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Perspective

Characterising common and range expanding species

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ABSTRACT

Climate change and biological invasions have increased the likelihood of the establishment, growth, spread and survival of some species. With the recent and strongly motivated call for balanced consideration of the ecology and conservation of common and rare species, species undergoing range expansion are of particular interest. The notion of essential biodiversity variables has also re-focussed attention on the value of abundance and occupancy observations for assessing conservation values, threats and targets – species rare or common, contracting or expanding. Changes in the distribution and abundance of common and range expanding species deserve further attention, not only to better understand their dynamics, but also as the basis for monitoring range expansions and their consequences. With the aim of characterising range expansion, here we combine perspectives from typological approaches to studying species conservation status with perspectives from spread ecology and macroecology. Closer examination of the properties and dynamics of common species is important not only because declines in their conservation status are underappreciated, but also because those species becoming more common have significant implications for biodiversity, ecosystems and society.

Keywords

Abundance, biodiversity assessment, climate change, dispersal kernels, invasive alien species, monitoring, occupancy, range shift, spread ecology.

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INTRODUCTION

Conservation biogeography concerns the conservation-relevant dynamics of species distributions. Its central aim is to better describe, explain and predict these dynamics (Ladle & Whittaker, 2011). Species ranges are characteristically dynamic over their evolutionary lifespans, with sequential periods of contraction and expansion (taxon cycles) that are weakly conserved phylogenetically (Ricklefs, 2015). Range changes can happen rapidly, the time period over which species are widespread tends to be brief, and species with larger ranges tend to have lower speciation rates and lower extinction probabilities (Gaston, 1998; Roy *et al.,* 2009). However, contemporary species distributions are changing at rates that are considered to be greater on average than historical rates (Chen *et al.*, 2011). This has been brought on by the rapid rate of contemporary habitat loss, climate change and human-facilitated transport of species. The changes in range location occurring across species are in some instances also more strongly directional than predicted by natural variation in species ranges; made so by species tracking clines in rapid temperature change as well as movement along clear pathways of human trade and transport (Hulme, 2009; Hiddink *et al.,* 2015). These comparatively rapid changes have narrowed the gap between the study of population dynamics in ecology, and the dynamics of species ranges that has more commonly been the purvey of biogeography and macroecology (Gaston, 2008; Roy *et al*., 2009; although see Hengeveld, 1989).

Species distribution, measured as presence-absence records, and often collated as occupancy or range maps, is one of the two essential variables for quantifying the conservation status of species, along with measures of abundance or population size (Gaston, 1998). Well known and widely adopted schemes for classifying and grading rarity (Rabinowitz, 1981) and for evaluating extinction risk (IUCN Red List, Mace *et al*., 2008) rely on these measures to track the dynamics of species threatened by multiple drivers of

biodiversity loss (Channell & Lomolino, 2000). These schemes are most often applied to rare species and those undergoing declines in range and abundance, but have recently also been applied to common species and those with improving conservation status (Godet *et al*., 2015). Although there are comparatively few widespread and abundant species in nature (Gaston 2011), there are several reasons why attention to the value of common species has grown (Gaston, 2010; Connolly *et al.,* 2014). Common species are important to the structure and function of assemblages and ecosystems and many, once common species, are now declining (e.g. Evans *et al*., 2005; Inger *et al*., 2015). Whether the starting condition is common or rare, species undergoing range and abundance decline have been the main focus of conservation attention.

The opposite condition is also of significant evolutionary and biogeographic interest, that is species increasing in geographic range (and population size), or becoming more common. Although many species are in decline, a subset of species is becoming more common, or more common in certain locations, and is undergoing some form of range expansion (Godet *et al*., 2015; Hiddink *et al*., 2015; Inger *et al*., 2015). Three reasons predominantly account for why some species are becoming more common. First, in a few cases species conservation status is improving as a result of successful management interventions to avoid their extinction (Neel *et al*., 2012). This may include positive responses by species to indirect actions such as habitat restoration, but also as a result of direct interventions such as breeding programs or assisted dispersal (e.g. Willis *et al*., 2009). Second, some populations and species are responding positively to climate change-driven increases in temperature at higher latitudes and elevations (Wilson *et al*., 2005; Hiddink *et al*., 2015). Although range contractions are prevalent, range expansions are also taking place in some cases (Slaton, 2015). There is a steady increase in evidence for species expanding along at least one range margin in response to climate change, accompanied by variable

responses in overall range size, abundance and direction of the shift (Mair *et al*., 2012; Hiddink *et al*., 2015; Lenoir & Svenning, 2015). Third, species can reach novel localities through human agency. Direct introduction of species outside of their native ranges (Wilson *et al*., 2009) can be followed by the establishment and spread of these species and the establishment of novel ranges (Lockwood *et al*., 2013). Species can also reach novel localities and increase their abundance within their historical extent of occurrence, for example due to increased disturbance (Carey *et al.*, 2012). Broadly defined, range expansion is set to continue into the foreseeable future as range margins expand in response to warming, and as species continue to spread as a consequence of human-mediated introductions and increasingly homogenous habitats (Bellard *et al*., 2013).

Observing range expanding and common species is important for understanding the homogenisation and diversification of biota (Godet *et al*., 2015), as well as the significant impact that common species have on spatial variation in biodiversity and on ecosystem function (Evans *et al*., 2005; Sizling *et al*., 2009). Moreover, invasive and pest species have significant negative socio-economic impacts (Xu *et al*., 2006; Scalera, 2010). However, while there is a well-developed literature on the dynamics of abundance-range relationships and its application to understanding and monitoring the dynamics of rare species, the same is less true for common ones (Gaston, 2011). Unlike the systematic evaluation and monitoring process in place for prioritizing and tracking the status of threatened species at multiple spatial scales (Mace *et al*., 2008), no such process is currently in place for range expanding species or those species becoming more common (Blackburn *et al*., 2014) (although the IUCN Red List does track improvements in conservation status). The variables and metrics for standardised tracking of range expanding species necessary to underpin a robust observation system have not been fully developed or adopted (Foden *et al*., 2013; Blackburn *et al*., 2014).

Here we discuss and combine complementary approaches to studying common species and range expansions. We include in our definition of range expansion any species with at least one range margin expanding via leading-edge, jump, extreme long-distance or mass (multiple source) dispersal (*sensu* Wilson *et al*., 2009). In this sense we are concerned with contemporary expansion by species into novel geographic areas. First we build upon previous work on rarity to propose a typology of commonness applicable to species reaching new areas, and identify seven forms of common. We then briefly outline some of the key insights on range expansion trajectories from the field of spread ecology and from the macroecological relationship between abundance and distribution. We simulate range expanding species with different dispersal strategies and show (1) how these perspectives can be combined and integrated to quantify, understand and predict the dynamics of species that are becoming more common, and (2) to better understand the multiple ways in which species may expand their ranges. This integration achieves a synthesis of typological and continuous approaches to conceptualising and quantifying commonness and range expansion. Our intention is to start to reconcile the ongoing use and call for pragmatic approaches to inform species management (in the form of lists, categories and classification schemes, e.g. Mace *et al.,* 2008; Essl *et al*., 2011; Gillson *et al*., 2013; Blackburn *et al*., 2014) with the insights provided by the theory of geographic ranges and current understanding of range expansion processes (Gaston, 2003; Hastings *et al*., 2005; Arim *et al*., 2006; Lenoir & Svenning, 2015).

SEVEN CATEGORIES OF COMMON

Just like rarity, commonness is not a single condition. Rabinowitz's (1981) influential typology clarified the concept of rarity by identifying different forms of the condition. The typology identified eight species conditions, classified by small and wide geographic range, small and large local population size and narrow and wide habitat specificity. Seven of these

conditions are considered to encompass some element of rarity. The eighth category, i.e. large ranges, high local abundance and broad habitat specificity, represents not rare, but common species.

Commonness and rarity are relative notions. Therefore, species range and population size can be interpreted through the lens of a species on a trajectory towards becoming common (although they may be rare to begin with). In this way seven of Rabinowitz's (1981) eight original types could, alternatively, each be considered a form of common (Fig. 1a). Combinations of range (occupancy) and population size (abundance) in such a typology are fundamental properties that are as valuable for understanding the ecological and conservation consequences of common species as they are for rare ones (e.g. Godet *et al*., 2015). For example, a large local population size means low extinction risk from stochastic population dynamics and greater likelihood that a species will undergo range expansion. An increase in the number of established populations in the novel range of a species provides greater opportunity for the rescue effect to play a role in maintaining and supplementing populations, potentially enhance the genetic heterogeneity of existing populations, and over longer time scales lead to increased species success (Havel *et al*., 2002; Webb *et al*., 2012; Chown *et al*., 2015). Increasing novel geographic range, measured as extent of occurrence, also means increasingly independent survival likelihoods of distant populations exposed to different environmental conditions. Range expanding species therefore potentially signify double trouble (Gaston, 1999) for extant and historical characteristics of biodiversity structure and function.

In the context of range expansion, or of species on a trajectory towards becoming common, time since establishment in the novel range provides a more useful third axis for classification (Fig. 1) than does habitat specificity (used in the typology for rarity (Rabinowitz, 1981)). Habitat specificity, or the relative degree of generalism versus

specialism in the resource requirements of species, is both difficult to measure objectively and to compare across a broad range of taxa (Lawton, 1993). By contrast, the concepts of 'novelty', 'expansion' or 'growth' are inherently temporal and provide the typology for defining common with an explicitly dynamic dimension (as they would for rarity) (Hengeveld, 1992). Importantly, time also provides conceptual continuity within the typology across the domains of ecology, conservation and biogeography (Gaston & Chown, 1999; Roy *et al*., 2009). Using novel geographic range, local population size and time since establishment (rather than habitat specificity), seven forms of common emerge (which we term newly established, incipient, constrained, sparse, dispersed, successful and highly successful; Fig. 1a, Table 1).

Examples in each of these categories of commonness are provided in Table 1 from the broad suite of alien plants and animals present in South Africa. For example, a 'sparse' species with small local populations, but widely distributed across a novel (alien) range after a substantial time since establishment is considered naturalized (reproducing independently in its novel range, Simberloff & Rejmánek, 2011), such as Johnson grass in South Africa (Table 1). This is an alternative interpretation for the rare condition of a species with similar properties in its native range. Similarly, a locally abundant, narrowly distributed species in a recently reached novel range could be considered a potentially common or 'incipient' species (Fig. 1a) (Bennett *et al*., 2013), such as the House crow (Table 1). This is in contrast to the status of such a species as geographically restricted in its' native range.

The non-mechanistic clarification of the concept of common in this way is useful for multiple reasons. It provides a foundation for classifying and studying range expanding and common species. It draws attention to the value of occupancy and abundance as essential biodiversity variables (*sensu* Pereira *et al*., 2013) for assessing and monitoring species status regardless of their state within the typology, or of the typology itself: both common species in

decline and those becoming more common pose an increasing threat to broader biodiversity (Gaston, 2011; Blackburn *et al*., 2014). This clarification argues for the inclusion of all species in standard biodiversity surveys, regardless of their geographic origin (i.e. whether native or alien) or conservation status (as threatened or invasive). This is especially true for species presence-absence (occupancy) data, which is the fundamental building block for a broad range of conservation and species management objectives (Pereira *et al*., 2013). Finally, with further development the typology may provide a basis for prioritizing range expanding and common species for monitoring, policy and management intervention (Foden *et al*., 2013). Monitoring species that are recovering (e.g. from overharvesting), invasive alien species and those impacted by climate change, as well as improving the scientific basis for doing so, forms the basis of several of the Aichi Targets that underpin the Convention on Biological Diversity's Strategic Plan for Biodiversity 2011-2020 (e.g. Targets 6, 9, 12, 19; UNEP, 2011).

The categories of common are clearly not static, and can be interpreted as successive, temporary states within a range of possible trajectories towards becoming more common (Fig. 1b). There are multiple time scales and routes by which species become common, via changes in abundance, distribution and various combinations of these (Kunin & Gaston, 1993). This inherent scale dependence will have to be dealt with when monitoring, assessing and comparing range expanding species, for example using scale domains and hierarchical modelling frameworks (e.g. Pearson and Dawson 2003). Spread ecology and macroecology have significantly advanced understanding of the properties and dynamics of species ranges, including their scale dependence (McGeoch & Gaston, 2002). These fields also provide approaches by which the various routes to common can be more closely examined. In the next section we provide an overview of some of the key insights from this work. We then integrate the categorical (i.e. the typology of common) and continuous approaches (range

expansion trajectories and macroecological signatures formed by their abundance-occupancy relationships) to examine range expansion and the dynamics of species on trajectories towards becoming more common.

CHARACTERISING RANGE EXPANSION

Trajectories to common

Species distributions, abundances and their dynamics (measured as time or number of generations) are naturally continuous variables and readily modelled (Fig. 2, see Appendix S1 for methods). Some of the earliest studies in invasion biology modelled population spread as the increase in distribution of species in their novel range (Elton, 1958; Hengeveld, 1989; Lockwood *et al*., 2013). This and later work have shown how population structure, species interactions, properties of the historical range, evolution and spatial and temporal environmental variability all play important roles in the dynamics of species spread (e.g. Roques *et al*., 2012; Gilbert *et al.,* 2014). Developments in spread modelling include those related to modelling properties of the environment being colonised, and the demography and dispersal of species colonising and their interactions (Bocedi *et al.,* 2014; Ferrari *et al*., 2014). However, acknowledging the many mechanisms involved, questions remain about whether there are systematic differences in the shapes of dispersal functions for different taxa (Lockwood *et al*., 2013), or for example between established populations of alien species undergoing range expansions versus populations responding positively to climate warming (Nullmeier & Hallatschek, 2013; Lenoir & Svenning, 2015).

One of the key insights from spread ecology is the distinction between three main types of dispersal. First, natural diffusion (or a travelling wave), is characterised by a Gaussian or normal dispersal kernel – such as the well-known spread of muskrats across Europe over a period of more than five decades from an initial source population in Prague

(Lockwood *et al.*, 2013). Second, spatially discontinuous jump, or fat-tailed, dispersal includes a larger proportion of long-distance dispersal events than Gaussian dispersal, and has often been found to characterise seed dispersal (Shigesada *et al.*, 1995; Kot *et al.*, 1996; Nathan 2006). Third, stratified dispersal includes a combination of short and long distance events and has been used, for example, to model species with a combination of natural and human-mediated dispersal (Hengeveld, 1989; Hastings *et al.*, 2005; Vanderploeg *et al.*, 2002). These three dispersal kernels characterise different trajectories to common that species follow, and the shapes of their expansion curves can be modelled either as changes in abundance (such as local mean population size) or distribution (measured as area of occupancy (AOO)) (Fig. 2).

The trajectories characterised by these dispersal kernels have significant practical implications (Lockwood *et al.*, 2005; Fisher, 2011). For example, long distance dispersal events play a key role in increasing rates of range expansion (Clark *et al.*, 1999), with maximum rates of range expansion higher and accelerating for fat-tailed and stratified trajectories compared with lower, constant rates for diffusive dispersal (Fig. 2). On the other hand, natural diffusion results in a faster increase in local mean abundance, as new individuals will first colonize nearby sites. Human-mediated jump dispersal, which is at least one of the mechanisms underlying the apparent speed of biological invasions, increases the length and fatness of the tail of the dispersal kernel, or gives rise to stratified dispersal (Hastings *et al.*, 2005). Accelerating rates of range expansion under fat-tailed or stratified dispersal kernels can thus result from natural long-distance dispersal events, human-induced independent establishment events that fall within or expand the tail of the distribution, or some combination of these (Shigesada & Kawasaki, 1997; Huttanus *et al.*, 2011).

The number and relative locations of novel populations also affects the shape of the range expansion trajectory (Fagan *et al.*, 2002; Altwegg *et al.*, 2013). For example, an

increase in the number of randomly distributed source populations on the outer edge of the novel range has a substantial, non-linear effect on the rate of range expansion, while keeping the local population growth mostly unchanged (resulting rather in a larger global population size) (Fig. 2). Multiple source populations and propagule pressure are considered to underpin most biological invasions, enabling faster spread and increasing invasion risk (With, 2002; Simberloff, 2009; Wilson *et al*., 2009; Pyšek *et al*., 2015).

When interpreted in the context of the typology of commonness (Fig. 1), the three dispersal functions start to reveal how species might move across the typology as their ranges expand (Fig. 2a) or as their populations grow or multiply (Fig. 2b). For example, the Quagga mussel (*Dreissena bugensis*, Andrusov) is an invasive species that was introduced to the eastern side of Lake Erie in the U.S.A. and that in addition to shorter distance natural diffusion has been dispersed in the lake over longer distances by boat (Vanderploeg *et al*., 2002). This species is likely to shift from a narrow to wide range category (Fig. 1b) as fast as it shifts from small to large population size, with possible fluctuations in abundance (Patterson *et al*., 2005). By contrast, the Marbled white butterfly (*Melanargia galathea*, Linnaeus) is likely to undergo a faster shift from small to large population size, rather than from a narrow to wide range category. This species underwent assisted colonization to two novel localities beyond its previous range margin in the U.K. (Willis *et al*., 2009). For this species, both populations followed Gaussian-like dispersal for the 6 years that were studied post introduction and establishment (Willis *et al*., 2009). These developments in characterising range and abundance changes of species over time have contributed significantly to effective species conservation and pest management (Mace *et al*., 2008; Lockwood *et al*., 2013).

Macroecological signatures of range expansion

Time series of novel range and population size changes, as outlined above, present one way of examining trajectories to commonness. However, combining information on abundance and distribution to examine the relationships between them provides the macroecological signature within which range expansion takes places (Fig. 3). The relationship between abundance and range size can be compared for different dispersal kernels to produce unique range expansion signatures (Fig. 3). The intraspecific abundance-occupancy relationship is almost universally positive (Brown, 1984; Gaston *et al*., 2000), and as a consequence has several implications for biodiversity measurement and management (Gaston, 1999). To parallel the double jeopardy argument (Lawton, 1993; Gaston, 1998), if there is a metapopulation dynamics-driven positive correlation between local abundance and area of occupancy, then ongoing novel introductions or population establishment events (for example human-mediated ones) will maintain and increase local population densities of existing populations. This will in turn result in ongoing increases in the number of sites occupied and trends towards commonness.

Although the positive intraspecific abundance-range size relationship is ubiquitous, variation associated with the relationship can be used to represent the boundaries within which a species' trajectory towards commonness takes place (Fig. 3). The macroecological signatures formed by different dispersal kernels provide a basis for comparing and inferring the dynamics of range expanding species (Fig. 3). When dispersal kernels are known or estimated, they also provide a means of forecasting future patterns of range expansion. For example, under Gaussian conditions, if the grain is large enough, an increase in area of occupancy never precedes an increase in local mean population size (LMA), because the increase in LMA takes place prior to space filling in the novel range (Fig. 3, Arim *et al*., 2006; Webb *et al*., 2012). Examining the abundance-range size relationship for different

dispersal kernels also shows that they have overlapping yet characteristic macroecological signatures (Fig. 3), with the signatures formed in different ways for different dispersal kernels. The signatures of Gaussian and fat-tailed kernels are particularly distinctive (Fig. 3) and suggest that interspecific comparisons of the abundance and occupancy of range expanding species may be informative. For example, the relative positions of alien species within the signature may inform risk assessment and prioritisation of species for management (Thomaz *et al*., 2012; Webb *et al*., 2012). Intraspecific comparisons of species populations in different parts of their range may provide early warning of incipient change (Veldtman *et al*., 2010).

With the necessary assumptions, modelled signatures can be used to formulate and test hypotheses for individual, or different, species expected to have particular dispersal kernels, or for species with kernels expected to vary over time or space (such as leading edge versus long-colonised populations (Channell & Lomolino, 2000; Phillips *et al*., 2008; Webb *et al*., 2012), or range expansion driven by human mediation versus natural diffusion (Bennett *et al*., 2013). Differences in the macroecological signatures associated with different dispersal kernels suggest that species may follow multiple routes towards becoming common. In the presence of evolutionary, dispersal or niche constraints species or populations may vary or be constrained at various points within these trajectories (e.g. Lawson *et al*., 2012; Nullmeier & Hallatschek, 2013). In this way different forms of commonness are not fixed (as in Fig. 1), but rather snapshots within a dynamic space bounded by measures of range, abundance, dispersal and time. These signatures are also a step towards integration of categorical and continuous approaches to characterizing the concept of common, as we will show below.

INTEGRATING THE APPROACHES

The different perspectives and approaches provided by the typology of commonness (Fig. 1), the trajectories to common (Fig. 2) and their macroecological signatures (Fig. 3) can be combined to better model and understand the dynamics of species range expansion (Fig. 4). We overlaid the relationship between range (AOO), population size (LMA) and time for the three dispersal kernels (Appendix S1) with the typology of commonness. The outcome shows how species with different dispersal kernels may follow different routes to becoming common (Fig. 4 b-d). For the purpose of illustration in Fig. 4, the Marbled white butterfly trajectory passes through the stage described as incipient, whereas the Quagga mussel's position remains within the 'newly established' category (differentiated based only on local population size (LMA)). Note that the spatial extent is important; because the Quagga mussel has spread across the full extent of Lake Erie it may be considered 'dispersed' at the scale of the lake, but only 'newly established' when considering multiple lakes. Fig. 4 also illustrates the implications of multiple independent introductions on the relative status of a species in its novel range (Simberloff, 2009). The more source populations, the higher the chance a species will become 'highly successful', and will become so by being 'dispersed' instead of 'incipient' (Fig. 4b-d). Long distance dispersal events and many independent introductions or range expansion events are also more likely, for example, to produce 'highly successful' species (Fig. 4a).

Three forms of boundaries are apparent in Fig. 4; those formed by the boundaries of the categories of common (from Fig. 1), those formed by the modelled boundaries produced by three different dispersal kernels (Figs 2 and 3), and those formed by the intersection between them (Fig. 4). Of particular interest, would be boundaries formed by empirical realisations of single species, or assemblages, expressed within this phase space for comparison with model outputs. Predicting the dynamics of species is challenging because

high quality empirical data on the temporal dynamics of species distributions is rare, and distribution data can be biased in a number of ways (Pyšek *et al*., 2008; Beck *et al.*, 2014). Nonetheless, with ongoing efforts to observe, collate and map species distributions, and the explosion of novel technologies for this purpose, such data are likely to become increasingly available (Fretwell *et al.*, 2012; Jetz *et al*., 2012; Berthouly-Salazar *et al*., 2013; Chown *et al*., 2015).

PROSPECTS

The rationale for assessing and monitoring common and range expanding species is strong, as is the use of species presence-absence or occupancy data as the basic building block for doing so (Gaston, 2003; Sagarin & Gaines, 2006; McGill *et al*., 2015). For these species, as well as rare species and those in decline, measures of range size and distribution are essential for informing conservation responses and management practice (Fagan *et al*., 2002; Fisher, 2011; Lawson *et al*., 2012). Further theoretical and empirical attention to the dynamics of species undergoing range expansion is needed to fill something of a gap in our understanding and in the relative attention paid to these species in biodiversity monitoring, assessment and conservation biogeography. Progress in understanding the fundamental properties of the distributions of these species, as we advocate here, will benefit more parameter rich approaches that also encompass, for example, genetic, environmental and niche information (Arim *et al*., 2006; Marquet *et al*., 2014). The integration of approaches to studying range expansion provides an information intensive perspective (Michener & Jones, 2012) that complements new impact classification schemes (such as Blackburn *et al*., 2014), and can be used to predict and contrast the potential future dynamics of species. It draws on a suite of well-developed theory for examining the properties and relationships between range, abundance, dispersal and time. Ongoing development of the theory of range expansion will

have multiple benefits, including application in support of national and global efforts to assess and monitor biodiversity change and its implications for society.

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SUPPORTING INFORMATION

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

Appendix S1 Description of the simulation model.

BIOSKETCHES

Melodie A. McGeoch is Associate Professor in Biological Sciences. Her research applies spatial and community ecology to the study of biological invasion, climate change impacts and biodiversity monitoring, particularly in protected areas.

Guillaume Latombe is a Postdoctoral Fellow at Monash University. He uses complexity-based and mathematical approaches to study the process-pattern relationships that shape community structure.

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Table 1 Examples of species across the typology of commonness, using naturalised plants (sources in table) and animals (Picker & Griffiths, 2011) that have established self-sustaining wild populations in South Africa. Note that the examples below are categorised using only information on novel range, local population size and time since establishment, without using any information on pathways of introduction or spread, or the ecological impact that the species may or may not have.

Novel range	**Local population size**	**Time since establishment**	**Terms in Fig. 1.**	**Example**
Narrow	Small	Short	Newly established	• Vermiculated sailfin (*Pterygoplichthys disjunctivus*) recorded in dams and rivers since 2000 in a few localities in the north-east of the country. • Invasive fruit fly (*Bactrocera invadens*) first recorded in 2010 and known from two localities bordering the country.
Narrow	Large	Short	Incipient	• Heath-leaved banksia (*Banksia ericifolia*) introduced in the 1970s, the few existing local populations have until recently been constrained by the absence of fire (Geerts *et al*., 2013). • House crow (*Corvus splendens*) first recorded between the 1960s and 1970s, is confined to two main centres where they have reached populations of several thousands.
Narrow	Large	Long	Constrained (by ecological processes or human intervention)	• Kangaroo thorn (*Acacia paradoxa*) was introduced pre 1930 and occurs as a single, high density population (Zenni *et al*., 2009). • Feral domestic pig (*Sus scrofa*) released between the 1920s and 1940s and now established in small groups in a few parts of the country.
Wide	Small	Long	Sparse	• Johnson grass (*Sorghum halepense*) widely distributed, but infrequently recorded (Bromilow, 2010). Date of establishment unknown, but pre-1930.
Wide	Small	Short	Dispersed	• Common peacock (*Pavo cristatus*)

				introduced in 1968 is broadly distributed across the country with several, small feral populations.
Wide	Large	Long	Successful	• Sweet prickly pear (*Opuntia ficus-indica*) introduced in the 19th century and now widely distributed forming large, dense stands in places (Bromilow, 2010). • Common carp (*Cyprinus carpio*) introduced in 1859 and is numerous across all major river systems.
Wide	Large	Short	Highly successful	• Harlequin lady beetle (*Harmonia axyridis*) first recorded in 2001, widespread across the country by 2010. Forms large overwintering aggregations.

Figure Legends

Figure 1a Seven types of common: A typology of common common species based on three characteristics; novel geographic range (wide or narrow), local population size (small or large) and time since establishment (long or short). The eighth condition of narrow range, small local population size and long time since establishment qualifies as rare ('not common'). **b**. Arrows show some of the various paths to increasing commonness from each category by varying one variable at a time: range (dashed arrows), population size (dotted arrows) or time (solid arrows). Changes in range or population size can of course only happen as time increases and arrows for these illustrate rapidly occurring change.

Figure 2 Trajectories to common for range expanding species during the early stages of range expansion. The shift towards commonness is measured by the increase in (a) the novel geographic range (area of occupancy, AOO) or (b) local mean abundance (mean abundance across occupied sites) for species undergoing natural diffusion (normal or Gaussian dispersal kernel), jump dispersal (fat-tailed or Cauchy kernel) and stratified dispersal (a mixture of Gaussian dispersal kernels with different means). Arrows show the effect of increasing numbers of founder populations on the trajectory at a particular point in time. The figures are schematics from the output of an individual based model (see Appendix S1). Two species (stars) are used as qualitative examples to show where individual species may lie on these trajectories. The Quagga mussel is invasive in Lake Erie (U.S.A.), where its distribution expanded from the eastern side of the lake and its overall population density decreased after an initial increase (Patterson *et al*., 2005), suggesting stratified dispersal (confirmed by Vanderploeg *et al*., 2002). Assisted colonisations of the Marbled white butterfly in the U.K. showed that although the dispersal mode included long-distance dispersal events, this did not

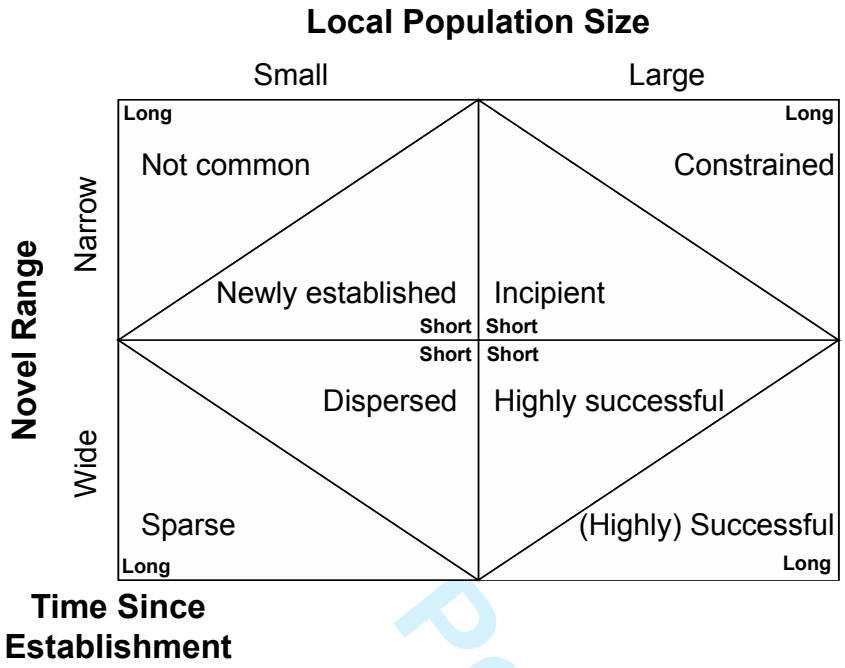
lead to population establishment (Willis *et al*., 2009), suggesting Gaussian-like distribution and population dynamics.

Figure 3 Macroecological signatures for range expanding species with different dispersal kernels; normally distributed (Gaussian), fat-tailed (Cauchy) and stratified. The relationship shown is between novel geographic range (measured as area of occupancy, AOO) and population size (local mean abundance, LMA, across occupied cells). As in Fig. 2, the arrows show the effect of increasing numbers of founder populations on the signature. The stars represent the same two species examples used in Fig. 2 and their corresponding positions within the relevant macroecological signature.

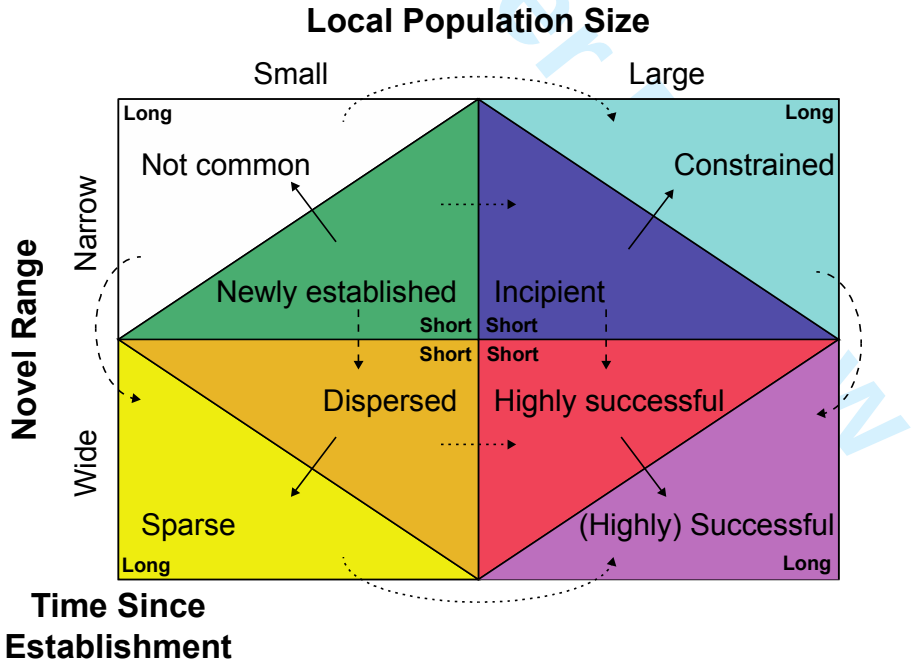
Figure 4 A three dimensional phase space for species becoming common, defined by novel range (AOO, area of occupancy), population size (LMA, local mean abundance) and time since establishment in the novel range. Colours represent the typological forms of common (a) with arbitrarily defined boundaries (as in Fig. 1b). The lines represent simulation outputs of the three dispersal kernels, Gaussian (b), fat-tailed (c) and stratified (d), within the phase space (Appendix S1). The typological forms of common for each model are represented using a 3D surface interpolated from the lines. The boundaries may therefore appear different in the 3 figures due to the 3D projection and the resulting differences in the surfaces. Arrows show increasing numbers of founder populations randomly distributed on the outer edge of the novel range. The stars represent the same two examples shown in Figs 2 and 3 and their corresponding positions within the phase space. For illustrative purposes, we defined a common set of boundaries for the three models, so that most of the forms of common (a) are represented by the trajectories shown (b-d). The model is implemented so that all trajectories start in the 'new introduction' category, and so that no trajectory leads to the 'not common'

or to the 'sparse' categories (a). The model specifically represents the range expansion process, and is limited only by carrying capacity.

(a)


Local Population Size
Small
Large
Long
Long
Not common
Constrained
Narrow
Novel Range
Newly established
Incipient
Short
Short
Short
Short
Dispersed
Highly successful
Wide
Sparse
(Highly) Successful
Long
Long
Time Since Establishment

(b)


Local Population Size
Small
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Long
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Not common
Constrained
Narrow
Novel Range
Newly established
Incipient
Short
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Dispersed
Highly successful
Wide
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(Highly) Successful
Long
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Time Since Establishment

Figure 1.

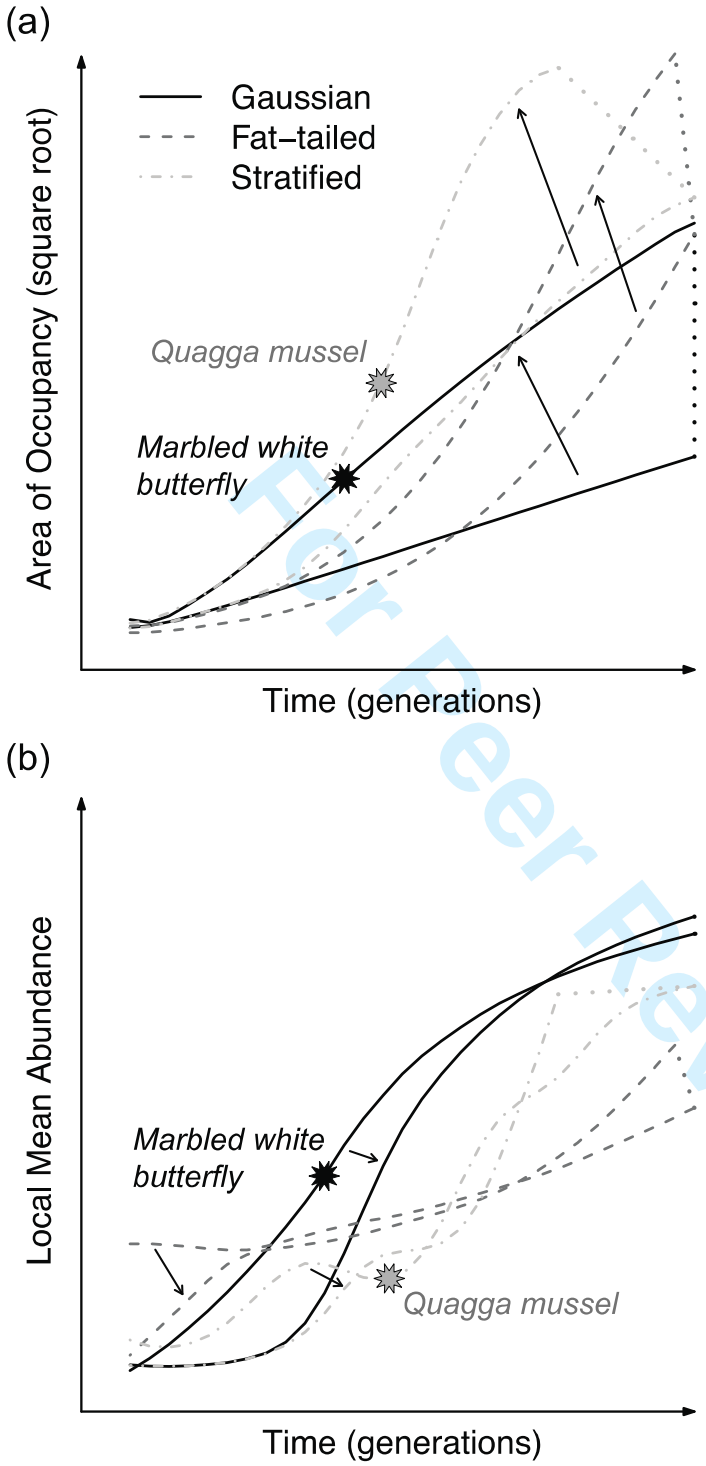

Figure 2

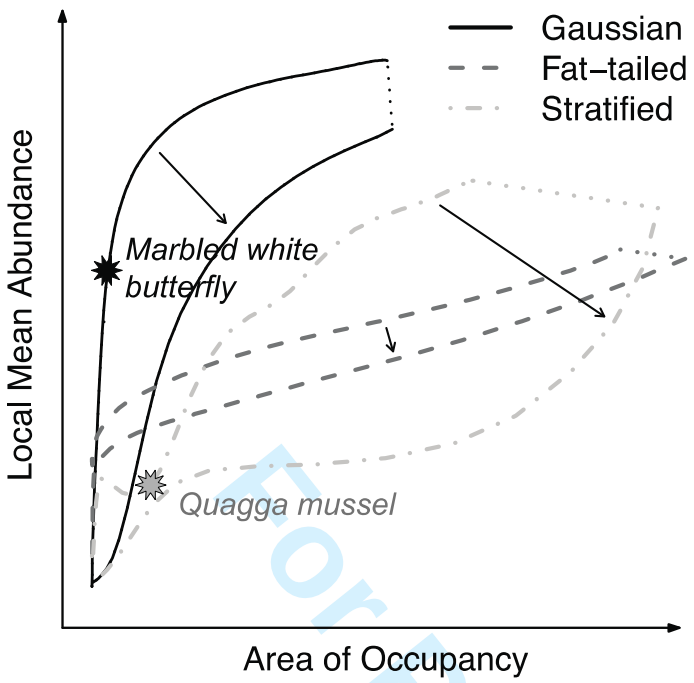

Figure 3

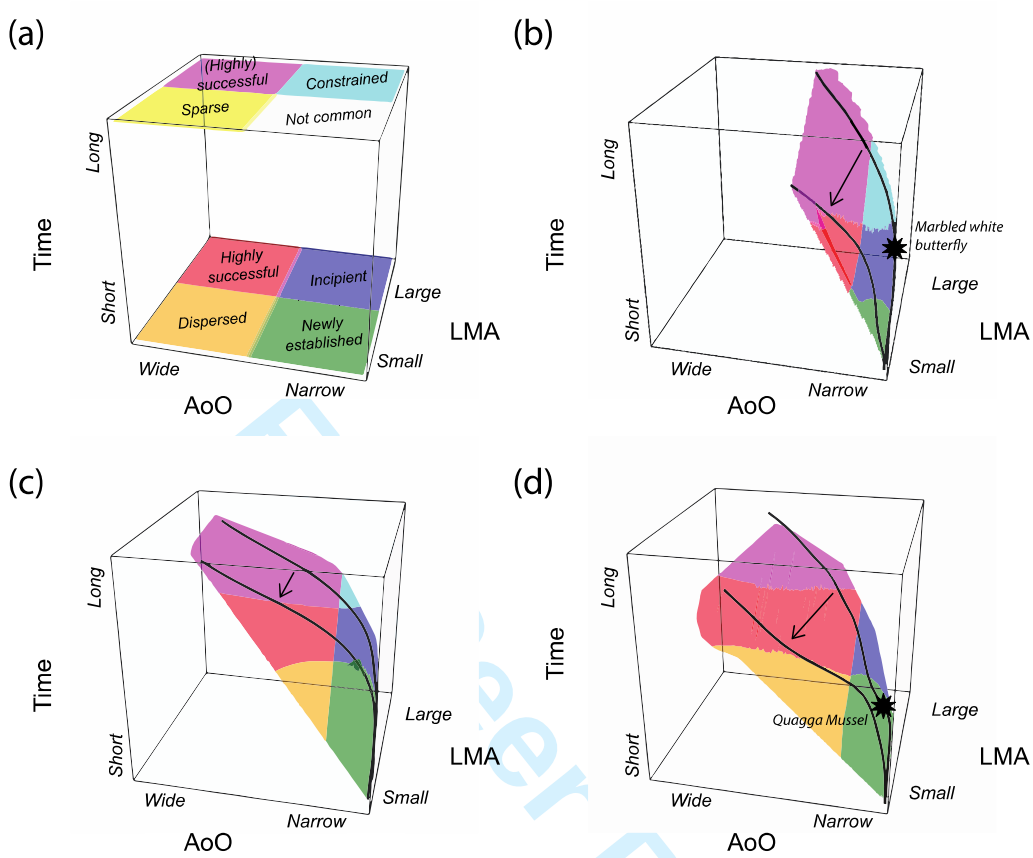

Figure 4

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SUPPORTING INFORMATION

Characterising common and range expanding species

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Appendix S1 Description of the simulation model used to illustrate the relationships between dispersal kernels, range expansion trajectories and macroecological signatures.

We implemented an individual-based model (IBM) of the spread of a fictitious sessile species. The environment consisted of a 401 × 401 lattice. Each cell had a carrying capacity of 50 individuals. Individuals are characterized by a set of continuous coordinates in the space. At each iteration, all existing individuals produced one offspring (a single individual therefore reproduced multiple times). The offspring then moved by some distance drawn from a dispersal function, in a random direction. If the destination cell was outside of the lattice, or if the number of individuals already present in the destination cell was greater than or equal to the carrying capacity, the offspring died. Otherwise it survived, and could not die during the rest of the simulation.

We tested 3 different dispersal functions (Figure S1). The first one was a Gaussian distribution, with a mean of 0 and a standard deviation equal to 5 cell widths. The second one was a Cauchy distribution, representing fait-tailed dispersal, with a location parameter of 0 and a scale parameter of 0.2. The third was a mixture of Gaussian distributions, representing stratified dispersal. In this case, individuals dispersed according to a Gaussian distribution with a mean of 0 and a standard deviation equal to 5 cell widths with a probability of 0.99, and according to a Gaussian distribution with a mean of 75 cells and a standard deviation equal to 10 cell widths with a probability of 0.01.

Simulations were initialized with one or ten source populations, and 100 individuals in total. For one source population, all 100 individuals belonged to the same population, whereas for 10 source populations, each population contained 10 individuals. A source population corresponds to 10 consecutive cells randomly located on the edge of the environment (i.e. on the first or last row or column of the lattice). The individuals from a source population were then randomly distributed over these 10 cells. Cells from a source population could therefore contain more individuals than the carrying capacity. We replicated 20 simulations for each dispersal function and for each configuration of the source populations. Each simulation ran until an average of 20 individuals per cell over all cells was reached.

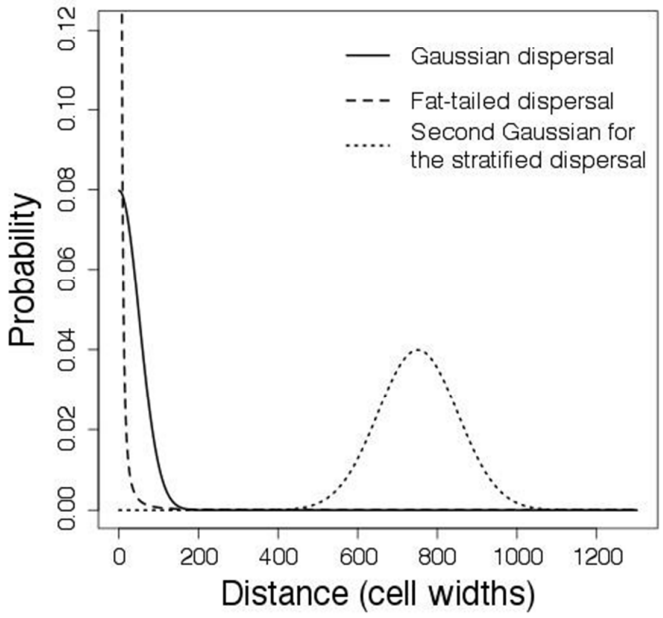
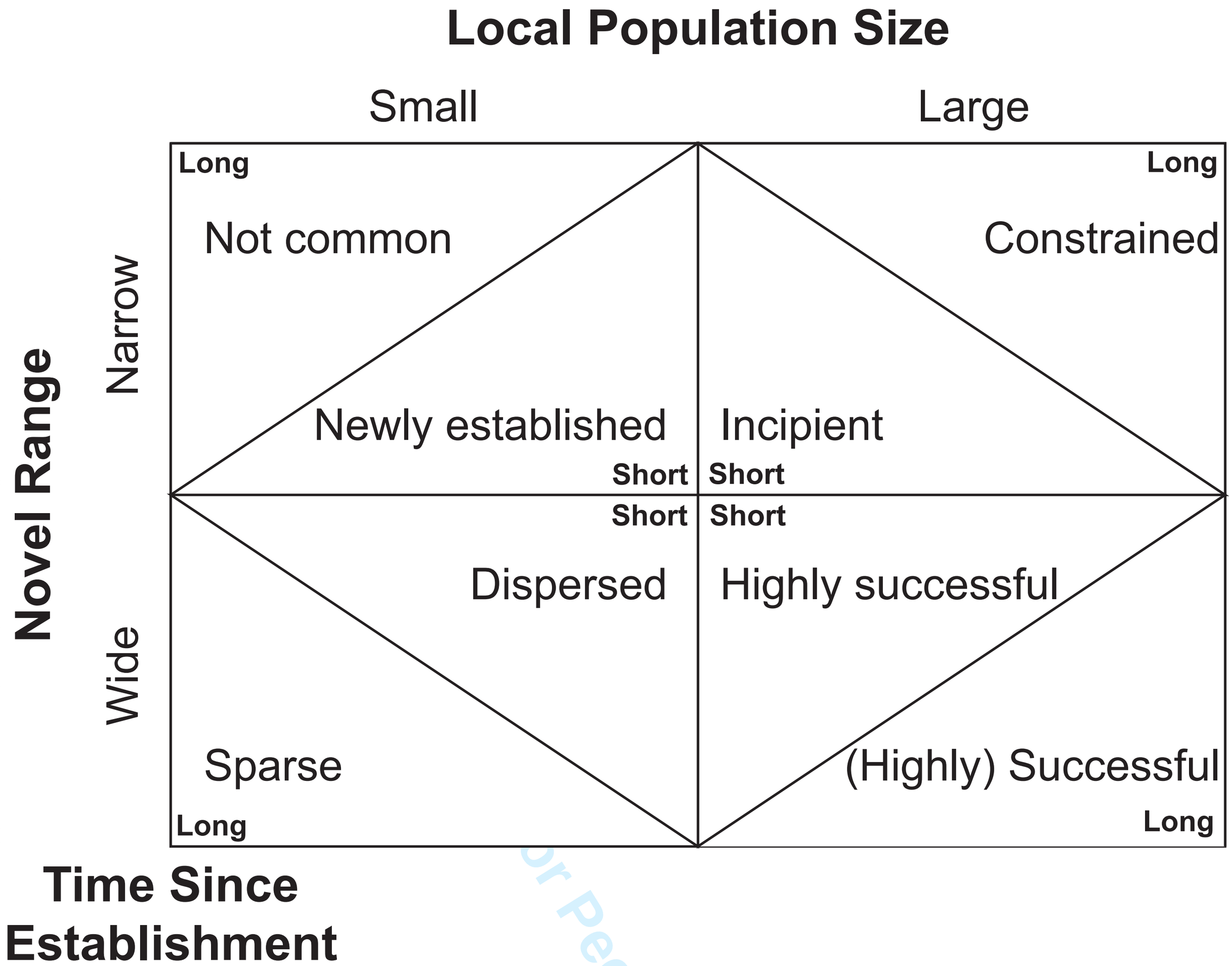


Figure S1. Dispersal functions used in the simulations. The stratified dispersal used the same function as the Gaussian dispersal 99% of the time, and the second Gaussian 1% of the time.

(a)



(b)