



## Understanding (insect) species distributions across spatial scales

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There is little doubt that multiple factors, operating across a hierarchy of spatial and temporal scales, shape species distributions (Levin 1992). However, while variation in the pattern and drivers of species richness with spatial scale has been extensively studied (Crawley and Harral 2001, Whittaker et al. 2001, Rahbek 2005), relatively less is known about how the determinants of the distributions of single species vary across spatial scales (but see, e.g. Mackey and Lindenmayer 2001, Pearson and Dawson 2003, Guisan and Thuiller 2005). Perhaps this dearth of information is due to the lack of a theoretical framework connecting these scale-variant effects, especially with regard to the most diverse group of eukaryotes – the arthropods.

Arthropods in general, and insects in particular, provide a powerful opportunity to study how species distributions are shaped by different factors across spatial scales. In this special issue, we present the papers arising from the symposium on “Sampling and modelling the spatial responses of insects across spatial scales”, held in July 2008 during the XXIII International Congress of Entomology (<[www.ice2008.org.za](http://www.ice2008.org.za)>) at Durban, South Africa. This collection of studies provides a sample of the different scales at which the distributions of species are studied, synthesizes how the different factors affecting the presence (and absence) of a species scale up from the locations of single individuals to the full extent of the geographic ranges of species, and highlights the analytical tools available for such purposes.

The opening paper in this special feature provides a unifying thread that links the study of species distributions across spatial scales. Soberón (2010) presents the most recent account of his theoretical framework merging the Grinnellian and Eltonian views of the niche (i.e. abiotic and biotic, respectively; Soberón 2007, Soberón and Nakamura 2009). His framework incorporates in a single formal mathematical definition three important elements (Soberón and Peterson 2005): the abiotic factors that affect the net growth rate of populations (i.e. scenopoetic factors), the biotic interactions that may affect fitness in a regulatory

manner (i.e. bionomic factors), and the effects of the spatial movements of individuals and populations on species distributions (i.e. movement-related factors) (Soberón 2007, see also Pulliam 2000). Soberón (2010, see also Soberón and Nakamura 2009) argues that abiotic conditions are fundamental at large scales and bionomic effects at smaller scales, thereby providing theoretical scaffolding to link the different descriptions of species distribution across scales and the factors which influence them (Fig. 1).

Scenopoetic factors determine the size and shape of species distributions at continental or regional scales, becoming negligible at site scales (Fig. 1). These factors are responsible of a number of processes affecting species distributions, including physiological constraints, responses to climatic and habitat gradients, active habitat selection and range shifts in response to changes in climate and/or habitat. Climate can constrain the ranges of species at large scales (i.e. from global to regional), while habitat-related variables seem to operate at landscape and local scales (Pearson and Dawson 2003, Thuiller et al. 2004). The mechanisms by which different factors influence species distributions may also vary with scale, as shown by, for example, the scale-dependent predictions of Kriticos and Leriche's (2010) models assessing the areas climatically suitable for two insect pests. In spite of eventual changes in the mechanism, the importance of scenopoetic factors may be still significant within hundreds or even tens of meters (Fig. 1). An excellent example is provided by Hartley et al. (2010), who show how small-scale variations in temperature limit brood development of the invasive Argentine ant at the edge of its distribution, thereby impeding these populations from further spread.

The influence of biotic factors is often negligible at continental scales, but becomes progressively important as scale decreases (Fig. 1). Many bionomic processes can affect species distributions, but their effects are often complex and do not have significant effects at scales larger than point or site. For example, the two congeneric fig wasp species studied by Warren et al. (2010) show similar scenopoetic

### Types of factors shaping species distributions

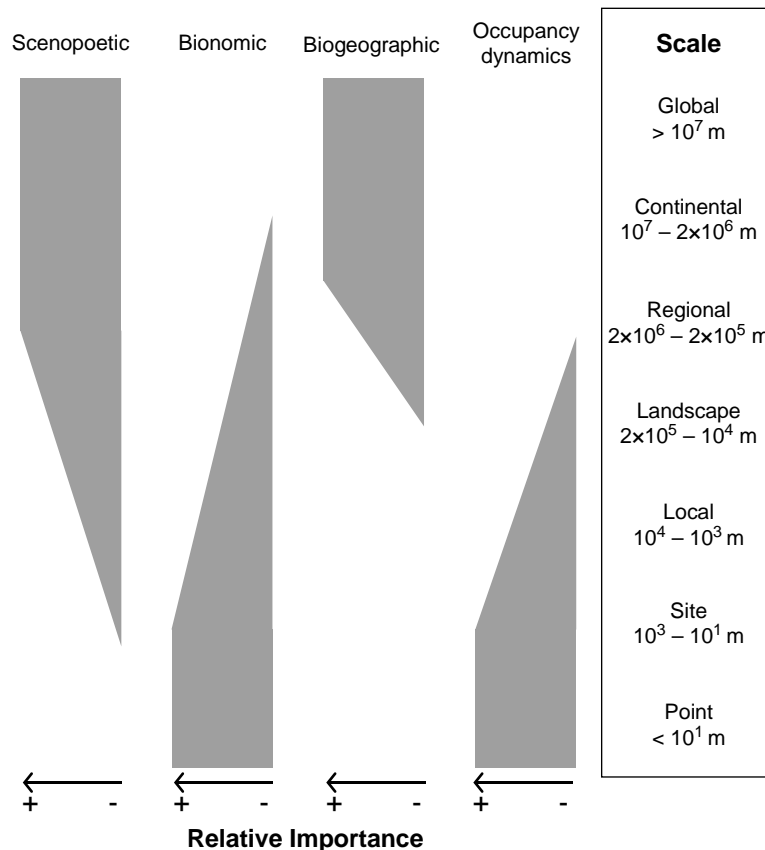


Figure 1. Relative importance of four types of factors affecting species distributions (see text and Soberón 2007, 2010) across spatial scales. Grey areas indicate relative importance; scale categories follow Pearson and Dawson (2003).

requirements and coexist in the same landscapes, in spite of their physiological and behavioural divergences, and their strong competition for sycamore figs. At large scales, only extreme (mainly trophic) specialists will have distributions constrained by the bionomic part of their niches (Araújo and Luoto 2007, Cornelissen and Stiling 2009). Such restriction scales down to the site scale. For example, viable populations of a silver-spotted skipper butterfly studied by Wilson et al. (2010) are unavoidably limited to the dry grasslands where its host plant, sheep's fescue grass, occurs. Similarly, Bell et al. (2010) used a spatially-explicit network model to show how predation of polyphagous beetles and spiders on other small arthropods, earthworms and slugs produces a negative relationship between the abundances of predator and prey species within a winter wheat field ( $< 5$  ha). These suppression effects occur at the small scale of a single cucumber plant or even a single leaf in the system integrated by the two-spotted spider mite and its mite predator studied by Nachman and Borregaard (2010). Importantly, in these latter two case studies the spatial structure of predator/prey co-occurrence is highly dynamic, and the dispersal rate of predator and prey individuals plays a major role in the observed patterns.

Although Soberón (2007, 2010, Soberón and Peterson 2005) presents all movement-related factors within a single group to understand species distributions throughout all scales, it might be necessary to differentiate between biogeographic factors and those related to occupancy

dynamics. Biogeographic factors have a significant effect on the large-scale processes that determine the size and shape of species distribution ranges (Fig. 1). Accounting for these factors is not straightforward because their precise effects on the distributions of individual species are often the subject of debate, or simply unknown. While modelling the niche and distribution of a Mexican endemic butterfly, Soberón (2010) used regions partly delimited from biogeographical considerations to account for the historical changes in the distribution. Similarly, Lobo et al. (2010) propose an analytical framework for species distribution modelling based on the selective use of absence data created *à la carte* to describe the absence of species due to biogeographical effects, but also from either lack of suitable environment or simply lack of recording effort. In both approaches, accounting for species absences from suitable areas is crucial to obtain a realistic description of the distribution of species.

Occupancy dynamics are the output of a series of processes affecting the demography of populations and the movements of their individuals, including metapopulation dynamics, small-distance dispersal and localized disturbances, among others. At scales smaller than the landscape these processes can determine the degree of aggregation of populations within the geographic range of the species (Cabeza et al. 2010, Wilson et al. 2010), or of individuals within a locality (Bell et al. 2010, Nachman and Borregaard 2010) (Fig. 1). The degree of aggregation is

certainly scale-dependent, as shown by Hui et al. (2010) and Procheş et al. (2010). However, describing the spatial aggregation of individuals is also difficult and perhaps counter-intuitive. Hui et al. (2010) propose categorizing the scaling patterns of aggregation measures, which will both clear up their meaning and make the terminology accessible to other ecologists working outside this particular topic.

In order to describe species distributions, and understand the effect of different factors that shape them, it is necessary to explicitly consider the effect of scale (Hui et al. 2010, Kriticos and Leriche 2010). For example, Procheş et al. (2010) study how the patchy distribution of pneumatophores within mangrove forests, and of these forests along the South African coast, affect the distribution and abundance of the arthropod species across a range of scales. Understanding scale dependencies can also inform conservation. In an interesting example, Cabeza et al. (2010) use different methods to describe the distributions of, and design conservation priorities for Finnish butterflies at three different scales (national, regional and landscape), showing that both targets and actions vary widely depending on the scale considered.

For simplicity, a primarily static perspective on species distributions (at least at the largest scales) is often used to describe how these distributions and their determinants vary across scales within a unified framework. But, species distributions are dynamic entities independently of the scale of analysis, and so are the factors affecting them. Integrating how the elements of niche, distribution and species-habitat association change through time will further improve our understanding of the dynamics of distributions of species across spatial scales. Leaving apart scaling variations due to the body size and life history of each taxonomic group, the relative importance across spatial scales of scenopoetic, bionomic, biogeographical and occupancy dynamics-related factors have been well addressed by the papers in this special feature of *Ecography*.

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