Bio 112 Literature Review Paper
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On The Defining Factors of Species Ranges

Grinnell's Classic Paper and Its Influence on Ecology

In 1914, Joseph Grinnell wrote a paper titled "Barriers to distribution as regards birds and mammals." In it, he set a foundation for the modern field of *biogeography*, which is the study of species distributions and the biotic and abiotic factors that control them. Grinnell identified the most obvious factors as mechanical barriers like land or bodies of water that become increasingly impassable with increased width. However, he also mentions "intangible" barriers that are just as important—certain climatic features like temperature, and the availability of food and breeding grounds. Individuals can temporarily transgress such boundaries without immediate harm, making "intangible" barriers fuzzier in nature, and more difficult to understand.

These were not entirely new ideas. In 1807 von Humboldt described latitudinal and altitudinal distributions of vegetative zones, and created interest for further study by showing how temperature strongly affected species distributions. In his Origin of Species, Darwin (1859) thought that distributions were controlled by some kind of interplay between interspecific interactions and the abiotic environment. Merriam (1898) described the life zones and crop zones of the United States, again implicating temperature as an important distribution-controlling factor. However, it wasn't until 1917 when biogeography took an important turn from being a largely observational science to a more experimental one.

In that year, Grinnell followed up on his 1914 work with a paper entitled "Field tests of theories concerning distributional control." Once again he argued that temperature was the most frequent limiter of distribution, though he added that humidity, food supply, and shelter were also strongly important. However, this was not why this paper had a greater impact on later ecological research than his mostly overlooked 1914 paper. This time, he emphasized the validity of field research and pushed for more. Grinnell argued that when studying distributional control factors, data obtained from the field could be used to obtain results similar to and just as conclusive as data obtained in the lab. This gave a big push for the field ecology studies necessary for the further development of biogeography. By getting ecologists out into the field to collect data, they were able to gain important and otherwise unobtainable insights into the landscape and climatic controls of distributions.

In later years, field work continued to be essential to the refinement of Grinnell's ideas. Whittaker (1956), through his work in the Great Smoky Mountains, recognized that the distribution of plant species varied across different environmental gradients. He and Curtis (1959) each developed a different gradient analysis method to explore how species composition in an area and environmental factors were related. In 1967, MacArthur and Wilson wrote *The Theory of Island Biogeography*, a book that remains influential today. By studying various islands, they were able to propose that island area and distance from mainland populations combined to regulate immigration and extinction in island populations. They hoped their book would stimulate new kinds of theoretical and empirical studies, to advance biogeography beyond the data collection phase they believed it was stuck in prior to 1967.

New studies were indeed done, but data collection was just beginning with the 1972 launch of the first LANDSAT satellite. Ecologists were able to move beyond field work to conduct previously impossible large-scale landscape studies, now that the ranges of thousands of kilometers of forests and grasslands, and in later years, even those of individual plant species, could be mapped all at once. In the last decade, remote sensing coupled with GIS have been heavily used for visualizing range limits at large scales, and to study the environmental factors controlling them (Bauer and Peterson 2005). However, remote sensing is not very useful for studying biotic factors that control species ranges, so field work continues to be crucial.

As a result of the research that stemmed from Grinnell's work, ecologists have identified three groups of distribution-controlling factors: abiotic (climate, topography, soil type), biotic (population dynamics, interspecific interactions like competition and predation, and metapopulation dynamics), and most recently, anthropogenic (human land use causing environmental change, and climate change).

Current Areas of Research, and Their Development Over Time

Four important areas of research, each stemming from Grinnell's work, involve investigating how species distributions will be affected by 1) climate change, 2) species interactions, 3) metapopulation dynamics, and 4) ecological processes generated by landscape patterns, an important focus of landscape ecology. Since the actions resulting from these factors are so complex, modeling has become an indispensable investigational tool in biogeography. An influential paper by Peterson (2001) on predicting species distributions with ecological niche modeling cited Grinnell directly, again demonstrating the importance of his work.

1. Climate Change Effects on Species Distributions

Grinnell cited temperature, humidity, and food availability as major factors controlling the distributions of birds and mammals. Unfortunately, these all have the potential to change in many places due to climate change. Research on how climate change will affect species distributions is relatively new, since only recently have all the computational tools, models, data, and motivation come together to make investigations of this question possible.

Bird species are one group of animals whose distributions may dramatically change due to climate change. Back in 1988, Root described environmental factors associated with the boundaries of bird species. It would seem that birds, because they can fly to new places, would be unaffected by environmental factors that limit land animal distributions. However, despite being capable of flying great distances, many birds do not, and thus remain susceptible to local and regional changes in climate. Even migratory birds cannot escape climate change. Root's paper was cited 98 times—Crick (2004) cited him when describing the negative impact of climate change on birds, and Lee and Rotenberry (2005) also cited Root's paper when describing how bird distributions strongly correlate with distributions of certain tree species in eastern North American forests. This indicates a habitat dependence—if trees shift their distributions due to climate change, bird distributions must likewise change. Iverson et al. (1998, 1999) used models to predict dramatic climate change-driven shifts for many of 80 eastern US tree species in the coming century, but interestingly, some birds have already begun to shift their winter distributions due to global warming and local habitat changes (Valiela and Brown 2003).

The advent of powerful statistical techniques and GIS tools have made possible the development of numerous models for predicting species distributions. Guisan and Zimmermann (2000) wrote an influential review, cited 254 times, that described the various types of statistical models then available. These were ordinary multiple regression, generalized linear models, ordination and classification methods, Bayesian models, environmental envelopes, neural networks, and various combinations of the above, all of which are still used today (Guisan and Thuiller 2005). Unfortunately, Guisan and Zimmermann point out that these models are all "static and probabilistic in nature," only able to relate the "geographic distribution of species or communities to their present environment." This leaves us to question how well these static models can predict future species distributions in a world facing unprecedented environmental changes. Only very recently has there been a focus on optimizing predictions of species distributions by evaluating the models used (Thuiller 2003, Segurado and Araújo 2004).

2. Species Interactions Define Distributions

One of Grinnell's "intangible" factors that defined species borders has already been identified as environmental gradients. Another important one is species interactions, first described by Darwin (1859), who thought an interplay between interspecific interactions and the abiotic environment was responsible for determining species ranges. Later, Haldane (1956) described how range limits could be determined intraspecifically by gene flow. He argued that the few individuals locally adapted to conditions on the periphery of the range would be routinely overwhelmed by gene flow from the many individuals at the core of the range, thus erasing the adaptations that would allow the species to expand its range.

In 1989, Oksanen and Oksanen described natural grazing as an interspecific interaction defining the ranges of plant species. Their paper was cited by Manseau et al. (1996), which found that caribou grazing and trampling affects vegetation composition and productivity. Since changes in composition and productivity affect habitat quality for a number of animal species, herbivory can thus limit animal species distributions. This paper was cited 39 times since then, due to the interest it created in herbivory as a range-defining mechanism.

However, it wasn't until 2000 in a well-cited paper by Case and Taper that both interspecific interactions and gene flow, combined with environmental gradients, were all shown to work together to define species borders. Biogeography had to await the development of suitable models and simulations before over 100 years of research on the nature and workings of these "intangible" species interactions could be brought together.

3. Fuzzy Range Boundaries From Metapopulation Dynamics

A metapopulation is a group of populations constantly immigrating to and emigrating from habitat patches within dispersal distance. Interestingly, their dynamics can give rise to species range boundaries where gradual environmental gradients like slope or moisture exist (Lennon et al. 1997). Unlike the sharp boundaries created by water and non-traversable landforms, these boundaries are fuzzy like those Grinnell had described as resulting from "intangible" factors.

The landscape model of metapopulation dynamics defines the landscape as a set of habitat patches varying in quality, surrounded by a spatially heterogeneous habitat matrix providing varying levels of resistance to dispersal. Thus, species distribution can be limited if some patches are more difficult to reach than others. We see this in Wolff (1981), which described the effects of habitat patchiness on the population dynamics of snowshoe hares, and Franken and Hik (2004), which described how habitat quality, patch size, and patch connectivity influenced the colonization and extinction dynamics of collared pikas. In both cases we have landscape patterns that affect metapopulation dynamics, thus indirectly affecting species distributions.

4. Landscape Ecology:
spatial patterns -> ecological processes -> definition of species ranges

Landscape ecology is the study of how spatial patterns affect ecological processes over space and time, and vice versa. In the previous section we saw that spatial patterns can define species ranges, making landscape ecology very closely allied with biogeography. Several highly influential papers have been written on the hot topic of pattern and process—Urban et al. (1987) with 269 citations, Wiens et al. (1993) with 351 citations, and Turner (1989), with an incredible 539 citations. Ideas from this field have permeated most ecological disciplines, and will become increasingly important in the future as we study how our continued large-scale alteration of landscape patterns will disrupt ecological processes and alter species distributions.

Turner's paper, "Landscape Ecology – The Effect of Pattern on Process," is one of the classic papers of landscape ecology. Like Grinnell, Turner wasn't the first to come up with the pattern-process idea, but her paper was pivotal because it summarized much previous thinking on the subject, and presented ideas for new research. A. S. Watt had already described pattern and process in plant communities back in 1947. In 1979, Hansson described the importance of landscape heterogeneity (pattern) in determining the population densities of breeding mammals (process). Pattern and process showed up again in 1988, when Fahrig and Paloheimo wrote that the spatial arrangement of habitat patches affects population size. These important experimental papers were all cited in Turner's 1989 review. This year, due to the rapid advances in landscape ecology in the past decade, she published a new synopsis of landscape ecology that describes its history, how far it has come, and where future research will likely be headed (Turner 2005).

Future Research Directions

Almost all research in this area prior to the past ten years has focused on factors that define species' geographic ranges. While this is still the case, the past ten years has seen a growing focus on how future species ranges will be altered due to changes in environmental and climatic factors. Researchers want to know if these ranges will shrink, grow, migrate large distances, and if so, how quickly? What factors will control these shifts in species ranges? What effects might they have on community composition and biodiversity? What can we do to help species migrate more quickly to avoid extinction? What effects might these shifts have on human life? These questions can be explored with models, but they need to incorporate dynamic instead of static variables to account for environmental and climatic changes.

Additionally, there has been a long thread of research focusing on the relationship between species diversity and latitude, which will likely see renewed importance due to the rapid rates of deforestation in tropical biodiversity hotspots (Fischer 1959, Pianka 1966, Sax 2001). We have long known that greater diversity exists in the tropics than at the poles, in part because many tropical species have smaller ranges than those at higher latitudes. What factors maintain these small species ranges? Physical factors like topography, soil type, and climate do not vary much over the small scales of these species ranges, so their ranges must be limited by biological factors. Future research will likely explore how competition, predator-prey dynamics, and metapopulation dynamics might be important in managing for biodiversity.

Conclusion

In 2004, Belovsky et al. wrote ten suggestions to strengthen the science of ecology. The second said ecologists should do more back-researching to avoid repeating ideas that had already been developed in the past. Grinnell's paper might seem to be a case in point, since many of the factors he described as being important to defining species distributions appear over and over again in modern research. However, the academic history of biogeography has been far from a constant reinvention of the wheel. Rather, like any science, it has been a gradual refinement of old ideas. Darwin had some early ideas about biogeography, but Grinnell went a step further by describing them and showing that theories of how species distributions are controlled could be tested in the field. Because of his work, we now know and understand so much more about the factors that define species ranges than we did in 1914. The body of knowledge that began with Grinnell will serve us well in the near future, as we try to predict how human activities will alter future species distributions and what the ecological ramifications might be.

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