancy may provide a practical proxy for range size that is suitable in the context of certain research questions, the two are not conceptually equivalent. Furthermore, a species with a small range but high occupancy may require different conservation and management measures compared to a species with a large range but low occupancy (Figure 1); this will be discussed in more detail in *Conservation implications*. Given that studies of rarity (or rare species) often have conservation objectives, the distinction between range size and occupancy is important to maintain.

There are four major advantages to replacing habitat specificity with occupancy: first, like range size and habitat specificity, occupancy describes a pattern of occurrence. Second, our proposal yields a system that

acknowledges the importance of scale in rarity, as the proposed dimensions of range size, occupancy, and local abundance correspond to global, regional, and local scales, respectively (Figure 2), thus filling the regional scale gap in the Rabinowitz framework. Third, as we will argue in more detail in *Conservation implications*, using occupancy rather than habitat specialisation will allow the framework to more accurately identify species that are truly uncommon, which has important implications when using the classification system for conservation purposes. Finally, because habitat specialisation is among the mechanisms that can influence occupancy , habitat specificity will remain embedded in the framework, but as a causal driver rather than a rarity dimension, as explained in the *Explaining rarity: Process* section.

Explaining rarity: Process

A key challenge in ecology is to identify generalities that transcend the idiosyncrasies of specific focal assemblages or regions. Through the use of traits (i.e., morphological, physiological, phenological, behavioural, biochemical, or other characteristics of species that influence their fitness), functional ecology offers a taxonomically-neutral approach to inferring information about ecological processes from species functional traits. Similarly, traits may offer a path towards identifying the key processes that drive different rarity dimensions. However, despite the large body of literature that has sought links between traits and rarity (Table 2), identifying generalities has proven difficult for a variety of reasons. First, rarity is defined differently across studies, e.g., species may be considered rare based on range size, conservation status, or frequency of occurrence within a study region. The traits associated with such different types of rarity can be expected to vary substantially. A second challenge is the large diversity of taxa and traits covered in studies focussing on trait-rarity relationships: the traits related to rarity may vary substantially among taxonomic groups owing to differences in physiology and life history. In addition, species exhibit numerous traits, not all of which will necessarily impact or even correlate with their degree of commonness or rarity. Furthermore, traits may interact within a single individual or species, and the effects of traits that promote rarity may be offset by other traits that promote commonness. Finally, studies on traits naturally focus on those traits for which we have adequate data, and it is unclear to what degree the available data correspond to the key drivers of rarity.

Owing to the difficulties in finding consensus among studies of the traits associated with rarity, we propose a top-down approach linking rarity to traits. Instead of inferring trait-rarity relationships by synthesising the available evidence, we instead propose a suite of trait dimensions that can be mechanistically linked to the three proposed rarity dimensions (i.e., range size, occupancy, and local abundance).

Trait dimensions

We propose four basic trait dimensions to aid in linking rarity to ecological processes: tolerance, movement, interactions, and life history. These dimensions are based in part on the trait dimensions proposed by for the study of metacommunities, and in part on concepts from relevant macroecological theories. Tolerance captures the breadth of conditions that a species can tolerate (or, conversely, the types of conditions it requires). The interactions dimension includes both interspecific and intraspecific interactions. These first two dimensions overlap to some degree: for example, a plant's requirement for light is both a physiological requirement and a source of competitive interactions. To distinguish between the two, we use tolerance for non-consumable environmental conditions (e.g., pH, temperature), and interactions for consumable resources (e.g., light, food, nesting sites). Movement includes both dispersal and establishment, while life history includes traits related to survival, mortality, sexual and asexual propagation, ontogeny, and growth rates. Together, these four trait dimensions capture numerous key ecological processes, including demography (life history, interactions), colonisation (movement, life history), density-dependence (interactions), competitive exclusion (interactions), and environmental filtering (tolerance).

Linking trait dimensions to processes

We consider our four trait dimensions to be indicative of different ecological processes: movement and interactions are indicative of the processes of the same name, whereas tolerance is analogous to the process of environmental filtering, and life history to demographic processes. Here, we seek to identify which dimensions most strongly influence each of the three rarity dimensions. Although in reality the three dimensions of rarity are, to some extent, likely influenced by all four processes for at least some species, our objective is to identify which of the processes are the key drivers of each rarity dimension (Figure 3).

A bundance

Theory suggests that abundance is largely driven by processes relating to life history and interactions. Life history theory captures the effects of several key demographic processes that directly affect abundance, and the related fast–slow life history continuum distinguishes between species with "slow" life histories (K-strategists), which are regulated by density-dependence, and those with "fast" life histories (r-strategists), which are more strongly influenced by growth and reproductive rates. Whereas in theory, r-strategists should have higher abundance than K- strategists owing to their higher population growth rates , there are significant indirect effects from the environment that make it difficult to generalise the relationship between life history strategies and abundance. For example, K- strategists can be quite abundant in resource-poor environments, where resource limitations constrain the feasibility of fast life history strategies . Conversely, r-strategists could hypothetically remain rare if disturbance occurs so frequently that there is insufficient time to rebuild populations between disturbances.

Interactions also play a significant role in regulating local abundance through resource–consumer dynamics and density-dependent effects. Consumers are limited by the availability of the resources they require and the pressure they exert on them; this may in part explain the widely observed negative correlation between body size and abundance , which may be attributable to the higher energetic requirements of larger organisms . Density-dependence, whether interspecific or intraspecific, can play a strong role in regulating population size. Predators and pathogens may constrain the abundance of their prey via cyclical (e.g., or non-cyclical (e.g.,) effects. Finally, negative intraspecific density dependence, which is stronger in rare species than in common species , may be an adaptive mechanism that promotes persistence in some naturally rare species .

Occupancy

Occupancy is governed by two primary factors: first, the ability for species to access various sites on the landscape, and second, their ability to persist at these sites. The former varies, in part, as a function of a species' dispersal capacity, suggesting that movement is important in determining patterns of occupancy. Once a species establishes at a site, its persistence will be driven by the balance between births and deaths, which, in turn, should be governed by the suitability of conditions at the site (i.e., environmental filtering) as well as demographic processes.

Theory supports the above hypotheses. Two concepts from metapopulation theory, which is the principal theory explaining patterns of occupancy, are relevant here. The first is the importance of the balance between colonisation and local extinction in driving occupancy. The second is the distinction between patch and matrix, that is, the presence and spatial arrangement of sites with suitable (patch) or unsuitable (matrix) habitat on the landscape. While the spatial arrangement of patches is a geographic contingency that is beyond the scope of the current discussion, the distinction between patch and matrix acknowledges the role of environmental filtering in driving patterns of occupancy.

The balance between colonisation and local extinction is somewhat more complex, as both processes are intimately tied to abundance: larger local populations produce more propagules, thus increasing the probability of colonising new sites , and are less prone than smaller populations to local extinction resulting from demographic stochasticity. These dynamics have been invoked to help explain the widely observed positive relationship between occupancy and abundance , further underscoring the relationship between these two rarity dimensions. As such, the drivers of abundance indirectly influence occupancy via their effects on colonisation and extinction (Figure 3).

Finally, the importance of colonisation in metapopulation theory underscores the importance of movement as a driver of patterns of occupancy. Based on the discussion in this subsection, we conclude that occupancy is directly driven by environmental filtering and movement, although the indirect effects of demography and interactions, through their influence on local abundance, should not be neglected.

Range size

Hutchinsonian niche theory suggests that, apart from sinks, species' occurrence will be constrained to sites where environmental conditions are conducive to their persistence (; that is, occurrence is spatially constrained by environmental filtering. Both island biogeography and metapopulation theories also highlight the importance of movement (dispersal), in conjunction with the geographic contingencies of habitat availability and connectivity, in determining species' geographic distributions . As such, theory suggests that the primary mechanistic drivers of species' distributions are environmental filtering and movement.

This importance of environmental filtering is strongly supported in the biogeographical literature. note that niche processes are among the most common explanations for interspecific variations in range size, an assertion supported by a metanalysis. Tolerance has also been invoked to explain Rapoport's rule (the general tendency for range size to increase with increasing latitude), as species living at higher latitudes experience, and thus must tolerate, a wider range of climatic conditions than those living in lower latitude regions. In addition, the popularity and efficacy of species distribution models suggests that tolerance is an important component of range size.

Dispersal has also frequently been cited as a driver of range size , though its importance is less clear than that of environmental filtering. Empirical studies of the relationship between range size and dispersal have produced mixed results; some have found that poor dispersal capacity is common among species with restricted distributions and references therein), while others have found only a modest relationship between range size and dispersal . A recent meta-analysis found a positive relationship between range size and dispersal capacity , but noted that the relationship is complex and is mediated by factors such as taxonomy, dispersal proxy, and biogeographic realm. In addition, of our three rarity axes, range size is arguably most influenced by the effects of historical contingencies, including phylogeny and long-term environmental changes . It is possible that these influences, which operate at very broad temporal scales, may obscure or even override the role of shorter-term processes such as movement .

Note of caution

Despite the advantages outlined above, replacing habitat specificity with occupancy may pose certain conceptual and technical challenges. First, occupancy is correlated with both range size and abundance, which may be perceived as problematic. Second, it may be difficult to quantify occupancy in practice, given that estimates can be influenced by the scale of observation and imperfect detection. However, similar problems exist for the other Rabinowitz dimensions; for example, habitat specificity and range size are also correlated (Slatyer et al., 2013), but this relationship has not hindered the utility of the framework.

With respect to the difficulty of quantifying occupancy, it is generally challenging to quantify any of the rarity dimensions in practice, and a good deal of creativity has been used in applying the framework. Each of the three rarity dimensions have been defined in remarkably variable ways in the literature. For example, some studies have defined species restricted to a particular ecological or administrative region of interest as having a small range size, and more broadly distributed species as having a large range (e.g., . Similarly, while most studies assess habitat specificity based on the number of ecoregions or habitat types within which a species occurs , others base their assessments on additional, related factors, such as habitat scarcity or species' reliance on a focal habitat type . The flexibility and creativity demonstrated by these examples can be used to assess occupancy in the literature is usually based on available information and study objectives. The strict definition of occupancy we proposed here may be impractical to quantify in many situations; however, the concept can be approximated, for example, by re-defining occupancy as the proportion of study sites within a dataset in which a species was observed, or by gridding the study region and estimating occupancy based on the proportion of occupied cells. In well-surveyed regions such as the United Kingdom or Switzerland , dot maps may also provide an excellent basis for assessing occupancy.

Finally, while our framework is intended to identify the key mechanistic drivers of rarity, it is impossible to

capture all the idiosyncrasies of individual species while also retaining a meaningful degree of generalisability. As such, our proposed framework is by necessity a simplification of reality. For example, for species that rely on biogenic habitats (e.g., epiphytes), interactions may be a key driver of range size as the presence of these species is dependent on the presence of the host or substrate species, a factor that is not accounted for in our framework. As such, the ecology and biology of focal taxa or groups must be considered when applying the framework.

Contingencies

Beyond the processes described above, rarity can also be influenced by historical and geographical contingencies. Perhaps the most obvious of these are the effects of habitat quality, availability, and accessibility on abundance, occupancy, and distribution. These effects are illustrated by studies of niche position (i.e., the commonness or rarity of species' habitat on the landscape), which has been found to be significantly correlated with occupancy and abundance across a range of taxonomic groups. Historical contingencies also affect species' occurrence: phylogeny is correlated with range size , and glaciation can leave a lasting imprint on species' range limits . Finally, neutral theory suggests that rarity can arise from random variations in species' demography (ecological drift). While the complexity and diversity of contingencies precludes generalising their effects on rarity and integrating these effects into our framework, the role of contingencies cannot be ignored when considering the drivers of rarity for species of interest.

Conservation implications

The practical implications of defining rarity axes

While some ecologists are interested in rarity from a theoretical perspective, many studies on rarity and rare species are explicitly conservation oriented. While rare species are not always of conservation concern, and many naturally rare species may be stable over long periods of time, rare species as a group are more likely to be at risk of decline and extinction. In addition, historically stable rare species may experience rapid declines because of anthropogenic pressures, as illustrated by the vaquita. As such, rare species are often the focus of conservation efforts such as monitoring and protected area planning. However, how rarity is defined determines which species are, or are not, targeted by such efforts, and what types of conservation measures are used. As such, any framework for structuring rarity should consider the practical implications of including or excluding particular dimensions of rarity.

Our proposed replacement of habitat specificity with occupancy implies that habitat specialists will not necessarily be classified as rare. However, habitat specialists may be quite common if their preferred habitat is widely available; such abundant, widespread habitat specialists stretch the definition of rarity, and are unlikely to be of conservation concern. For example, brown peatmoss (Sphagnum fuscum), a bryophyte, is a circumboreal habitat specialist that occupies relatively dry microhabitats in peatlands. However, this habitat type is widely available, and brown peatmoss is common and abundant throughout north temperate and low Arctic regions. Thus, while brown peatmoss would be considered rare under the original Rabinowitz classification, it would be considered common under our modified framework. Conversely, for specialists associated with uncommon habitat types, the effects of their high niche position will likely manifest as low occupancy or restricted distribution. The koala (*Phascolarctos cinereus*), which is range-restricted owing to its strong reliance on *Eucalyptus* forests, is an example of this phenomenon. A contrasting example is Porsild's bryum (Haplodontium macrocarpum), a moss species that occurs only in shaded, continually moist localities on calcareous substrates. While widely distributed throughout northern temperate and polar regions, populations are few and disjunct owing to the limited availability of suitable habitat. In contrast to brown peatmoss, both the koala and Porsild's bryum would be considered rare under our classification owing to the effects of the availability of their highly specific requirements on their range size and occupancy, respectively.

Conservation implications of the dimensions and drivers of rarity

Our framework (Figure 3) provides insight into the particular vulnerabilities of different types of rare species

and may help identify effective conservation measures for them. Each of the three rarity dimensions pose different challenges to persistence: species that occur at low abundance may be vulnerable to demographic stochasticity , Allee effects , inbreeding, and drift . Low occupancy is correlated with higher extinction risk , which may be explained in part by metapopulation dynamics: as occupancy declines, populations will become increasingly isolated, which in turn reduces the probability of demographic rescue and increases the risk of local extinctions. Similarly, isolation resulting from low occupancy may also promote drift and lack of gene flow , impacting fitness. Furthermore, species that are characterised by narrow ranges may be particularly vulnerable to correlated population dynamics owing to the spatial correlation in ecological processes and environmental conditions over the relatively small spatial extent of these species' ranges . For example, factors such as disturbance or habitat loss will affect a larger proportion of the range of narrow endemics as compared to more widespread species. Finally, species that are range restricted by a narrow climatic niche are particularly vulnerable to climate change .

The hypothesised relationships between the three rarity axes and the four underlying processes (Figure 3) may point to measures that could be used to conserve different types of rare species. Note that the measures proposed below are aimed at managing species whose persistence is threatened by their rarity, rather than those that are stable despite being rare.

We hypothesise that species characterised by low abundance are primarily limited by demography and interactions. Demographic challenges to persistence may be mitigated via measures such as assisted breeding and ex-situ conservation, which can increase the probability of survival for species on the brink of extinction, and help to maintain or increase the genetic diversity of very rare species . As for interactions, species may be threatened by new negative interactions (e.g., competition and predation), or, conversely, by the loss of positive interactions (e.g., pollination). Control of predators or invasive species may be necessary for conservation of some species (while avoiding unnecessary and unproductive persecution of predators;). In the case of facilitative interactions, the conservation of species with obligate symbioses requires the conservation of the symbiont. In some cases, facilitative interactions may be known or suspected to be involved in a species' rarity, but the identity of critical symbionts unknown; e.g., a rare plant may be threatened by insufficient pollination, but the specific pollinator is not known. In these cases, habitat- or landscape-scale efforts that promote the recovery or maintenance of biodiversity and ecological processes may be the most effective intervention. In short, it is essential to recognize the importance of the trophic network surrounding the target species.

Species characterized by small ranges and/or low occupancy are thought to be mainly limited by environmental filtering and movement. Species limited by environmental filtering may benefit from landscape scale measures to conserve or increase (i.e., restore) high quality habitat. Where movement is a limiting factor, increasing patch connectivity (at a grain size suitable to the target species' dispersal capacity) and assisted colonisation may be helpful to increase patch occupancy. Assisted migration to climate analogues may also help conserve range-restricted species threatened by climate change.

Conclusions

There are limits to the generalities that can be made about the causes of rarity. Species are rare due to unique combinations of factors, including traits, trait–environment interactions, biotic interactions, geographical contingencies, and historical contingencies. That said, there is value to using a conceptual framework to structure and guide our explorations of the phenomenon of rarity, as evidenced by the widespread use of the Rabinowitz framework. We have created a framework that can be used to infer potential causes of rarity depending on the type of rarity exhibited by a species. The generalities provided by the framework can be combined with empirical observations and natural history knowledge to more precisely determine the causes of rarity, stimulate the development of hypotheses about focal rare taxa, guide the selection of focal traits for future trait–rarity studies, and identify effective, targeted conservation measures for rare species.

References

Figure captions

Figure 1. Distinction between range and occupancy, illustrated with examples from the flora of the British Isles: (a) large range and high occupancy (*Fritillaria meleagris*), (b) small range and high occupancy (*Fumaria occidentalis*), (c) large range and low occupancy (*Maianthemum bifolium*), and (d) small range and low occupancy (*Alchemilla minima*).

Figure 2. Schematic diagram of the three proposed rarity dimensions and their relationship to spatial scale.

Figure 3. Hypothesised process-rarity relationships. Solid arrows indicate a direct relationship between processes (left) and rarity dimensions (right); dashed arrows indicate an indirect relationship, as described in-text.







Figure 2.



Figure 3.

Table 1. Rabinowitz rarity types based on Rabinowitz (1981).

Geographic range		Wide	Wide	Narrow	Narrow
Population size		Large	Small	Large	Small
Habitat specificity	Generalist	common	rare	rare	rare
	Specialist	rare	rare	rare	rare

 Table 2. Examples of studied traits and their relationship with one or more rarity dimensions.

Rarity dimension	Trait dimension	Study	Taxon	Trait
Range size	Tolerance		Birds	Niche breadth
				Diet breadth
			Plants	Habitat breadth
	Interactions		Plants	Herbivory levels
		Laube et al., 2013	Birds	Trophic level
	Movement	Laube et al., 2013	Birds	Dispersal ability
		Estrada et al., 2015	Plants	Dispersal potential
			Birds	Dispersal ability
	Life history	Lavergne et al., 2004	Plants	SLA
				leaf N
				LDMC
				Flower number
				Flower size
				Stigma-anther separation
				Pollen/ovule ratios
				Propagule structure
			Plants	SLA
		Laube et al., 2013	Birds	Fecundity
		,		Body size
		Estrada et al., 2015	Plants	Clonality
		, <u> </u>		Seed mass
				Age of maturity
				Reproductive frequency
				Self-fertilisation capacity
				SLA
		Bohning-Gaese et al., 2006	Birds	Body size
Range size (con't)		, , , , , , , , , , , , , , , , , , ,		Seed weight
			Plants	Seed production
				Seedbank longevity
		Lavergne et al., 2004	Plants	Seed mass
		0		Seed size
				Seed bank persistence
Occupancy	Tolerance		Aquatic invertebrates	Niche breadth (outlying m
			Birds	Niche breadth (outlying n
			Aquatic invertebrates	Niche breadth (outlying m
			Aquatic invertebrates	Niche breadth
			Diatoms	pH range
	Interactions	Hurlbert & White, 2007	Birds	Trophic level
			Plants	Mycorrhizal associations
	Movement		Aquatic invertebrates	Dispersal mode
		Heino & Gronroos. 2014	Aquatic invertebrates	Dispersal mode
		van der Veken et al 2007	Plants	Long distance dispersal ca
		,,		0

rearrey dimension	Trait dimension	Study	Taxon	Trait
	Life history	Hurlbert & White, 2007	Birds	Body size
	v		Birds	Foraging strategy
		Lachaise et al., 2021	Plants	Life history strategy (SLA
			Plants	Inflorescence type
				Ovule number
				Seeds/plant
Occupancy (con't)				Seed setting rate
				Seed mass
			Plants	SLA
				Seed number per reproduc
				Clonality
				Seed mass
		Vilmi et al., 2019	Diatoms	Body size
		Heino & Gronroos, 2014	Aquatic invertebrates	Body size
		van der Veken et al., 2007	Plants	Seed production
				Seed bank longevity
				Seed dispersal mode
				Seed weight
				Seed size
			Plants	Seed bank longevity
Abundance	Tolerance	Heino & Tolonen, 2018	Aquatic invertebrates	Niche breadth
		Marino et al., 2019	Aquatic invertebrates	Niche breadth (outlying m
		Kolb et al., 2006	Plants	pH range
		Heino & Gronroos, 2014	Aquatic invertebrates	Niche breadth
	Interactions		Butterflies	Food availability
		Lachaise et al., 2021	Plants	Mycorrhizal associations
			Plants	Herbivory
				Mycorrhizal associations
		Kolb et al. 2006	Plants	Pollination mode
	Movement		Plants	Dispersal ability
Abundance (con't)		Kolb et al., 2006	Plants	Long distance dispersal ca
		Heino & Gronroos, 2014	Aquatic invertebrates	Dispersal mode
	Life history		Plants	Clonality
	·			Seed number
				SLA
				Seed weight
		Reader, 1998	Plants	Growth rate
			Plants	Leaf longevity (life history
		Sporbert et al., 2021	Plants	SLA
				Seed number per reproduc
				Clonality
				Seed mass
		Vilmi et al., 2019	Diatoms	Body size
		Kolb et al., 2006	Plants	Clonality
				Seed number
				Seed size
				Seedbank persistence
		Heino & Gronroos, 2014	Aquatic invertebrates	Body size