

OPINION

Microclimatic challenges in global change biology

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Abstract

Despite decades of work on climate change biology, the scientific community remains uncertain about where and when most species distributions will respond to altered climates. A major barrier is the spatial mismatch between the size of organisms and the scale at which climate data are collected and modeled. Using a meta-analysis of published literature, we show that grid lengths in species distribution models are, on average, ca. 10 000-fold larger than the animals they study, and ca. 1000-fold larger than the plants they study. And the gap is even worse than these ratios indicate, as most work has focused on organisms that are significantly biased toward large size. This mismatch is problematic because organisms do not experience climate on coarse scales. Rather, they live in microclimates, which can be highly heterogeneous and strongly divergent from surrounding macroclimates. Bridging the spatial gap should be a high priority for research and will require gathering climate data at finer scales, developing better methods for downscaling environmental data to microclimates, and improving our statistical understanding of variation at finer scales. Interdisciplinary collaborations (including ecologists, engineers, climatologists, meteorologists, statisticians, and geographers) will be key to bridging the gap, and ultimately to providing scientifically grounded data and recommendations to conservation biologists and policy makers.

Keywords: body size, climate change, downscaling, fractals, grid size, maxent, refugia, spatial resolution, species distribution models, temperature

Received 7 March 2013; revised version received 8 May 2013 and accepted 10 May 2013

One of the great challenges in modern biology is to predict how climate change will affect species (Schwenk *et al.*, 2009). In many locations, changing climates will alter ecosystem functioning, reduce biodiversity, and drive some fraction of species extinct. In the last 10 years, such impacts of climate change have been well documented (Parmesan, 2006; Tylianakis *et al.*, 2008; Walther, 2010; Somero, 2012), and efforts have started to shift from documenting impacts to predicting how species, and their distributions, will respond to future climates. Statistical models for predicting distributions – called species distribution models (SDMs) – are now widely used to relate species distribution data and environmental or spatial characteristics of the known locations of individuals in a species (Elith & Leathwick, 2009). However, SDMs remain difficult to generalize (Araújo & Guisan, 2006; Heikkinen *et al.*, 2006; Kearney & Porter, 2009; Buckley *et al.*, 2010), both from one species to another and into novel environments. Here, we explore an important issue related to the spatial scale at which SDMs predict biological phenomena.

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Species distribution models use climatic data arrayed into grids having characteristic spatial scales. Although most SDMs use grid sizes of one to several degrees of latitude and longitude, corresponding to 1 to many kilometers on a side, the largest terrestrial animals are <10 m long, and the largest plants not much larger. Moreover, these largest animals and plants are outliers – the majority of animals are smaller than a few centimeters on a side (May, 1988). We find, in a meta-analysis of published SDMs, that the mismatch (in units of \log_{10} m) between grid lengths and organism lengths is, for animals, 4.20-fold (range 1.12–7.04) and, for plants, 2.84 (range 0.41–7.24) (Fig. 1; see also Supporting Information online). Using a linear scale, this corresponds to an average mismatch of ca. 10 000-fold in animal studies and ca. 1000-fold in plant studies. The relatively better performance by plant studies reflects that studied plants are larger than animals, rather than that plant studies use finer grained environmental data (of course, our analysis does not address the complexity of plant roots, which are in a different environment altogether). Current SDMs are therefore operating far from an ideal spatial resolution.

Our analysis highlights a key problem for predicting ecological effects of climate change: organisms do not

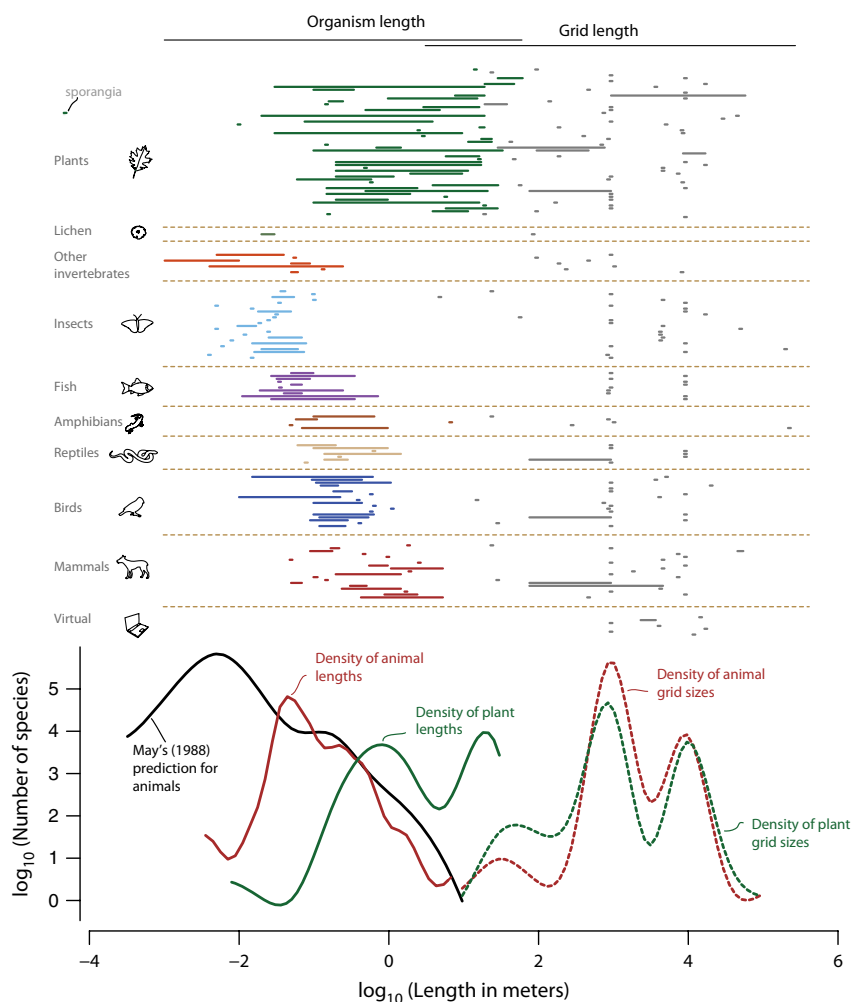


Fig. 1 Lengths of grid cells from published species distribution models (SDMs) compared to the lengths of the animals and plants they studied. See Supporting Information for methods of the literature search, the list of articles, and the data we extracted from them. Colored dots indicate the body size of a species from one study; colored horizontal lines indicate a range of body sizes if the study used multiple species. The corresponding grey dots and lines indicate the grid size (or range of sizes) of climate variables used in that study. The black density plot is a spline fitted to data from May's 1988 study [(May, 1988), fig. 6], which represents his estimate of the body size distribution of all terrestrial animals. Density plots of the rest of the terrestrial data are shown at the bottom for comparison. The two peaks in the grid-size density plots correspond to the commonly used grid scales of 1 and 10 km (e.g., these are the most common resolutions exported from the WorldClim database). We compared pairs of distributions by bootstrapping a two-sample Kolmogorov–Smirnov test (10 000 iterations), using samples ($N = 50$) drawn with replacement from the observed empirical distributions. The distribution of terrestrial animal sizes was significantly shifted toward large body sizes compared to May's predicted distribution (mean P -value was 0.0028, and 99.0% of iterations had $P < 0.05$). The distributions of animal and plant grid sizes were not statistically distinguishable (mean P -value = 0.31).

sample environmental data at the spatial scales currently used in SDMs. Rather, organisms live in microclimates, which can be highly heterogeneous in space and time (Bakken, 1992; Kearney & Porter, 2009; Sears *et al.*, 2011), and can differ strongly from surrounding macroclimates (Bartholomew, 1966; Willmer, 1982; Oke, 1987; Geiger *et al.*, 2009). For example, the microclimates on the leaves of a single plant can easily be 10 °C warmer or colder than the surrounding air (Potter *et al.*, 2009; Pincebourde & Woods, 2012). In general, an organism's

body size determines the microclimates it can access. Indeed, smaller organisms integrate conditions over smaller spatial (and temporal) scales. Moreover, shifts in size, and in other properties like shape and reflectance, affect the relative importance of different components of heat budgets (Stevenson, 1985a, b). Thus, despite sharing the same habitat, two organisms may have markedly different body temperatures because each filters its environment according to its own thermal properties, shape, and size (Gates, 1980; Broitman

et al., 2009; Sears *et al.*, 2011). Current SDMs [except some biophysical models, e.g., (Kearney *et al.*, 2009)] do not include such effects, meaning that they implicitly consider all organisms within a grid cell to experience the same coarse abiotic conditions.

Predicting how organisms will respond to climate change will require radically reducing the mismatch between the spatial [and temporal (Kearney *et al.*, 2012)] scales of models vs. organisms. This problem must be addressed from both sides: there is no point in using information on organisms that is much finer than information on their climates, or *vice versa*. How fine is fine enough? The question of optimal grid cell size (or grain) has been debated since the birth of SDMs, with some authors suggesting that finer scaled SDMs provide better predictions (McPherson *et al.*, 2006; Austin & Van Niel, 2011; Franklin *et al.*, 2013) and others that they do not (Guisan *et al.*, 2007), in some cases making them perform even worse. However, simulation studies on the effects of grain size generally test spatial resolutions down to ca. 100 m, which is still far from the ideal resolution we propose. Ignoring practical constraints (for the moment), we propose that the ideal spatial resolution is related to organismal body size and lies between 1 and 10 times the length or height of the organism.

Reaching the proposed optimal resolution will require serious effort on several fronts. Current climate data are coarse because it is difficult and expensive to sample simultaneously at fine scales and large geographic extents. Below, we highlight three approaches that will help bridge the gap. These are not alternatives but complementary, mutually reinforcing approaches that should be pursued together if we are to bridge the gap rapidly.

Advances in data collection

The first approach is the obvious one of sampling organisms and climates at finer scales. To do so, we need smaller, more robust sensors with enough power and memory to collect data for long periods without requiring much attention. One class of effective devices would be small robots whose sizes, modes of movement, and 'home range sizes' match those of the organisms of interest. Robots that operate in swarms and communicate among themselves are rapidly becoming available for military and medical use (Baisch *et al.*, 2011; Wood *et al.*, 2012), and they could be adapted to scientific aims. Alternatively, small sensors could be attached to live organisms, which would simultaneously solve the problems of directing robots to behave like organisms and of obtaining high-resolution information on organismal distributions. Although

autonomy would create new communication problems of obtaining data from sensors, there are increasingly sophisticated ways to create ad hoc wireless networks for funneling data to central receivers (Johnson *et al.*, 2009; Rubenstein *et al.*, 2012). Autonomy is key, as it will free researchers from time-consuming efforts to get sensors into place and keep them functioning.

It is obviously neither desirable nor possible to cover the world with sensors. Rather, densely arrayed sensors should be deployed, in structured designs, within focal environments, which will allow us to better understand in particular cases how microscale variation depends on macroscale predictors. Until robots with realistic behaviors are cheap and readily available, sampling may be most practical in agricultural contexts, or other relatively homogeneous environments. In those environments, a small area of well-sampled microclimates will more accurately describe the total variability throughout the whole environment.

A second step would be to integrate these better sensors into smaller scale operative temperature models (Grant, 1990; Bakken, 1992; Angilletta, 2009). Operative temperature models integrate complex microenvironmental conditions into realistic measures of body temperature by replicating the biophysical filtering that arises from the shape, size, and surface characteristics of particular organisms. Although this approach has been used successfully with organisms such as mussels (Helmuth *et al.*, 2010), sea stars (Pincebourde *et al.*, 2008), reptiles (Shine & Kearney, 2001), and a few large insects (Harrison & Fewell, 1995; Kingsolver, 2000), it has not been used with the small organisms positioned on the left half of May's distribution (Fig. 1). For very small body sizes (<1–2 mm), bare thermocouples provide accurate measurements, as convection dominates heat exchange.

Remote infrared (IR) sensing (Tomlinson *et al.*, 2011) – via satellites or portable IR cameras – will continue to play an important role at medium to large spatial scales. Remote sensing is less informative about physical environments of large organisms, as they are more coupled to air temperature and incoming solar radiation than to surface temperature (except large animals such as snakes that lie flat on the substrate). For small organisms, satellites provide inadequate spatial resolution (>60 m), and neither satellites nor ground-based cameras can 'see' everywhere that small insects and other metazoa could go in complex microhabitats – under bark, in leaf litter, deep in flowers, etc. Although technical advances in remote sensing at fine scales would be valuable, especially to estimate surface temperature when parameterizing process-based models, it probably will not substitute for more direct sensing of microclimatic variables.

Advances in downscaling

A second approach is to 'downscale' climatic variables, which refers to translating climatic variables across spatial scales, e.g., from global circulation models to regional or local scales (Hewitson & Crane, 1996; Winkler *et al.*, 2011a, b). Downscaling has been developed independently by meteorologists and by ecologists. For meteorologists, the problems have been to predict regional climates from the outputs of global circulation models and, for ecologists, to predict microclimates or body temperatures from regional and local information. Clearly, local efforts (by ecologists) could be nested within the coarser grained downscaling done by meteorologists, but such cross-level downscaling remains rare in studies of climate change (Fridley, 2009; Sears *et al.*, 2011). Progress will require joint efforts to downscale climatic variables into the microclimates around organisms, to scales <1 m.

Downscaling methods developed by meteorologists fall into two categories: dynamic (or process based) (Murphy, 1999) and empirical (or statistical) (Wilby *et al.*, 1998). Dynamic methods incorporate the physical processes (e.g., energy and mass fluxes) of the focal system, and can involve a cascade of nested models that run at different scales; the output of one model becomes the input at the scale below. Empirical approaches use statistical relationships between observed local and global climates. Like the antagonism between mechanistic and statistical models of species distribution (Buckley *et al.*, 2010), process-based models are computationally expensive while empirical approaches suffer from the assumption that future relationships between global and microclimates will be like those observed now. The most productive way forward likely will be to use both methods, as they provide complementary insights. Indeed, the recent emergence of statistical–dynamical approaches has led to significant progress in the precision and validity of climate downscaling methods at regional scales (e.g., regional circulation models) (Boé *et al.*, 2006; Najac *et al.*, 2011). Alternatively, the use of gridded weather data sets, which are a source of dynamic meteorological data over large spatial and temporal scales, may provide directly downscaled information (Mislán & Wethey, 2011). The spatial resolution of such gridded data sets remains coarse (>12 km), but can predict thermal stress events for intertidal organisms (Mislán & Wethey, 2011) and should be expanded to other biomes.

From a microclimate perspective, downscaling methods are still inadequate: they give resolutions of ca. 30 m at best (Fridley, 2009), which is not fine enough to describe variability relevant to small

organisms (Scherrer & Körner, 2010). There has been, however, a separate effort over the past 40 years, by physiological and biophysical ecologists, to develop mechanistic models for predicting animal body temperatures from local-scale environmental information (Porter *et al.*, 1973; Gates, 1980; Helmuth, 1998; Pincebourde & Casas, 2006; Kearney & Porter, 2009; Saudreau *et al.*, 2013). In effect, this parallel work bridges the gap between the local-scale climates and microclimates. It remains, however, to establish the link between the output from nested regional climate models and the local-scale climates. The lack of such local-scale models has led researchers to connect microclimatic models directly with regional circulation model outputs (Kearney & Porter, 2009), which is problematic because the climatic variability generated by local environmental topography is not considered. We suggest that a high priority should be to develop local-scale climatic models within this biophysical framework to further integrate microclimatic biophysical models with regional or global circulation models.

The development of local-scale climatic models is not straightforward. Constraints include potentially exorbitant computational expenses, the problem of obtaining other fine-scaled environmental information (e.g., microtopography, coordinates in 3D space of tree leaves) that can be coupled to broad-scale climate data, and the difficulty of generalizing model predictions to new landscapes and climates. The development of hybrid models (semimechanistic and semistatistical) may be the best way to trade-off between the methods' advantages and disadvantages.

Fine-scaled predictions can be obtained by specifying how broader scale climates interact with finer scaled measures of environmental topography, thermal properties of substrates, and other local abiotic and biotic factors (Helmuth, 1998; Sears *et al.*, 2011). The heat budget of organisms is strongly influenced by numerous factors, including air temperature, solar radiation, wind speed, humidity, and precipitation (Gates, 1980), which can all be variable at small spatial scales depending on local and microtopography. All these factors therefore need to be downscaled based on topographical information. For example, we can use simple geometrical relationships to compute the amount of radiation (the main heat source in the environment) received by each 'pixel' of a surface from zenith angle and azimuth of the sun, and slope and azimuth of the substrate (McCullough & Porter, 1971). Using the spatial distribution of angles for a given landscape, we can then estimate the landscape thermal heterogeneity at scales relevant to a small organism. For surfaces with heterogeneous microtopography and multiple elements (e.g., bare rock, bark, leaves), the spatial heterogeneity in

radiative heat absorption can be estimated from the statistical distribution of slope and absorbance values (Huey *et al.*, 1977). Other components of the heat budget, namely, surface evapotranspiration and heat loss via convection, can be estimated from surface wetness and ambient air temperature. Such hybrid models allow us to estimate statistical distributions of microclimates at the scale of small organisms, even when spatially explicit information on environmental architecture is unavailable.

Advances in multiscale spatial statistics

A third approach is to develop better statistical descriptions of spatial patterns of microclimates. There is now an enormous literature on using spatial statistics to characterize environmental variation and landscape

structure (Bell *et al.*, 1993; Garrigues *et al.*, 2006; de Knegt *et al.*, 2008), and a diverse set of techniques is available for describing the scale dependence of spatial data, including wavelets, spatial regression, and fractals (Sun *et al.*, 2006; Florindo *et al.*, 2012). These techniques have less often been applied to problems with characteristic scales of a few centimeters or less (Baraloto & Coutron, 2010; Meager *et al.*, 2011), suggesting that the statistical tools exist and we simply need finer scale data to which they can be applied. However, the statistical problem can also be asked in broader ways. For example, are there general rules to describe how the spatial distributions of physical factors in microhabitats scale with organismal body size? Do small or large organisms have more thermal heterogeneity available to them? Can we predict spatial patterns of variation at fine scales from those observed at

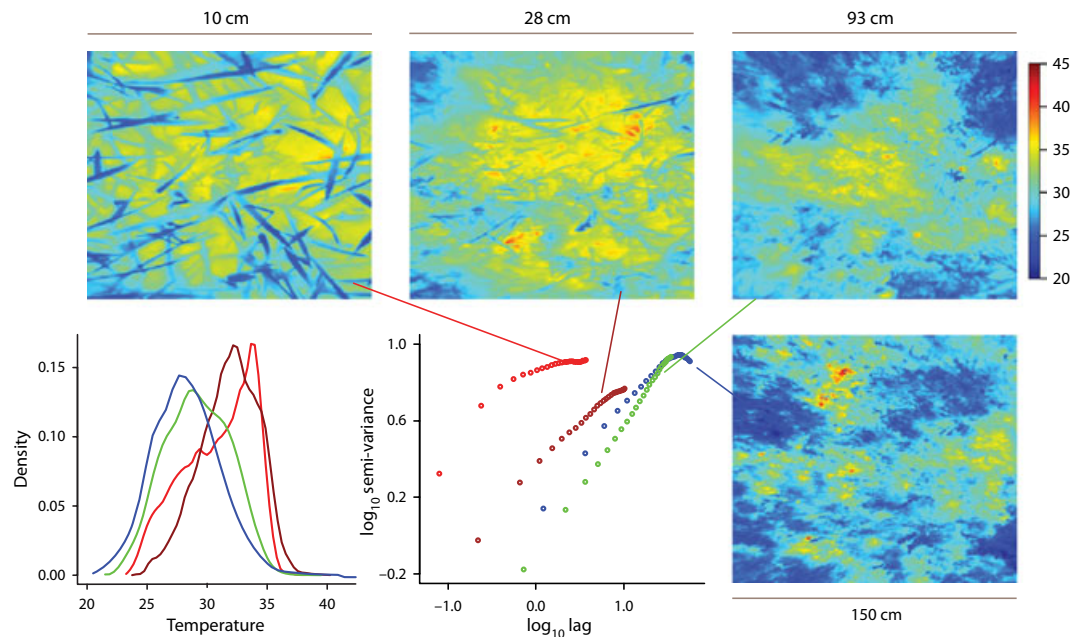


Fig. 2 Scale-dependent thermal variation. Small and large organisms may experience local thermal variation differently, even when they share the same habitat. To illustrate this effect, we took thermal images at different heights above a single patch of grass and forbs along the banks of the Loire River, France (numbers associated with each image represent the length of that side). The images differ both in total area sampled (their spatial extent) and in the real-world size represented by each pixel; the close-up images have smaller extents and higher spatial resolutions (i.e., smaller pixel size). In the close-up images, the distributions of pixel temperatures (bottom left panel) are shifted toward higher temperatures. A more spatially explicit way to examine temperature distributions is with semivariograms (bottom center panel), which show thermal variance as a function of distance between pixels (lag). The variograms indicate that, within each image, smaller lags contain lower variance. In other words, nearby pixels are more similar to each other than they are to distant pixels. Across images, however, the close-up images show higher total variance. Relating these patterns to body size depends on recognizing that smaller organisms will usually sample smaller total extents but will do so at finer spatial resolutions. The latter effect corresponds roughly to changing the pixel size of the image, and smaller organisms therefore sample smaller pixels (as in the upper left image) (Emerson *et al.*, 1999; Al-Hamdan *et al.*, 2010). By contrast, at a fixed spatial resolution, sampling smaller extents will give lower total variance. Thus, two offsetting processes influence the available variation—less variation associated with smaller total extents but greater variation associated with sampling at finer scales. The net outcome for an organism, both in the patches we sampled and more generally for any nested set of measurements like this, will depend on the relative influence of those two effects. Although our sample is only a single series ($N = 1$), and the quantitative patterns may not be general, this example reinforces our recommendation that the biological community needs to systematically search for and characterize patterns across biomes (see also Fig. 3).

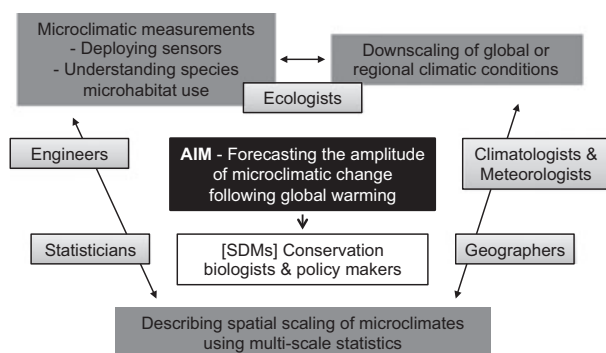


Fig. 3 Roadmap for bridging the spatial gap between the scales of organisms and of species distribution and climate models. This challenge is strongly multidisciplinary. Ecologists should work with engineers to develop new sensors, and with climatologists and meteorologists to develop better methods for downscaling to microclimates at submeter scales. Statisticians and geographers should also work with ecologists to improve our statistical understanding of microclimatic spatial structure across scales. Interdisciplinary collaborations will be key to forecasting the effects of global warming on species, and to providing scientifically grounded data and recommendations to conservation biologists and policy makers.

larger scales? Which physical processes generate patterns of variation at different spatial scales? Because different energy- and mass-transport processes contribute to variation in scale-dependent ways, and because organisms also move around their environments in scale-dependent ways, we suspect that there will be no simple answer. The most productive outcome would be to identify systematic changes, if any, in patterns of spatial variation during the transition(s) from large to small scales (Fig. 2).

The statistical problem is magnified by scale-dependent changes in environmental rugosity, which is a measure of roughness defined as the draped surface area divided by the surface area projected onto a flat plane. Rugosity usually increases at finer scales – i.e., an ant foraging in a field perceives it to be more rugose than does an ungulate grazing on the same field. For fine-scale phenomena, high rugosity is problematic because spatial statistics are designed primarily for 2D data (i.e., their locations are specified using latitude and longitude). Moreover, adding a third axis for specifying position is unsatisfying because often there will be no straight-line path from one point in 3D space to another. Finally, high rugosity at fine scales limits the utility and quality of remotely sensed data, especially if there are crevices or pockets not visible to the sensor.

In summary, we do not know how most organisms will respond to future climates, and a fundamental source of uncertainty is the complexity of the physical and biotic filters between macroclimates and the micro-

climates where organisms live. Taking microclimates seriously will raise other important problems. For example, most animals have complex life cycles, with each life stage living in a distinct microclimate. In complex life cycles, which microclimate is most important? Changes in microclimate may strongly affect some life stages but not others (Kingsolver *et al.*, 2011). Animals also grow, which alters the set of microenvironments available to them (Porter & Tracy, 1983). Finally, in communities, interacting species often spend most of their lives in different microclimates, which implies that understanding the effects of climate change on ecological processes will require understanding its effects on entire suites of microclimates. Despite this complexity, the three research directions advocated above promise rapid advances. Importantly, although each alone has significant weaknesses, the approaches are mutually reinforcing and should therefore all be pursued (Fig. 3). For example, advances in data collection at fine scales will provide key data for developing and validating the robust spatial statistics needed for connecting macro- to microscales. It is urgent that we resolve these problems: macroclimates are changing faster than the worst-case scenarios predicted just a few years ago (Oldenborgh *et al.*, 2009), with essentially unknown effects at the smallest scales.

Acknowledgments

Thanks to Lucas Jones for discussing fractals and the statistical approaches for analyzing them, and to Jérôme Casas and two anonymous reviewers for helpful comments on a previous version of the manuscript. This work was supported by NSF grant IOS-0844916 to HAW and by ANR Blanc MicroClimite (ANR-2010 BLAN-1706-02) to SP.

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Supporting Information

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

Data S1. Methods of the meta-analysis.

Table S1. List of articles and the extracted data.