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Review

How and why species are rare: towards an understanding of the ecological causes of rarity

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The three-dimensional rarity typology proposed by Rabinowitz in 1981, based on geographic range, habitat specificity, and local abundance, is among the most widely used frameworks for describing rarity in ecological and conservation research. While this framework is descriptive and is not meant to explain the causes of rarity, recent advances in ecology may be leveraged to add explanatory power. Here we present a macroecological exploration of rarity and its underlying causes. We propose a modification of Rabinowitz's typology to better distinguish between the dimensions of rarity and the ecological processes that drive them, and explore the conservation implications of our modified framework. We propose to add occupancy (the proportion of occupied sites within a species' range) as a rarity axis, and recast habitat specificity as a cause of rarity, thus yielding a modified classification based on range size, occupancy, and local abundance. Under our framework, habitat specialists are no longer considered rare if they are widespread and abundant; 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 macroecological and theoretical 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. We further use ecological theory to hypothesise the conservation concerns associated with each rarity axis, and propose conservation measures that may be suitable for conserving different types of rare species. Our work may provide a basis for developing hypotheses about the causes of rarity of particular focal taxa or groups, and inform the development of targeted conservation strategies.

Keywords: conservation, Rabinowitz, rarity, theory



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Introduction

Rare species have long been the focus of considerable attention in ecology and conservation biology (Myers et al. 2000, Bonn and Gaston 2005). Rare species have been found to be particularly vulnerable to extinction due to factors such as high habitat specificity and small range size (Harnik et al. 2012, Chichorro et al. 2019), and are often among the targets of conservation efforts (Prendergast et al. 1993, Flather and Sieg 2007, IUCN WCPA 2019). 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 (Gaston and Blackburn 2000, Scheiner and Willig 2008); 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, rarity is complex, multifaceted, and complicated by contingency (Lawton 1999), and identifying generalities has proven difficult.

Numerous ecologists have sought to bring order to the unwieldy phenomenon of rarity. Early research attributed rarity to a single causal factor. For example, Willis (1922) proposed that rare species were newly evolved taxa which have not yet occupied their full niche, whereas Fernald (1925) hypothesised that they are relictual species that have decreased in abundance or distribution. Cain (1940) argued that low heterozygosity limits species' ecological amplitudes, leading to rarity. While overly simplistic, these early studies began the work of identifying species-level characteristics that predict rarity, thus laying the foundation for later work to identify the traits associated with rarity (e.g. poor dispersal ability, high trophic level, large body size; Gaston and Kunin 1997).

More recent efforts to understand rarity have taken a less monolithic (sensu Rabinowitz 1981) perspective and include the development of frameworks that conceptualise rarity as a multidimensional phenomenon. Some of these focus on describing different patterns of rarity, i.e. different ways in which species can be rare. The most well-known of these is the framework developed by Rabinowitz (1981), which classifies species based on three dimensions of rarity: local abundance, habitat specificity, and geographic range. Local abundance refers to a species' typical population size at the local scale; habitat specificity refers to the range of habitat types in which a species occurs, and is roughly analogous to the concept of niche breadth; and geographic range denotes the 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 (Birsakis-Barros et al. 2019, Reed et al. 2020), identify conservation priorities (Sykes et al. 2020), and assess extinction risk (Harnik et al. 2012).

While Rabinowitz focused on describing patterns of rarity, other ecologists have focused on identifying the underlying processes that generate these patterns, and developed theoretical frameworks to explain the causes of rarity. Fiedler and

Ahouse (1992) created a rarity typology based on two factors – range size and the persistence of the species over time (i.e. taxon age) – which are dichotomised (i.e. narrow versus wide range and short versus long persistence) and combined to form four different rarity types. They then propose a different hierarchy of explanatory causes for each of the four resulting groups. Stebbins (1980) emphasized the need for a synthetic approach to understanding rarity, and proposed a system that incorporates the roles of historical, genetic, and ecological processes.

We reviewed all the studies (peer-reviewed articles, government reports, theses, etc.) that cite either Fiedler and Ahouse (1992) (n=209) or Stebbins (1980) (n=213) until the end of 2022 according to Google Scholar, and found that although these two papers have been frequently cited, these theories have rarely been used to classify species or assemblages (though see Yates et al. 2007). While this is in striking contrast to the popularity of the Rabinowitz framework (with 1977 citations according to Google Scholar), 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 distribution, 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 and 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). Rabinowitz (1981) 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.

Stebbins' emphasis on synthetic explanations is 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 (Stebbins 1980, Sheth et al. 2020). However, data on many rare species are scarce: for example, of the species assessed under the IUCN red list criteria, one in six is listed as data deficient (Chichorro et al. 2019), and estimates are higher for diverse, understudied groups such as invertebrates (Hochkirch et al. 2021). To provide practical value for conservation, a framework for explaining rarity must be

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

Geographic range		Wide		Narrow	
Local abundance	Habitat specificity	Large	Small	Large	Small
		common	rare	rare	rare
	Generalist				
	Specialist	rare	rare	rare	rare

usable despite the knowledge gaps that often exist for rare species, a feat that the Rabinowitz framework appears to have accomplished, based on its widespread application.

We sought to increase the robustness of the conceptual underpinnings of studies of rarity by developing a process-based framework to identify the ecological causes of different types of rarity. We used the Rabinowitz framework as the basis for our work owing to its evident utility, and took a top-down, macroecological approach focused on linking patterns of rarity to their predominant underlying ecological causes. Our objective was to add an explicative component to this popular model, while also retaining its accessibility. To this end, we propose adding occupancy as an additional rarity axis, and we reconceptualise habitat specificity as a trait that leads to rarity, rather than a rarity axis. By basing our framework on common, accessible metrics related to abundance and distribution, we hope to maintain the utility exhibited by Rabinowitz' original framework. Following these modifications, we use ecological theory to explore the possible mechanisms underlying each rarity axis. Finally, we discuss the implications of our proposed framework for the conservation of rare species.

Describing and explaining rarity: pattern versus process

The field of macroecology seeks to understand the relationships between pattern – broadly-occurring ecological phenomena – and process – the underlying drivers of these phenomena – from a multi-scale, multi-taxon perspective (McGill 2019). Historical approaches to understanding rarity can be divided along this pattern–process dichotomy: the causal theories of Stebbins and Fiedler and Ahouse sought to identify the fundamental processes that result in rarity (i.e. why species are rare), whereas the Rabinowitz framework took the approach of describing different patterns of rarity (i.e. how species are rare).

While patterns are driven by ecological processes, they are also significantly affected by a second class of causal factors: contingencies, which are unpredictable, often stochastic external factors that impact ecological patterns (Pickett et al. 2007). Examples of contingencies include climate change, ecological drift, evolutionary history, past glaciation events, the availability of specific habitats, and human or natural disturbances. Here, we use an expanded definition of contingencies that also accounts for geographic and environmental 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 the product of interactions between ecological processes and contingencies. Contingencies can complicate and obscure the search for general patterns in ecology (Lawton 1999); however, by recognizing the separate, but interrelated roles of both contingency and process, we hope to identify the key processes underlying rarity despite the vast diversity in patterns of rarity that stem from the influence of contingencies.

Due to their inherent unpredictability, it is not possible to generalise the effects of contingencies in a framework. As such, the remainder of our argument focuses on the relationship between process and pattern in generating rarity, but we stress that it is important to remain mindful of the role of contingencies in driving rarity.

Describing rarity: pattern

There is no universally agreed-upon definition of rarity or what exactly constitutes a rare species, but the term is most commonly used to refer to species characterised by a restricted distribution, low abundance, or both (Fiedler and Ahouse 1992, Kunin and Gaston 1993, 1997, Gaston 1994), and we will follow this convention. Furthermore, while rarity 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 rare. Thus, species that are rare only within a certain context, such as a particular jurisdiction or community, are not considered here.

While the popularity of the Rabinowitz framework is a testament to its practicality and value, it is somewhat problematic when viewed through our pattern–process lens, in that the three rarity dimensions (geographic range, local abundance and habitat specificity) represent a combination of pattern and process. Creating a process-based framework for rarity requires a clear distinction between the processes that generate rarity, and the outcomes of these processes, which are patterns. Range size and local abundance are emergent properties which arise from the interactions between species and their environment (including other species). The are a manifestation of the effects of ecological processes on species. Above, we describe patterns as the product of the interaction between ecological processes and contingencies; in this sense, local abundance and range size may be classified as patterns. Habitat specificity, by contrast, is an inherent characteristic or trait of species, not property that emerges from the influence of processes (at least, not on an ecological time scale). Rather than being a pattern of occurrence, habitat specificity is among the factors that may influence these patterns.

The Rabinowitz framework captures patterns of occurrence either at very broad (i.e. geographic range) or very fine scales (i.e. local abundance), but not at an intermediate scale. As scale can substantially affect patterns of rarity, along with related issues such as population decline (Hartley and Kunin 2003), this omission may create an important gap in assessing rarity. Finally, while the Rabinowitz framework captures abundance at the local scale, a species' overall abundance is influenced not only by local-scale population size, but also by the frequency at which the species occurs across the landscape. For example, a species that is characterised by small local populations, but which occurs frequently throughout its range, will have a higher total abundance than a species with similarly-sized local populations, but few occurrences. The effects of these larger-scale dynamics on abundance are not captured by the Rabinowitz framework.

We propose addressing both these issues by making three modifications to the Rabinowitz framework. First, we propose to more narrowly define Rabinowitz' geographic range axis the geographic extent within which a species occurs (excluding vagrants and sink populations), which we call 'range size' here. This resembles (but is not identical to) the IUCN's concept of extent of occurrence (IUCN Species Survival Commission 2012). Second, we propose reconceptualising habitat specificity as an underlying cause of rarity instead of a rarity dimension. We will address this change in more detail in the following section ('Explaining rarity: process'). Third, we propose adding occupancy to the framework as a novel rarity axis. These three changes yield a modified version of the seven forms of rarity (Table 2) that can be used to classify species in the same way as the original Rabinowitz framework. We define occupancy as the proportion of habitat patches within a species' range that is occupied. Our definition of occupancy bears some similarities to the concept of 'Area of Occupancy' (IUCN Species Survival Commission 2012), though our measure is a proportion rather than an area, and need not be measured on the basis of a grid. Our proposal to add occupancy as a rarity axis is not altogether novel, as Rey Benayas et al. (1999) also proposed adding habitat occupancy (proportion of suitable sites occupied), but as fourth rarity axis in addition to the three put forth by Rabinowitz.

The distinction between occupancy and range size warrants some further precision, as occupancy is frequently used a proxy for range size, including in some studies that have applied the Rabinowitz framework (Harnik et al. 2012, Maciel and Martins 2021). However, Fig. 1 illustrates the differences in how we define the two concepts: whereas range size refers to the global limits of the area within which a species occurs, occupancy denotes the frequency of occurrence within those limits. As such, the two metrics provide complementary information about species' geographic distributions. Furthermore, the conservation implications of low occupancy differ from those of geographic restriction; we discuss these considerations in the 'Conservation implications' section. Given that studies of rare species often have conservation objectives, the distinction between range size and occupancy is important.

There are two major advantages to adding occupancy as a rarity axis: first, like range size and local abundance, occupancy describes a pattern of occurrence. Second, the addition of occupancy provides additional information on abundance and distribution that is complementary to the other two rarity axes. Like range size, occupancy describes the geographic distribution of a species, but at a finer scale (i.e. within-range versus global) (Fig. 2). Similarly, occupancy provides additional information about species' abundance, but at a different scale

than local abundance, by capturing information about the frequency at which a species occurs within its range.

The practical implications of defining rarity

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 (e.g. 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 conceptualization of habitat specificity does not mean that habitat specialists cannot be classified as rare; species can be rare at along any of our axes due to specialisation; alternatively, a specialist species may be abundant if its preferred habitat is abundant (Venier and Fahrig 1996, Vela Díaz et al. 2020). 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 (Vitt and Lüth 2017). However, this habitat type is widely available, and brown peatmoss is common and abundant throughout north temperate and low Arctic regions (Blockeel et al. 2014). Thus, while brown peatmoss could 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 the low availability of their required habitat on the landscape 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 (Melzer et al. 2000). A contrasting example is Porsild's bryum *Haplodontium macrocarpum*, a moss species that occurs only in shaded, continually moist localities on calcareous substrates (COSEWIC 2017). While widely distributed throughout northern temperate and polar regions, populations are few and disjunct owing due to the limited availability of suitable habitat (COSEWIC 2017). 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. While examples of common specialists such as brown peatmoss exist, we expect them to be in the minority. Narrow habitat requirements are commonly associated with small ranges or low occupancy (Slatyer et al. 2013), and we expect an inverse correlation between the degree of

Table 2. Rarity types under our proposed framework.

Range size		Wide		Narrow	
Local abundance		Large	Small	Large	Small
Occupancy	High	common	rare	rare	rare
	Low	rare	rare	rare	rare

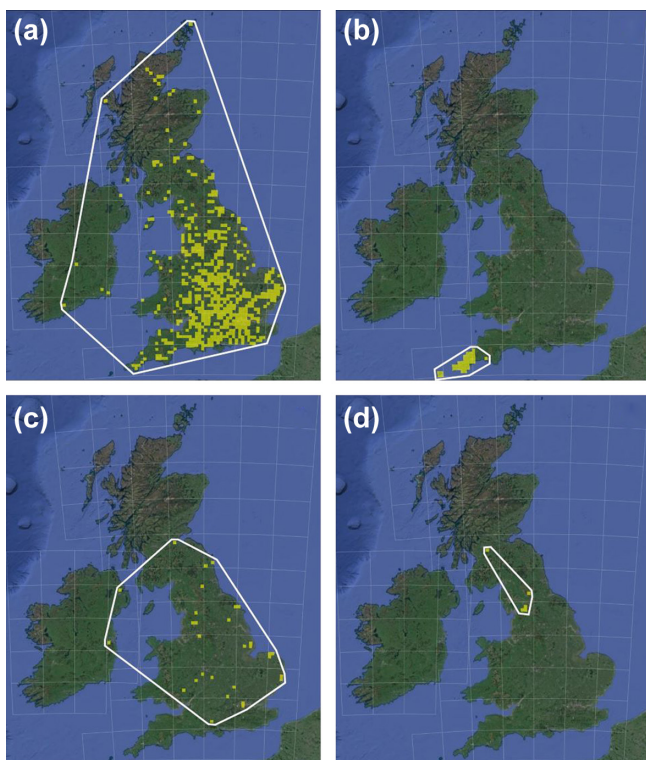


Figure 1. Distinction between range and occupancy, illustrated with examples from the flora of the British Isles: (a) large range and high occupancy *Fritillaria meleagris*, (b) small range and high occupancy *Fumaria occidentalis*, (c) large range and low occupancy *Maianthemum bifolium* and (d) small range and low occupancy *Alchemilla minima* (Botanical Society of Britain and Ireland 2022).

specialisation and the amount of suitable habitat available. That is to say, as species' requirements become increasingly specific, less habitat will satisfy these requirements.

Explaining rarity: process

In this section we seek to link each of our three rarity axes (range size, occupancy and local abundance) to the processes that drive them. This section represents a thought exercise to

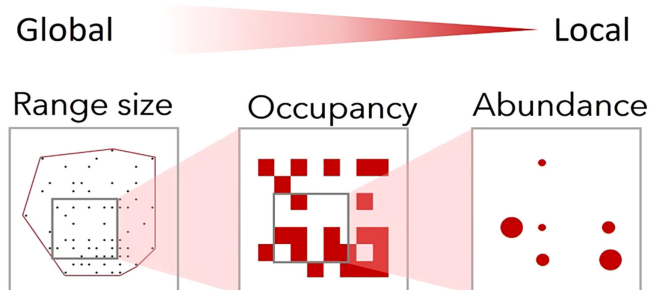


Figure 2. Schematic diagram of the three proposed rarity dimensions and their relationship to spatial scale. Note that while occupancy is shown as a gridded measure, this is simply for convenience in the figure, and occupancy can equally be measured based on a natural division of the area within a species range (e.g. into habitat patches).

attempt to create a macroecological and theory-driven framework organizing the various causes underlying our three rarity dimensions. We begin by identifying traits we hypothesize are associated with rarity, as traits are a tool for inferring the mechanisms underlying species' occurrence patterns. We then review ecological theories to glean insight into the links between our three rarity axes and processes, using traits as an indicator of processes.

A key challenge in ecology is to identify generalities that transcend the idiosyncrasies of specific focal assemblages or regions (McGill et al. 2006). Functional ecology offers a taxonomically-neutral approach for inferring information about ecological processes from species' functional traits (Funk et al. 2017). Similarly, functional traits may offer a path towards identifying the key processes that drive different rarity dimensions. For example, in vascular plants, specific leaf area is a component of the suite of traits known as the leaf economics spectrum, which are indicative of plant life history strategies along a spectrum ranging from conservative to acquisitive (Wright et al. 2004). Higher specific leaf area is associated with the rapid production of leaf tissue, thus facilitating the uptake of resources from the environment (Adler et al. 2014), which in turn promotes higher growth rates and greater competitiveness for light resources (Wright et al. 2004). As such, specific leaf area is commonly considered a proxy for productivity and competitive ability (Sporbert et al. 2021). Higher leaf area has been found to be associated with higher local abundance (Sporbert et al. 2021), and occupancy (Lachaise et al. 2021), suggesting a mechanistic link between traits (here, specific leaf area), functions (resource acquisition), environmental processes (competition for light), and species' degree of commonness. Given the mechanistic relationship between traits and processes, we would expect to see similar relationships between other traits and species' degree of commonness or rarity.

However, despite the large body of literature that has sought links between traits and rarity (Table 3), 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 (Walck et al. 2001, Lavergne et al. 2004), conservation status (Gabrielová et al. 2013), or abundance within a study region (Rabinowitz et al. 1984, Laliberté et al. 2012). Traits associated with such different types of rarity can be expected to differ (Heino and Grönroos 2014, Sporbert et al. 2021). A second challenge is the large diversity of taxa and traits covered in studies focusing on trait–rarity relationships, as the traits related to rarity may vary substantially among taxonomic groups owing to differences in physiology and life history. For example, diet breadth has been found to predict range size in birds (Laube et al. 2013) and abundance in butterflies (Curtis et al. 2015), whereas leaf traits, including specific leaf area, are important in plants. In addition, species exhibit numerous traits, not all of which will necessarily impact or even correlate with their degree of commonness or rarity (Estrada et al. 2015, Lachaise et al. 2021). Furthermore, traits may interact within a single individual or species, and the effects of traits

Table 3. Examples of studied traits and their relationship with one or more rarity dimensions.

Rarity dimension	Trait dimension	Study	Taxon	Trait
Range size	Tolerance	Laube et al. (2013)	Birds	Niche breadth
				Diet breadth
	Interactions	Estrada et al. (2015) Lavergne et al. (2004)	Plants	Habitat breadth
				Herbivory levels
	Movement	Laube et al. (2013)	Birds	Trophic level
				Dispersal ability
	Life history	Estrada et al. (2015) Böhning-Gaese et al. (2006) Lavergne et al. (2004)	Plants	Dispersal potential
				Dispersal ability
				SLA
				leaf N
				LDMC
				Flower number
				Flower size
				Stigma–anther separation
				Pollen/ovule ratios
				Propagule structure
		Matesanz et al. (2009)	Plants	SLA
		Laube et al. (2013)	Birds	Fecundity
				Body size
		Estrada et al. (2015)	Plants	Clonality
Occupancy	Tolerance	Heino and Tolonen (2018)	Aquatic invertebrates	Seed mass
				Age of maturity
	Interactions	Hurlbert and White (2007)	Birds	Reproductive frequency
				Self-fertilisation capacity
	Movement	Marino et al. (2020)	Aquatic invertebrates	SLA
				Body size
	Life history	Heino and Grönroos (2014) Vilmi et al. (2019)	Aquatic invertebrates	Seed weight
				Seed production
		Hurlbert and White (2007)	Birds	Seedbank longevity
				Seed mass
		Lachaise et al. (2021)	Plants	Seed size
				Seed bank persistence
		Kneitel (2018)	Aquatic invertebrates	Niche breadth (outlying mean index)
				Niche breadth (outlying mean index)
		Heino and Grönroos (2014) Vilmi et al. (2019)	Aquatic invertebrates	Niche breadth (outlying mean index)
				Niche breadth
		Hurlbert and White (2007)	Birds	pH range
				Trophic level
		Lachaise et al. (2021)	Plants	Mycorrhizal associations
				Dispersal mode
		Heino and Grönroos (2014) Van Der Veken et al. (2007)	Aquatic invertebrates	Dispersal mode
				Long distance dispersal capacity
		Hurlbert and White (2007)	Plants	Body size
				Foraging strategy
		Lachaise et al. (2021) Miller et al. (2021)	Birds	Life history strategy (SLA)
				Inflorescence type
		Sporbert et al. (2021)	Plants	Ovule number
				Seeds/plant
		Vilmi et al. (2019) Heino and Grönroos (2014)	Diatoms	Seed setting rate
				Seed mass
		Heino and Grönroos (2014)	Aquatic invertebrates	SLA
				Seed number per reproductive unit
		Sporbert et al. (2021)	Plants	Clonality
				Seed mass
		Vilmi et al. (2019) Heino and Grönroos (2014)	Diatoms	Body size
				Body size

(Continued)

Table 3. Continued.

Rarity dimension	Trait dimension	Study	Taxon	Trait
Abundance	Tolerance	Van Der Veken et al. (2007)	Plants	Seed production Seed bank longevity Seed dispersal mode Seed weight Seed size
		Kolb et al. (2006)	Plants	Seed bank longevity
		Heino and Tolonen (2018)	Aquatic invertebrates	Niche breadth
	Interactions	Marino et al. (2020)	Aquatic invertebrates	Niche breadth (outlying mean index)
		Kolb et al. (2006)	Plants	pH range
		Heino and Grönroos (2014)	Aquatic invertebrates	Niche breadth
		Curtis et al. (2015)	Butterflies	Food availability and diet breadth
		Lachaise et al. (2021)	Plants	Mycorrhizal associations
		Reader (1998)	Plants	Herbivory Mycorrhizal associations
	Movement	Kolb et al. (2006)	Plants	Pollination mode
		Rabinowitz and Rapp (1981)	Plants	Dispersal ability
		Kolb et al. (2006)	Plants	Long distance dispersal capacity
	Life history	Heino and Grönroos (2014)	Aquatic invertebrates	Dispersal mode
		Austrheim et al. (2005)	Plants	Clonality Seed number SLA Seed weight Growth rate
		Reader (1998)	Plants	Leaf longevity (life history strategy)
		Sporbert et al. (2021)	Plants	SLA Seed number per reproductive unit Clonality Seed mass Body size
		Vilmi et al. (2019)	Diatoms	Clonality
		Kolb et al. (2006)	Plants	Seed number Seed size Seedbank persistence
		Heino and Grönroos (2014)	Aquatic invertebrates	Body size
		Lachaise et al. (2021)	Plants	Seed weight

that promote rarity may be offset by other traits that promote commonness, or vice versa. 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 (Brown et al. 2003).

Owing to the difficulties in finding consensus among studies of the traits associated with rarity (Table 3), 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 priori, 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 (Bauer et al. 2021) for the study

of metacommunities, and in part on concepts from relevant ecological theories, including metapopulation theory (Levins 1969, Hanski 1999), various concepts that fall under the umbrella of life history theory (e.g. r/K selection; MacArthur and Wilson (1967), allocation theory; Weiner (2004), niche theory; Hutchinson (1957), and resource–consumer theory; Tilman (1982)), which we used to identify additional trait dimensions that could influence one or more of our three rarity axes. Tolerance captures the breadth of conditions that a species can tolerate (or, conversely, the types of conditions it requires). This trait dimension captures the important role of habitat specificity in rarity. As noted above, habitat specificity is an intrinsic characteristic of species, and, as such, is more akin to a trait than to a pattern of rarity. Note that studies of species’ environmental tolerances often rely on environmental proxies (e.g. habitat breadth) rather than traits in the strict sense, as we lack trait-based measures of the range of conditions a species can tolerate. For example, while cavitation resistance (i.e. the capacity to prevent the formation of air pockets in sap-conducting tissues) may provide information

about the drought tolerance of a plant species, we cannot use cavitation resistance to infer the full range of moisture conditions that the species can tolerate. Until we have accessible measures of the physiological correlates of niche breadth, environmental proxies remain the best available tool for quantifying tolerance. 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. food, nesting sites). Movement includes both dispersal and establishment, whereas 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 indicative of the process of environmental filtering, and life history of demographic processes. In the following sections, we conduct a thought exercise in which we hypothesize the processes most strongly influencing each of the three rarity dimensions. Furthermore, we apply our framework to two very different rare species (Box 1), to demonstrate utility of the framework for explaining rarity. 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 (Fig. 3).

Local abundance

Life history theory, along with the concepts of density dependence and resource-consumer dynamics, suggest 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 (birth, death and reproduction), and the related fast-slow life history continuum distinguishes between species with 'slow' life histories (K-strategists; e.g. elephants), which are regulated by density dependence, and those with 'fast' life histories (r-strategists; e.g. many rodents), 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 (Salguero-Gómez et al. 2016), there are significant indirect effects from the environment that make it difficult to generalise the relationship between life history

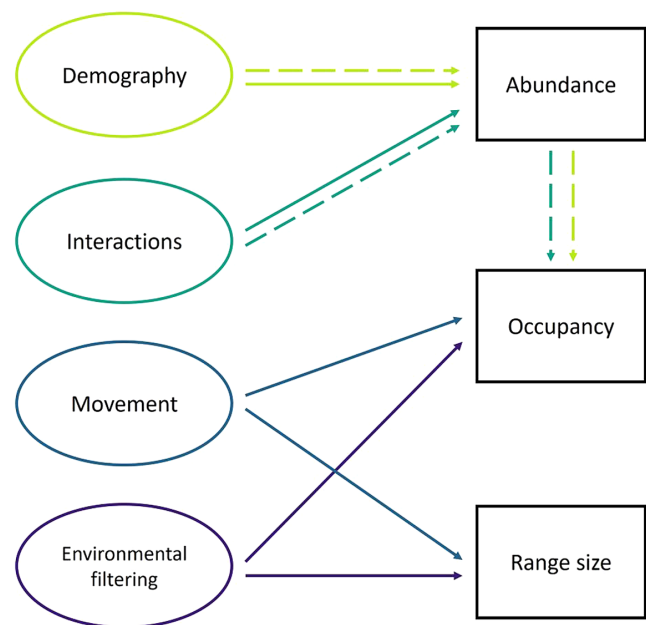


Figure 3. Hypothesised process-rarity relationships. Solid arrows indicate a direct relationship between processes (left) and rarity dimensions (right); dashed arrows indicate an indirect relationship, as described in-text.

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 (Reznick et al. 2002). 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 (Gaston and Kunin 1997), which may be attributable to the higher energetic requirements of larger organisms (Blackburn et al. 1993). 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 (Blasius et al. 2020) or non-cyclical (Bagchi et al. 2014) effects. Finally, negative intraspecific density dependence, which is stronger in rare species than in common species (Comita et al. 2010), may be an adaptive mechanism that promotes persistence in some naturally rare species (Yenni et al. 2012).

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

Box 1.

We illustrate the potential of our proposed framework by applying it to two rare species. The first, impoverished pinweed (*Lechea intermedia* var. *depauperata* Hodgdon, Supporting information), is a narrow endemic plant characterized by large local populations but low occupancy. The second, the wolverine (*Gulo gulo* Linnaeus 1758, Supporting information), is a mammal characterised by a large geographic range, but very low occupancy and local abundance.

Impoverished pinweed

Impoverished pinweed is restricted to northeastern Alberta and northwestern Saskatchewan, Canada (Supporting information). This taxon has a global range size of approx 118 km², based on a minimum convex polygon encompassing all known populations (COSEWIC 1996, Crisfield et al. 2019). Only 10 populations have been recorded since the taxon was first described, four of which may be extirpated (COSEWIC 1996, Lamb et al. 2011). Though remote, the region in which impoverished pinweed occurs has been well-surveyed (Raup and Argus 1982, COSEWIC 1996, Allen et al. 2003, Meijer 2002a, b, Lamb et al. 2011, Pinno and Errington 2016), and the taxon is morphologically distinct; as such, its low occupancy is unlikely to be an artefact of poor detection. While populations are few in number, they are often quite large, generally comprising hundreds and sometimes thousands of individuals (Crisfield unpubl.). As such, the taxon is characterised by a small geographic range, low occupancy, and high local abundance.

The restricted range and low occupancy of impoverished pinweed are likely attributable to the specificity of its habitat requirements (tolerance), the uncommonness of its habitat (i.e. high niche position), and dispersal limitations (movement). The taxon is restricted to the Athabasca Plain ecoregion, which is ecologically unique in the context of the western boreal forest owing to its loose, sandy soils, sparse vegetation communities, relatively high light levels, and relatively warm summers (Natural Regions Committee 2006, Pinno et al. 2013). Owing to its distinctiveness, the Athabasca Plain is a rare, boreal centre of endemism, and nine other endemic plant taxa have been documented in the region (Lamb and Guedo 2012). Impoverished pinweed is associated with recently burned sites, and heat is known to facilitate germination of impoverished pinweed seeds, which are physically dormant; however, excessively high fire temperatures may also kill the seeds (Crisfield et al. 2019). Impoverished pinweed produces large numbers of small, gravity-dispersed seeds, which are mostly deposited locally beneath parent plants, with very few seeds occurring outside of established populations (Crisfield et al. 2019). As such, its small range and low occupancy can be explained by the combination of highly specific habitat requirements (including the role of fire in facilitating germination), the restricted distribution of its preferred habitat, and very poor dispersal. While our framework predicts that high local abundance could have a positive effect on occupancy, the very low dispersal capacity of impoverished pinweed may preclude this effect.

Whereas seed dispersal is restricted, seed production and viability are both very high. Once dormancy mechanisms are broken, seeds germinate readily (Crisfield et al. 2019). The combination of these reproductive traits – high seed production, viability, and germination – may explain the high local abundance of the species. In addition, while the taxon's competitive ability is not known, its association with sparsely-vegetated and recently burned sites may allow it to escape competition, thus further facilitating its high local abundance. Conversely, its presumed disappearance as succession progresses (COSEWIC 1996), along with the tendency for members of the Cistaceae to be shade intolerant (Thanos et al. 2002) suggests that impoverished pinweed may be sensitive to competition for light, and may be unable to persist as post-fire environments become increasingly vegetated. As such, interactions may limit the occupancy of the taxon by limiting the persistence of individual populations, though this remains speculative.

Impoverished pinweed may not require active conservation at this time, given the remoteness of its preferred habitat and the absence of evidence of decline. Owing to its small range, however, impoverished pinweed may be vulnerable to catastrophic disturbance. This is particularly true given that five of the six known extant populations occur within an area of ~ 30 km² (Crisfield unpubl.), and a high intensity forest fire in this area has the potential to destroy the majority of extant populations, including soil seedbanks. In the event of such catastrophic disturbance, assisted colonisation in suitable habitats may be an effective intervention for this taxon.

Wolverine

The wolverine is characterised by a very large geographic range, being circumboreal and circumarctic in distribution (Abramov 2016, Fisher et al. 2022, Supporting information); however, both local abundance and occupancy are very low. In Canada, for example, the species occupies < 0.5% of available habitat (COSEWIC 2014). Individuals have large home ranges, which may be related to food availability (Hornocker and Hash 1981, Landa et al. 1998).

The wolverine is a habitat generalist and occurs in a range of boreal, alpine, and Arctic habitats (Fisher et al. 2022, Glass et al. 2022). Furthermore, the species is a dietary generalist, hunting and scavenging many species including caribou, reindeer, and a variety of other ungulates, small mammals, and birds (Fisher et al. 2022). In addition, wolverines

have a high dispersal capacity (Packila et al. 2017), and have successfully recolonised regions from which they were extirpated (Aronsson and Persson 2017). As such, species' large range may be attributable to its broad ecological and dietary tolerances (environmental filtering), as well as its strong dispersal (movement).

The local abundance of the wolverine is limited by the large home range requirements of individual animals (Landa et al. 1998) as well as low reproductive output (Weaver et al. 1996). The large home ranges required by the species are thought to be related to its high energetic requirements (Fisher et al. 2022) and the distribution of food resources on the landscape (Hornocker and Hash 1981, Landa et al. 1998), suggesting that, for this species, low local abundance is driven by resource–consumer dynamics. The species' partial reliance of scavenging may further increase the importance of interactions, as it may rely on the presence of other predators (Fisher et al. 2022). As such, the species' low local abundance can be explained by demographic factors (low reproductive rates) and resource requirements (interactions).

The wolverine's low abundance in turn drives low occupancy. Although the species has a broad ecological tolerance and high mobility, its large home range size implicitly limits its density at the landscape scale. Given the apparent role of food resources in determining home range sizes, we hypothesise that the species' low occupancy can be attributable to interactions (resource–consumer dynamics) via their effects on the species' local abundance.

Given that the wolverine is strongly and negatively affected by human presence, it is important to consider the impacts of anthropogenic activities on the species' rarity patterns. The wolverine has recently experienced a contraction in its range owing to habitat disturbance, fragmentation, and conversion by humans (Venier et al. 2014). Considering the species' aversion to humans, functional habitat losses (i.e. the avoidance of otherwise suitable habitat due to noise or other sources of stress) are likely much higher than absolute losses (Venier et al. 2014). Furthermore, humans have reduced wolverine populations through trapping (Venier et al. 2014). These anthropogenic impacts can be interpreted in the language we use in our framework. For example, the effects of trapping on wolverine abundance constitute a form of predation, and thus are captured by the 'interactions' category in our framework. Human disturbance and infrastructure have resulted in a decline in suitable habitat, or, in other words, an increase in the species' niche position. This represents a contingency that has affected the size of the wolverine's range.

As the wolverine naturally occurs at low local densities, increasing local abundance may not be a suitable conservation goal; however, encouraging the species to re-occupy areas from which it has been extirpated may ensure the long-term persistence of viable populations. Considering the species' aversion to human activity, along with its high mobility and capacity to recolonise areas within its historic range (Aronsson and Persson 2017), this could likely best be achieved via habitat protection and restoration, with an emphasis on providing large tracts of intact, continuous habitat.

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 (including stochasticity) and disturbance.

Theory supports the above hypotheses. Two concepts from metapopulation theory (Hanski 1999) 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 (Colautti et al. 2006, Cassey et al. 2018), 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 (Gaston et al. 2000), 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 (Fig. 3).

Finally, the importance of colonisation in metapopulation theory underscores the importance of movement as a driver of patterns of occupancy (Ims and Yoccoz 1997). 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 (Hutchinson 1957, Pulliam 2000); 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 (MacArthur and Wilson 1967, Hanski 1999, Holt and Keitt 2000). 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. Brown et al. (1996) note that niche processes are among the most common explanations for interspecific variations in range size, an assertion supported by a meta-analysis (Slatyer et al. 2013). 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 (Gaston and Blackburn 2000). 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 (Brown et al. 1996, Gaston 1996), 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 (Kunin and Gaston 1997), while others have found only a modest relationship between range size and dispersal (Lester et al. 2007). A recent meta-analysis found a positive relationship between range size and dispersal capacity (Alzate and Onstein 2022), 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 (Gaston 2009) and long-term environmental changes (Svenning and Skov 2004). 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 (Lester et al. 2007).

Conservation implications

Our framework (Fig. 3) provides insight into the particular vulnerabilities of different types of rare species and may help identify effective conservation measures for them. Note that these interventions are aimed at the conservation of species that are not naturally rare rather than species which are naturally rare and not in decline. Each of the three rarity dimensions poses different challenges to persistence: species that occur at low abundance may be vulnerable to demographic stochasticity (Gilpin and Soulé 1986), Allee effects (Stephens and Sutherland 1999), inbreeding, and drift (Ellstrand and Elam 1993). Low occupancy is correlated with higher extinction risk (Broennimann et al. 2005, Harnik et al. 2012), 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 (Honnay and Jacquemyn 2007), 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 (Joppa et al. 2016). 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 due to a narrow climatic niche are particularly vulnerable to climate change (Yu et al. 2017).

The hypothesised relationships between the three rarity axes and the four underlying processes (Fig. 3) may point to measures that could be used to conserve different types of rare species. We hypothesise that species characterised by low abundance are primarily limited by demography and interactions. The challenges associated with low abundance 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 (Santymire et al. 2014), and help to maintain or increase the genetic diversity of very rare species (Witzenberger and Hochkirch 2011). As for interactions, species may be threatened by new negative interactions (e.g. competition and predation), or, conversely, by the loss of positive interactions (Aslan et al. 2013, Ballal 2022). Control of predators or invasive species may be necessary to conserve of some species (while avoiding unnecessary and unproductive persecution of predators; Harding et al. 2020). In the case of facilitative interactions, the conservation of species with obligate symbioses requires the conservation of the symbiont (Pleasants and Oberhauser 2013). In some cases, facilitative interactions may be known or suspected to be involved in a species' rarity, but the identity of critical symbionts remains 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 recognise the importance of the trophic network surrounding the target species.

Species characterised by low occupancy may be impacted by drift and lack of gene flow (Honnay and Jacquemyn 2007). The degree to which low occupancy results in isolation will depend, in part, on the species' movement capacity relative to the distance between occupied patches. As such, species' intrinsic characteristics must be considered when assessing the conservation implications of low occupancy. Under our framework, occupancy is hypothesised to be driven by movement, environmental filtering, and abundance. Metapopulation theory suggests that species with low occupancy may benefit from increased local abundance, as this provides increased propagule pressure for colonising new sites (Stenseth 1983, Ims and Yoccoz 1997). Thus, measures to support the growth of local populations may also increase occupancy over time. However, this is contingent on the availability of suitable, accessible sites

on the landscape. As such, the conservation of species with low occupancy may also require landscape-scale measures to conserve or restore habitat, and to maintain or increase habitat connectivity at a scale that is suitable to the target species' dispersal capacity. Where such landscape-scale measures are not possible, assisted colonisation may be an effective intervention (Regan et al. 2012).

We hypothesise that species characterized by small ranges are mainly limited by environmental filtering and movement. Effective conservation measures for these species may include habitat protection and/or restoration, particularly for species with narrow requirements. Species limited by movement may benefit from measures to increase connectivity between habitat patches, and, in some cases, from assisted migration. The latter may be particularly helpful for narrow endemics that are vulnerable to climate change (Loarie et al. 2008).

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 range size (Venier and Fahrig 1996, Hanski 1999). These effects are illustrated by studies of habitat availability, which has been found to be significantly correlated with occupancy and abundance across a range of taxonomic groups (Seagle and McCracken 1986, Heino and Tolonen 2018, Vela Díaz et al. 2020). Habitat availability may play an important role in determining whether species are not only rare but also of conservation concern, particularly for species with strong affinities to habitats that have been subject to large-scale disturbance or conversion by humans (e.g. plains rough fescue; Elsinger et al. 2023). Historical contingencies also affect species' occurrence: for example, past glaciation events have left a lasting imprint on species' range limits (Svenning and Skov 2004). In the context of the present discussion, with its inclusion of traits as drivers of rarity, environmental conditions are another important contingency, as traits that confer an advantage in one environment may be detrimental in another. As such, the same trait may lead to diverging outcomes in different environments; for example, traits associated with a highly acquisitive strategy may be beneficial within a resource-rich habitat, but detrimental in a resource-poor environment. Finally, rarity may arise from demographic or environmental stochasticity (Hubbell 2001, May and McLean 2007). 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.

Note of caution

Despite the advantages outlined above, adding occupancy as a rarity axis may pose certain conceptual and technical

challenges. First, occupancy is correlated with both range size and abundance (Gaston 1994, Quinn et al. 1996), which may be perceived as problematic. 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. Furthermore, given that the conservation consequences of the three rarity axes differ, we maintain that despite being correlated, the three rarity axes are not redundant. Second, it may be difficult to quantify occupancy in practice, given that estimates are influenced by the scale and grain of observation (Gaston and He 2010), imperfect detection (Guillera-Arroita et al. 2010), and variations in search effort. It is thus critical to account for these potential pitfalls when assessing occupancy. We strongly recommend that occupancy be assessed based on presence-absence data collected using standardised methods, rather than opportunistically collected presence-only data (e.g. iNaturalist), in which 'absences' may be indicative of a lack of search effort. It is important to note that occupancy is not the only rarity axis to suffer from challenges associated with implementation; 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 (Harnik et al. 2012). Similarly, while most studies assess habitat specificity based on the number of habitat types within which a species occurs (Harnik et al. 2012, Birskis-Barros et al. 2019), others base their assessments on additional, related factors, such as habitat scarcity (Broennimann et al. 2005) or species' reliance on a focal habitat type (Kattan 1992). 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. Ideally, occupancy would be quantified based on biologically significant units, such as habitat patches within a species' range. However, like with the other Rabinowitz axes, this sort of ideal measure is not always feasible. In such situations, occupancy may be approximated, for example, based on the proxies such 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 (Broennimann et al. 2005, Pescott et al. 2015), dot maps may also be used to calculate occupancy (i.e. the proportion of grid cells within the species' range that are occupied). Regardless of the method used, the grain and method of measurement should be biologically appropriate to the organism or assemblage being studied and the research questions being investigated.

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. Additionally, our framework is based on ecological theory, which might itself be biased towards certain well studied taxonomic groups (e.g. vertebrates and vascular plants) and regions (e.g. temperate regions). It is unclear how well the framework might explain rarity among less studied groups and regions.

Finally, we acknowledge that our removal of habitat specificity as a rarity axis may be objectionable to defendants of Rabinowitz' framework. We argue that habitat specificity is best understood to be embedded on the causal side of our framework, within the trait dimension of tolerance. While the three axes of rarity we propose consistently, by definition, characterise rarity, habitat specificity does not systematically associate with rarity. We provided examples where a specialist may nonetheless be abundant if its habitat is widely available. Others may however continue to view it as a pattern of rarity and of practical importance. Our intent is not to invalidate the Rabinowitz framework, to discourage its continued use, or to dismiss the importance of habitat specificity in rarity. Rather, we sought to add an explicatory element to the framework. If some readers would prefer to continue to view habitat specificity as originally proposed by Rabinowitz, we welcome constructive discussion on the concept.

Conclusion

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 (Espeland and Emam 2011), 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 in particular species. Our hope is that this work will spur further explorations into 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.

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Author contributions

Varina E. Crisfield: Conceptualisation (lead); Funding Acquisition (lead); Writing – original draft (lead); Writing – review and editing (lead). **F. Guillaume Blanchet:** Conceptualisation (supporting); Writing – original draft (equal); Writing – review and editing (equal); Supervision (equal). **Ciara Raudsepp-Hearne:** Conceptualisation (supporting); Writing – original draft (equal); Writing – review and editing (supporting); Supervision (equal). **Dominique Gravel:** Conceptualisation (lead); Writing – original draft (equal); Writing – review and editing (equal); Supervision (lead).

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Supporting information

The Supporting information associated with this article is available with the online version.

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