

commentary

## Scale-dependence of spatial patterns of insect distribution and abundance

The most recent issue of *Ecography* (February 2010) contained eight papers devoted to patterns in the distributions and abundance of insects, and to the dependence of these patterns on spatial scale.

It has been known for some time that our perception of patterns of biodiversity, and the relative importance of the factors that determine these patterns, vary with the spatial scale considered (Whittaker et al. 2001). However, as Hortal et al. (2010) point out in their introduction to the *Ecography* special issue, most previous analyses have focused on species richness patterns, not on the distributions of individual species. Furthermore, in these previous studies, as in conservation and ecology research more generally (Clark and May 2002), there has been strong bias towards vertebrate animals and plants: in a meta-analysis of 394 studies of species richness patterns across different spatial scales (Field et al. 2009), only 68 focused on insects. The growing number of macro-ecology studies that do focus on insects is probably a reflection of increasing knowledge about the distributions of these species. In relation to the number of species they represent, insects are still massively under-sampled (Newbold 2010), but there are now nearly 15 million geo-referenced distribution records for insects in the Global Biodiversity Information Facility database (<http://www.gbif.org>), spread across all continents except Antarctica.

Covering a wide range of taxa, geographical regions and methodologies, these papers together make an important contribution to our understanding of patterns of insect biodiversity at different spatial scales.

### Scale-dependence in the drivers of biodiversity patterns

The different studies in this special issue considered patterns of insect distribution and abundance at a wide range of scales. This is reflected in

the different factors identified as important in explaining observed patterns and in the different methods used for analysis.

Several of the studies considered very broad (country-level or continental) scales, successfully using species distribution models with climate variables to explain distribution patterns (Lobo et al. 2010, Kriticos and Leriche 2010, Warren et al. 2010, Soberón 2010). At finer scales, other factors emerge as more important. In agricultural fields in the UK, arthropods showed patterns of co-occurrence that suggest an effect of biotic interactions (Bell et al. 2010). At small scales, micro-climate and topography are also important. In a national park in Hawaii, the extent of an Argentine ant (*Linepithema humile*) invasion was modelled better using microclimate data than landscape-level climate variables (Hartley et al. 2010), and a metapopulation model for the silver-spotted skipper butterfly (*Hesperia comma*) in Britain suggested that as the global climate warms, the ability to inhabit more northerly-facing aspects with warmer micro-climates is allowing faster rates of range expansion (Wilson et al. 2010).

Although it has been suggested several times that multi-scale models with different sets of drivers would help to better understand diversity patterns (e.g. Mackey and Lindenmayer 2001) and to make better predictions of species' responses to environmental change (Randin et al. 2009), this approach remains relatively rare in practice (but see e.g. Anderson et al. 2007). The marked variation with scale in the relative importance of different explanatory variables, and the decline in the importance of landscape-level climate variables at the finer resolutions, lends weight to the argument for including factors such as biotic interactions, habitat, and microclimate into models in a multi-scale framework.

Several of the studies explicitly tested the effect of spatial scale on the conclusions drawn from biogeographical analyses (Cabeza et al. 2010,

Hui et al. 2010, Kriticos and Leriche 2010).

Mar Cabeza and colleagues (Cabeza et al. 2010) presented a very interesting study looking at the outcome of systematic conservation planning exercises for butterflies in Finland at three spatial scales. The relative importance of areas was assessed using different methods at each of the scales: species distribution models with climate variables at the national scale, relating abundance to habitat variables at the regional scale, and using metapopulation models at an even finer (landscape) scale. Each of the three approaches revealed something different regarding the relative importance of areas for conservation, highlighting the advantages of a multi-scale approach.

On the other hand, distribution and abundance patterns can sometimes be explained successfully in spite of the scale-dependency of patterns. For two insect species in Australia, distribution models developed with climate data at different resolutions were very similar overall (Kriticos and Leriche 2010). However, in this case the aim was always to explain the same broad-scale distribution data, and climate variables were generally sufficient. If the aim is to explain fine-scale distribution patterns, then models developed with coarse-scale climate variables might well be inadequate.

If the factors that determine the occurrence of species at fine scales are themselves correlated with coarse-scale climate patterns, then models based on the latter might be able to explain the finer-scale patterns. Jorge Soberón (Soberón 2010) showed that this is the case by simulating a species distribution, determined at large scales by climate but with an effect of competition at finer resolutions. Distribution models based on climate variables were able to explain the simulated distribution at a coarse resolution very well, supporting the use of such models for estimating the current distribution of species. Nevertheless, this highlights the importance of choosing explanatory variables carefully when the aim of the model is predictive. A model that appears to explain current distributions will not necessarily capture the real response to the environment (Austin 2007).

## Data issues

Although our knowledge of the distribution of species is increasing rapidly, data remain scarce, patchy and biased for many taxa, especially for insects (Newbold 2010). Two of the studies in the special issue considered data availability, specifically the lack of data on species absence, and how it affects our ability to model the distributions of insect species (Lobo et al. 2010, Soberón 2010).

Species distribution models often require data on species absence as well as data on species presence, but a record of species absence can occur for a number of reasons: unsuitable environment, inability of the species to disperse to an area, or failure to detect a present species (Lobo et al. 2010). For an Iberian dung beetle, modelled distributions were markedly different depending on the type of absence data used (Lobo et al. 2010). Grid cells with no presence record were divided into three types of 'absences': those in environmentally suitable areas (estimated using an exploratory model, with a technique that requires only presence data) and within the observed extent of occurrence of the species were assumed to be unrecorded owing to inadequate sampling; those in environmentally-suitable areas, but outside of the extent of occurrence, were assumed to be unoccupied as a result of other factors, such as interactions among species or dispersal limitation; grid cells that were not within the initial modelled distribution were assumed to be genuinely environmentally unsuitable.

For modelling the distribution of the short-horned Baronia butterfly (*Baronia brevicornis*) in Mexico, Jorge Soberón (Soberón 2010) took a different approach to dealing with a lack of data on species absence, modelling the potential distribution using a simple climate envelope approach and then assuming that the butterfly is only able to disperse to those ecoregions in which it has been observed. This idea is a very promising one, although assessing whether the models really capture the distribution better will require evaluation with independent data, since the refined models by definition fit the data used to train them better than unrefined models.

These two studies highlight the importance of having clear objectives when modelling the distribution of species: whether one is interested in modelling actual distributions versus potential distributions, or in predicting distributions under new conditions versus explaining current distributions, will strongly affect the appropriate choice of data and methods.

Data on the abundance of insect species are even more scarce than data on the occurrence of species. Gösta Nachman and Michael Borregaard (Nachman and Borregaard 2010) adopt an interesting solution to this problem, using a spatially implicit model of the proportions of patches inhabited by either or both of a spider mite (*Tetranychus urticae*) and its predator (*Phytoseiulus persimilis*) to help understand the population dynamics of the system where spatially explicit data on abundance are lacking.

## Conclusions

The papers in this special issue of *Ecography* show how far we have come in understanding spatial patterns in the occurrence and abundance of insects. They also demonstrate techniques for making use of the incomplete and patchy spatial data on insects. Importantly, they also show how different the factors that shape observed patterns can be depending on the spatial scale considered. A proper understanding of the distributions of species will require models that incorporate as many of these different factors as possible at the appropriate scale.

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## symposium summary

# Introduced conifer invasions in South America: an update

One-day symposium at 6th Southern Connection Congress – Bariloche, Argentina, 16th February 2010

Species in the family Pinaceae are currently among the most widely distributed trees in the world. Although almost exclusively native to the northern hemisphere, many species have been introduced and widely planted throughout the southern hemisphere. Introduced conifers have been mainly used for plantation forestry, amenity, shelter and erosion control, and in the last few decades a number of species have become increasingly invasive. On February 16th, 2010, we held a symposium entitled “*Pine Invasion In South America: Patterns, Process, and lessons to be learned*” during the 6th Southern Connection Congress in Bariloche, Argentina (<http://www.sccongress2010.com.ar>). The symposium was organized by the Southern Hemisphere Network on Conifer Invasion (SHNCI), a group of concerned scientists working on conifer invasions in the southern hemisphere (details in Richardson et al. 2008). Speakers from different parts of the world, especially the Southern Hemisphere, shared their research experiences and presented studies on the ecology and management of invasive conifers. The aim of this note is to highlight the key ideas presented and discussed at the meeting on the study and management of conifer invasions in South America.

An introduction by Dan Simberloff et al. suggested that there are few problems more unique to the southern hemisphere, specifically to

parts of the former Gondwanaland, than introduced conifer invasion. Pinaceae native to the northern hemisphere have been widely planted in the last few decades. Today the invasion of these species is occurring outside managed areas, and is expected to increase in the next decades. Given the ecological and economic impacts that invasive conifers can produce, a better understanding is essential if they are to be most cost-effectively controlled and managed in the future (Simberloff et al. 2010).

## History, Patterns & Processes

A better understanding of the history and the current status of conifer invasions in South America is urgently needed. For Chile, Aníbal Pauchard et al. described how the Chilean government and forestry companies began massive reforestation programs during the late 20<sup>th</sup> century, using fast-growing conifer species to stop soil degradation, even in protected areas. Commercial *Pinus radiata* plantations began in the late 1960s and boomed in the 1980s. In southern areas, other species such as *Pinus sylvestris*, *P. ponderosa*, *P. contorta* and *Pseudotsuga menziesii* were also planted and are now becoming invasive, especially *P. contorta* (Langdon et al. 2010).

Pine invasions have been used as a model for understanding plant invasions (Richardson 2006) and South America provides exciting new