Moving forward with species distributions

Understanding and predicting the responses of natural ecosystems to global change is a "grand challenge" of modern ecology (Thuiller, 2007). To predict how species will respond to climate change, we need to first understand their climatic tolerances. Toward this aim, a common practice is to use a species' observed occurrences to estimate its physiological tolerances for various environmental and climatic variables and then to map the species' potential geographic range as the full extents of "suitable" areas (i.e., where all environmental variables are within the bounds of these tolerances). The same process can then be used to predict areas that will be suitable for the species in the future based on the conditions forecast under different general circulation models and emissions scenarios. This is the general approach of species distribution modeling (SDM), which is now one of the most widely used and influential techniques in biogeography and conservation biology (Franklin, 2009).

The use of observed occurrences to estimate species' current and future geographic ranges is based on two critical assumptions. The first assumption is that the observed occurrences of species accurately reflect the species' full range of environmental tolerances (i.e., that there is no difference between the species' realized and fundamental niches). The second assumption is that all conspecific populations have the same tolerances (i.e., that there is no local adaptation). Despite their seeming naivety, these two assumptions remain largely unchallenged and untested for most species. Changing these assumptions can have dramatic effects on the mapping of species' geographic ranges, as well as on our predictions for how species will respond to climate change.

Assumption 1. The observed occurrences of species accurately reflect their fundamental climatic tolerances. The range of environmental conditions in which populations can persist are unknown for most taxa (Fig. 1). The potential for species to tolerate and persist under a wider range of conditions than where they presently occur is referred to as "range underfilling" (Sunday et al., 2012). In other words, a species that exhibits range underfilling may have broader climatic tolerances and a larger fundamental niche than what is estimated based on its observed occurrences and associated distribution models.

There are several potential causes of range underfilling. First, the observed ranges of species may be "truncated" by lack of opportunity. This lack of opportunity may be due to dispersal limitation, which prevents species from reaching areas that have suitable conditions or to the absence of areas with certain suitable conditions under the Earth’s current climate (Terborgh and Weske, 1975). For example, species that occur in the hottest areas of the tropics may be capable of tolerating even hotter conditions but are unable to express this heat tolerance simply due to fact that there are no places with higher temperatures (Feeley and Silman, 2010a). Likewise, abiotic conditions such as soil type or topography may exclude species from areas that are climatically suitable (Ibáñez et al., 2006). Range underfilling may also result from biotic interactions. Indeed, it has long been posited that species’ realized geographic ranges are limited by the species’ physiological climatic tolerances at the “harsh” end of climatic gradients (e.g., high elevations or latitudes) in contrast to biotic interactions at the more “benign” ends of environmental gradients (e.g., at low elevations or latitudes; Connell, 1961). Finally, anthropogenic disturbances can also cause range underfilling. It has been suggested, for example, that human activities such as cattle grazing and burning in the high tropical Andes are “depressing” alpine treelines to elevations below where trees could physiologically grow (Young, 2009).

Whatever the cause(s), range underfilling will greatly impact our ability to model and predict how species will respond to climate change. One potential effect of range underfilling was illustrated in studies by Feeley and Silman (2010a) and Feeley et al. (2012a). These studies showed that if the fundamental thermal tolerances of Amazonian plant species are accurately reflected by their geographic occurrences, then even modest rises in temperatures can cause catastrophic losses of diversity. On the other hand, when range underfilling was accounted for and the thermal tolerances of species were allowed to be broader than reflected in their current distributions, then predictions were much more sanguine. In other cases, range underfilling can actually have the opposite effect on our predictions. Specifically, we may underpredict extinction risk if we fail to account for some species being excluded from high latitude or high elevation areas by nonclimatic factors. This is because these species will experience range compression as low latitude/elevation areas become unsuitably hot, but nonclimatic limitations continue to prevent the species from migrating upslope/poleward as would be predicted under simple distribution models (Feeley and Silman, 2010b). Finally, if range underfilling is driven by species interactions, then the emergence of novel communities will have complex and largely unpredictable effects—in some cases allowing species to fill greater proportions of their potential ranges and in other cases leading to greater range restrictions.

Assumption 2. There is no local adaptation. Most models predicting the impacts of climate change on species’ distributions ignore the potential for local adaptation. Indeed, most models implicitly assume that the climatic tolerances of a species’ different populations are all the same as for the species as a whole. Contrary to this assumption,
many species exhibit strong local adaptation. With local adaptation, the range of conditions under which individuals from any given population can occur will always be a subset of the climatic tolerances of the entire species.  

The potential for local adaptation will clearly have important implications for predicting how species will fare in the face of climate change. In essence, if local adaptation is strong, then different conspecific populations will need to be treated as independent “species-like” units in modeling studies. Since these populations will always have narrower climatic tolerances than the entire species, future climates will more rapidly become “unsuitable”, thereby more often requiring adaptive or migratory responses if the populations are to avoid extinction. The elevated risk of extinction for populations will result in elevated risk of species-level extinctions, or at the very least, risk of genetic diversity loss (Hampe and Petit, 2005; Jump and Peñuelas, 2005; Sork et al., 2010).  

Moving forward. To move beyond these crass assumptions and to better understand how species will respond to climate change, we need additional data on where species currently occur and under what conditions (i.e., species’ realized ranges and niches), species’ physiological limitations to climate and other environmental factors (i.e., their fundamental niches), and how these tolerances vary in relation to the environment and pedigree (i.e., phenotypic plasticity and local adaptation). This is not easy and will require new hard-won data for many groups of species that are currently only poorly represented in the scientific literature and databases. The impediments to advancing our understanding of species’ current and future distributions are especially strong in tropics where diversity is the greatest, data are often sparse or nonexistent, and logistical constraints can limit our ability to collect new data.  

The rapid increase in open-access online databases has greatly expanded our ability to model species’ distributions and niches. That said, many species remain unidentified or understudied (Feeley and Silman, 2011) so ongoing data collection campaigns remain of high value; in other words, we are still very far from overcoming either the Linnean or the Wallacean shortfall (Lomolino, 2004). Furthermore, experiments are required to help understand species’ fundamental tolerances and their ability to acclimate or adapt to changing conditions (Feeley et al., 2012b). For example, growth chamber, common garden, and transplant experiments can all be used to look at physiological constraints, intraspecific variation, and strength of local adaptation. Controlled experiments are not feasible for many species due to their large stature, long generation times, lack of funding, etc. For some of these species, we may be able to exploit uncontrolled experiments such as those offered by the occurrence of individuals outside their natural ranges as exotics or invasives, in botanical gardens, or in nursery settings (Early and Sax, 2014). Studies of species’ tolerances also need to explicitly consider the impacts of species interactions (e.g., Trainor et al., 2014) and be augmented with information about intra- and interspecific genetic and functional variation. In other words, we need to adopt an “all hands on deck” approach in which disparate forms of information are integrated to generate a more complete understanding of the factors limiting species’ distributions and their potential to respond to changing climates.
approach is only possible through large-scale, open-access, cooperative endeavors. We are faced with a global-scale challenge, and we must respond as a global community of scientists.

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