

PREDICTING BIODIVERSITY CHANGE: OUTSIDE THE CLIMATE ENVELOPE, BEYOND THE SPECIES–AREA CURVE

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Abstract. Efforts to anticipate threats to biodiversity take the form of species richness predictions (SRPs) based on simple correlations with current climate and habitat area. We review the major approaches that have been used for SRP, species–area curves and climate envelopes, and suggest that alternative research efforts may provide more understanding and guidance for management. Extinction prediction suffers from a number of limitations related to data and the novelty of future environments. We suggest additional attention to (1) identification of variables related to biodiversity that are diagnostic and potentially more predictable than extinction, (2) constraints on species dispersal and reproduction that will determine population persistence and range shifts, including limited sources or potential immigrants for many regions, and (3) changes in biotic interactions and phenology. We suggest combinations of observational and experimental approaches within a framework available for ingesting heterogeneous data sources. Together, these recommendations amount to a shift in emphasis from prediction of extinction numbers to identification of vulnerabilities and leading indicators of change, as well as suggestions for surveillance tools needed to evaluate important variables and the experiments likely to provide most insight.

Key words: biodiversity; climate change; climate envelopes; limited source; species–area curves; species–area prediction.

INTRODUCTION

Research on future threats to diversity has focused on predicting extinctions that will result from climate change and habitat loss (e.g., Davis and Zabinski 1992, Walker and Steffen 1996). Species richness prediction (SRP) attempts to summarize complex responses to global change in terms of numbers of extinctions. The most widely used SRP approaches involve methods developed independently to understand the consequences of climate change and habitat loss, i.e., climate envelopes and species–area relationships, respectively.

The challenges of SRP are especially evident at the regional scale. For example, like much of the globe, climate in the southeastern United States is expected to change dramatically. By mid-century, we can expect changes as extreme as a mean annual temperature increase of 1–7°C, a 30% decrease in summer precipitation, and a 25% increase in spring rainfall (Mearns et al. 2003). Increased aridity could result in a dramatic shift from temperate deciduous forest to southern mixed forest or even savanna, with increased importance of

species from lower latitudes and elevations (Bachelet et al. 2001).

Responses to global warming will be superimposed on complex landscapes. Three major subregions in the southeastern United States, the Coastal Plain, Piedmont, and Southern Appalachians, not only possess distinct climates, but they are also characterized by contrasting topography and soil parent material. The southeastern Piedmont could become too arid for Virginia pine (*Pinus virginiana*), and possibly even for loblolly and shortleaf pines (*P. taeda* and *P. echinata*). On the basis of climate relationships, the plant species predicted to expand in the Piedmont, such as longleaf pine (*Pinus palustris*), currently occupy lower latitudes and elevations of the Coastal Plain (Iverson et al. 1999; Fig. 1). However, Coastal Plain soils are dominated by sand and peat, with low nitrogen availability, high water tables, and historically high fire frequency (Christensen 2000). Species adapted to these conditions may not thrive on the clay-rich soils of the Piedmont. Clearly, a simple pole-ward shift in climate envelopes is not likely to provide useful predictions of future diversity in this region. Instead, the southeastern United States may see a combination of climate, soil, and land cover changes best suited to species that are not currently in the region. Uncertainty associated with the source of future occupants suggests that ecosystem function may differ in ways that are not captured by approaches now in use

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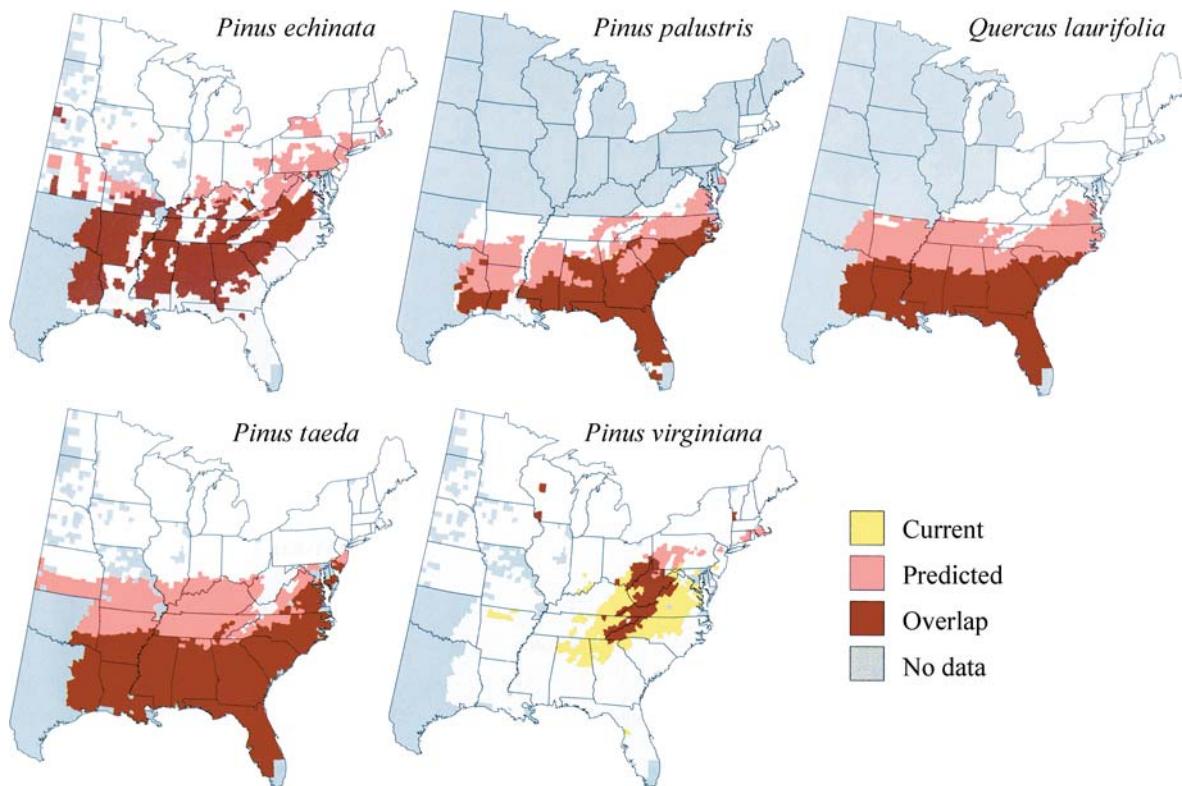


FIG. 1. These maps represent potential shifts in suitable habitat of four species of southeastern U.S. pines (from Iverson et al. 1999). Also detectable is the potential shift of laurel oak, *Quercus laurifolia*. For this species, January temperature is the major environmental variable affecting its migration northward (Iverson et al. 1999).

for SRP. This region illustrates the challenges faced by ecologists globally. Can we anticipate the redistribution of species and the composition of communities at regional and local scales under plausible climate scenarios?

Well-recognized limitations of SRP techniques are related to the empirical nature of such correlative methods and their application to novel and uncertain settings. Moreover, many factors shaping biodiversity tend to be omitted from SRP efforts. Physical geography and land use patterns will conspire to restrict the potential ranges of many species. Future migrations are likely to differ from past patterns, with fragmentation demanding new modes of dispersal for some species, while facilitating the passage of others (Malanson and Cairns 1997, Collingham and Huntley 2000). For habitat loss, a regression of number of species against habitat area is commonly used to predict extinctions; however, the regressions are usually not parameterized at a scale or in a setting appropriate for their application to future climate and land use conditions. Despite its potentially severe limitations, SRP has become one of the most visible applications of ecological understanding to global change research (Sala et al. 2001).

In addition, changes in biodiversity will imply more than just a decline in number of species. Biodiversity

losses may deeply affect ecosystem functioning (Loreau et al. 2001, Kinzig et al. 2002). Changes in biodiversity have the potential to impact productivity (Naeem et al. 1996, Tilman et al. 2001). Higher diversity has been connected to higher resistance to invasions (Rejmánek 1996). And, diversity may ensure stability under environmental fluctuations (Peterson et al. 1998). Thus, merely predicting numbers of extinctions will not provide much insight on ecosystem response to species losses.

Here we consider how ecological research is used to anticipate potential change in biodiversity. Several recent synthetic efforts to identify the direction and application of ecological research have begun to reshape priorities (National Research Council 2001). While a number of the recommendations from these efforts bear directly on biodiversity assessment and prediction, we believe that several specific issues related to how we approach biodiversity change could benefit from additional consideration. First, we outline reasons to question the emerging prominence of SRP, especially the limitations of climate envelopes and species-area approaches. We suggest that not only do climate and habitat area play indirect roles in the contemporary extinctions, but they also are not good surrogates for the combination of factors that will place species at risk in the future. We suggest that the next steps may involve

increased emphasis on specific processes, and the use of emerging methods for better exploiting information that is already available. We revisit several factors still needing better understanding, including (1) identification of variables related to biodiversity that are diagnostic and potentially more predictable than extinction, (2) constraints on species dispersal and reproduction that will determine population persistence and range shifts (including identification of limited sources of potential immigrants for many regions, and (3) changes in biotic interactions and phenology. “Limited sources” for diversity exist in regions where changing climate will select for combinations of characteristics not possessed by species that currently reside within migration distance.

THE PRACTICE OF SPECIES RICHNESS PREDICTION

Most species richness prediction (SRP) efforts focus on the number of species that will survive under climate change, habitat loss, or both. The ability to predict extinctions or species richness under these scenarios appeals to both scientific and pragmatic needs. Rough estimates of species richness help to identify the regions where threats are large: they help to communicate comparative risks for different taxonomic and functional groups and to identify critical drivers of diversity. However, number of extinctions may be neither the most reliable nor the most important variable to predict. In the next four sections, we summarize the two most popular SRP approaches (species–area relationships and climate envelopes), we provide examples where they can be misleading for a large, diverse region (the eastern United States), and we offer reasons why it is important to move ahead with other aspects of biodiversity research.

The use of species–area relationships

Ecologists have long known that species richness tends to increase with sample area and with habitat area (e.g., Gleason 1925). Preston (1960) proposed the power function in common use today, $S_j = cA_j^z$, where S_j is the number of species at location j , A_j is the area represented by the sample, and c and z are parameters. Much attention has been focused on z , the fractional change in S for a fractional change in A , $z = (d \log S)/(d \log A)$.

While the general pattern of increased species richness with area is widely accepted, the causes are still debated, as is the application for SRP in the context of future habitat loss. Many recent studies apply species–area relationships to endemic species only, as species occurring outside the fragmented area could presumably reinvade. Regressions are sometimes based on sampled area and other times based on the area of habitats. The value of z is often taken to be 0.25, although different sampling strategies and settings yield z values from 0.12 to 1 (Rosenzweig 2003). While many studies use species–area relationships to predict extinction over time following habitat loss, the relationship does not

incorporate changes that often accompany habitat loss or fragmentation and that can affect rates of species loss (Brashares et al. 2001). In summary, as discussed with examples below, species–area relationships have substantial and widely recognized limitations. Following a brief overview of climate envelopes, we discuss additional concerns with this method when it is combined with climate envelopes.

The use of climate envelopes

One of the most common methods for predicting species responses to climate change involves drawing an “envelope” around the domain of climate variables where a species is found today and then identifying regions predicted to fall within that domain under scenarios for the future. These future envelopes are taken to be the predicted species ranges (e.g., Fleishman et al. 2001, Lasch et al. 2002). Predicting species richness would require mapping such ranges for all species and is therefore typically restricted to groups for which data are deemed sufficient. The climate envelope can be determined in a number of ways, including simple regression (Huntley et al. 1995), distance-based methods (Carey 1996), genetic algorithms for rule-set prediction (GARP; Peterson and Cohoon 1999), and neural nets (Pearson et al. 2002). Variations on this theme can include other covariates related to the species “niche” (Peterson et al. 2003, Thuiller 2004). The assumptions regarding how species might move from the current to the predicted envelope range from no dispersal, in which case the species goes extinct in those parts of the current range that do not overlap with the future envelope (Midgley et al. 2002), to limited dispersal (Kirilenko and Solomon 1998), to unlimited dispersal, where the new envelope equals the new range (Thomas et al. 2004).

Limitations of climate-envelope-based predictions are well known, including the treatment of the realized niche as though it were the fundamental niche (Pacala and Hurtt 1993, Pearson and Dawson 2003). The control of climate over distributions is often highly indirect. Dispersal in novel climate and land cover is poorly understood and complicated by changing dispersal vectors. Elevated atmospheric CO₂ may change reproductive effort (Fischer et al. 1997, LaDeau and Clark 2001), and thus have a large impact on migration potential (Clark et al. 2001, 2003). Invading species may be faced with Allee effects, which slow the rate of spread (Veit and Lewis 1996), and accelerate decline when densities are low or mutualistic relationships, such as pollination, are disrupted (Hughes 2000). Human demographics, economic trends, and associated habitat degradation will combine with biotic interactions and new climate–soil combinations to affect migration routes and the suitability of sites for future species ranges. These interactions limit the predictive capacity of correlations based on the current realized niche.

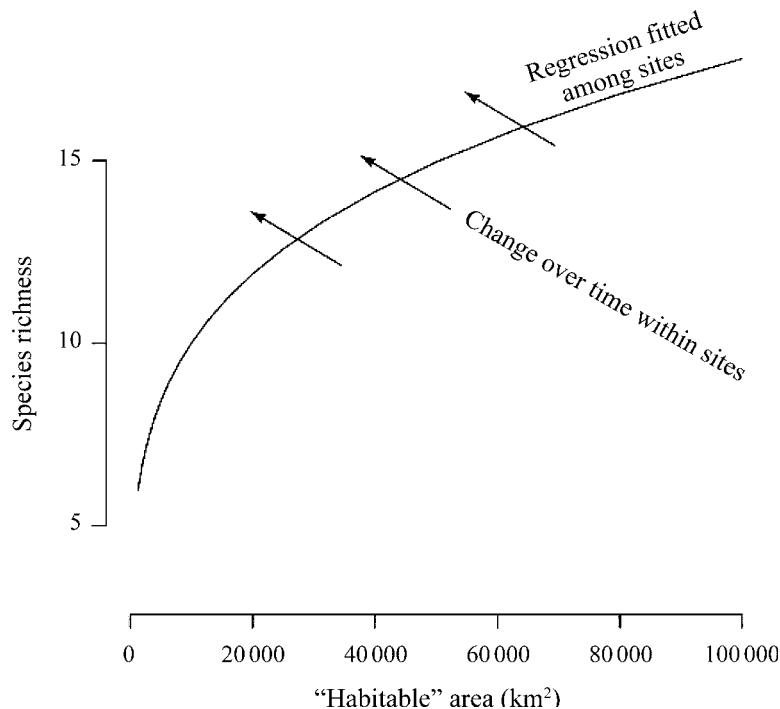


FIG. 2. Species–area curve showing incompatible reference for inference of change within a site based on relationships among sites. In principle, we could have an increasing relationship between richness and area among habitats, while having a decreasing relationship within sites.

Combining species–area relationships and climate envelopes

The correlative nature of species–area relationships and climate envelopes remains problematic when they are used in combination. Species–area relationships correlate area and species richness; climate envelopes correlate climate variables and the ranges of individual species. To combine these influences, Thomas et al. (2004) adapted the species–area relationship to the extinction risk of groups of endemic species occupying a region. In general, the approach consists of predicting the climate envelope under a climate change scenario, determining its area, and using the species–area relationship to estimate extinction risk. If the climate envelope expands, and the population can migrate to the new range, then no risk is assumed. If it contracts, some variation of the species–area regression is applied to a single species.

The correlation methods involved in climate envelopes and species–area curves usually predict at one scale (change within a site and risk for one species) based on data collected at another scale (differences among sites and changes in number of species). With its translation from relationships between plots, islands, habitats, or regions to inference and prediction to change within plots, islands, habitats, or regions, SRP embraces the scale-dependent problem that arises when relationships from aggregate data are applied to individuals (Cressie 1993, Clark 2003), and also from applications of

estimates taken from, say, birds to stream invertebrates. For a hypothetical example, consider a pattern of increasing richness with area among sites, where fragmentation increases diversity by attracting edge species (Fig. 2). Change in species within a site does the opposite of what we would conclude from the pattern we infer by looking across sites. Of course, many SRPs are restricted to endemic species, which, by definition, means that diversity can only decline with reduced habitat area. This has implications for hypothesis testing that we do not take up here. We include this hypothetical example because it illustrated an extreme, yet plausible, error that comes when inference and prediction for one scale (within habitats) are based on relationships at another scale (across habitats), the predicted change is not based on information about change.

Some examples from the eastern United States

Documented extinctions and range shifts over the last two centuries in Eastern North America illustrate problems with the assumptions behind SRP. The peak of land clearance in the eastern United States was reached in the mid-19th century, when 50% of forests (Pimm et al. 1995) were cleared for agriculture, forest products, and urbanization. In simplest terms, a z value of 0.25 would predict a loss of 16% of forest species and a 33–68% loss of tallgrass prairie species. Yet actual extinctions are not consistent with such simple relation-



PLATE 1. The North Carolina Southern Appalachians is a region of great diversity and high levels of endemic species. Photo credit: I. Ibáñez.

ships. Extinctions of endemic vascular plants in the eastern United States are $\sim 4\%$ (Stein et al. 2000). Remarkably high levels of endemism in the Southern Appalachians (see Plate 1) and the Coastal Plain can be attributed to geological history, and many species that are narrowly restricted to specific habitats, such as rocky outcrops and bogs (Stein et al. 2000). Despite extensive land conversion in the southeastern United States, these rare habitats have escaped alteration and permit a disproportionate number of species to persist relative to the area of the habitats. Even with widespread loss of tallgrass prairie, most of the native plant species are extant. The threats to prairie biodiversity that come with habitat loss are related to individual patch size, edges, and the surrounding matrix, and how those effects vary among species (Reis and Debinski 2001). The impacts of land conversion are not captured by species–area relationships, which would predict far too much extinction, while failing to illuminate the actual threats, which come from combinations of habitat changes that affect reproductive capacity, movement, and animal behavior (Haddad 1999).

The amount of forest habitat lost did not predict the number of bird extinctions in eastern North America, unless only endemic species were considered, in which case numbers of extinctions were higher than those predicted only on the basis of habitat loss (Pimm and Askins 1995). Recent mammal extinctions are linked to causes other than habitat loss, such as overgrazing by

domestic animals (which may or may not constitute “habitat loss”) and the introduction of feral species that act as predators or competitors (Lunney 2001, Mellink et al. 2002).

The southeastern United States hosts an unusually diverse assemblage of freshwater mollusks that are rapidly going extinct due to human pressures. In Alabama alone, 31 of 147 (21.1%) species of freshwater snails and 11 of 171 (6.4%) of freshwater mussels are considered extinct, while an additional 43.5% and 42.7%, respectively, are classified as either threatened or endangered (Lydeard and Mayden 1995). These extinctions are generally not attributable to changes in habitat area but rather to specific alterations caused by damming, channel modifications, siltation, pollution, and interactions involving introduced species (Lydeard and Mayden 1995). Similarly, a global assessment of amphibian declines does not recommend application of a species–area or climate envelope approaches. Many recent declines are related to habitat degradation, disease, direct exploitation, or are of unknown cause (Stuart et al. 2004). Many of the enigmatic declines occur in protected areas, not subject to land-cover change. Disease and exotic predators are implicated for some.

Of course, many of the concerns with SRP mentioned in this section have been raised before. Despite such concerns, SRP may now be having a disproportionate influence on the science and policy of global change as

compared to other ecological research (Pipkin 1996). The threats to biodiversity are grave, they are poorly described by SRPs, and they can be better understood by shifting the focus of research and how it is applied to future prospects.

SHIFTING THE RESEARCH FOCUS

It may be time to move beyond SRP and the traditional correlation approaches used for these predictions. We believe that future efforts will place more emphasis on process, and they will benefit from methods that permit more efficient exploitation of information than has been possible in the past. Here we summarize several opportunities and key processes needing specific attention. Some of these issues, including reproduction and dispersal, the consequences of phenological imbalances, and physical barriers to species migrations, have already been the subject of important empirical research, synthesis, or both. Other important issues, such as the constraints imposed by the absence of potential sources of colonizing species, have received relatively little attention.

A broader view of impacts

The focus of SRP on extinction may represent an inefficient use of resources. Despite its appeal as a forceful communication tool concerning ecosystem health and irreversible impacts, ecologists are less prepared to predict extinction than a number of other important variables. Predictions of extinction time are highly sensitive to parameter uncertainty (Ludwig 1999, Ellner 2003). The relationships that affect extinction risk are inherently difficult to estimate, because they occur in populations at low densities. Parameter estimates for demographic rates obtained at moderate densities are not expected to apply to populations nearing extinction, for example, due to Allee effects. Population heterogeneity has an even larger effect on predictions of population growth than does parameter uncertainty (Clark 2003, Cam et al. 2002). Almost no consideration has been given to model uncertainty, which is especially relevant, because the models for which parameters are estimated today have context that may not directly apply to a novel future (Clark et al. 2001, Peterson et al. 2003).

Although plausible extinction predictions are not yet feasible, ecologists are in the position to provide deeper insight into potential consequences of global change on biodiversity. This will include not only new technology to extend the list of variables that can be observed at appropriate scales, but also developing models to more fully exploit information that is already available, but hard to assimilate. For example, information on variables that affect community composition, such as weather, climate, and landscape configuration, are indirectly assimilated in ecosystem models. Statistical computation methods that have emerged over the last decade provide opportunities to accommodate relation-

ships between biodiversity and the weather, climate, and land cover variables that control it. A growing number of applications to ecology show that variability in population change over time is complex and not easily summarized by an extinction time. Modern methods of inference have helped identify the challenges and address the complexities (Clark 2005). For example, Ver Hoef and Frost (2003) developed a high-dimensional model to determine change in harbor seal abundance over 10 years at 25 locations in Prince William Sound, accommodating the errors in aerial survey counts and the heterogeneity in trends among sites over time. It should be no surprise to ecologists that population growth trends varied among sites from positive to negative, a result highly relevant to predictions of population risk and one that is not captured by a low-dimensional model that ignores the sources of variability and uncertainty. Stage-structured models that accommodate life history show similar heterogeneity in population growth for common terns on coastal Long Island and furry rats in Kenya's Taitu Hills (Clark et al. 2005). The manager needs this understanding of heterogeneity to assess current population trends and to anticipate the complexity of potential future responses. Population variability in space, over time, and among individuals and groups contributes to population risk, but has not been tractable with traditional modeling approaches.

The growing number of applications can broaden our understanding of how to ingest large, disparate data sets that show variability in populations dispersed over complex landscapes. Of course, one can take the results of such studies as the basis for forward simulations of extinction times, but those predictions may not be the most important application. The understanding of the heterogeneity of responses to climate and land-cover change could provide far more tangible guidance for management than SRPs. Such understanding can be applied to identification of risks, vulnerabilities, and leading indicators of change, quantification of the factors that affect risk, definition of early warning systems, and recommendation of where and when surveillance tools are needed for which variables and the experiments likely to provide most insight. In the next few sections, we highlight some aspects of population health of particular concern.

Species differences in dispersal and reproduction

Vegetation models suggest that current climate trends may require much faster rates of spread than those observed in the past, and as a consequence, many species will be at risk (Malcolm et al. 2002). How can we hope to understand constraints on decade- and continent-scale migratory potential based on observations that are short term and local?

Modeling and field data can help identify the key variables and provide a basis for evaluating predictive capacity. In the absence of other evidence, models of vegetation change parameterize dispersal to reproduce

high migration rates interpreted from the paleorecord (e.g., Dyer 1995, Collingham et al. 1996). Such parameterizations yield “optimistic” predictions that migration potential is high (Pitelka et al. 1997, Clark 1998). An example from our own research involves methods for combining observations of dispersal and fecundity with migration models and suggests (1) that Holocene tree migration rates may have been slower than we previously thought and (2) that life history differences should have more impact (Clark et al. 2001). Subsequently, molecular evidence and fossil records from North American populations has supported the interpretation of slower spread (e.g., Jackson et al. 1997, McLachlan et al. 2005; but see alternative interpretations of similar data from Europe [Petit et al. 1997]). When applied to contemporary climate change, the developing evidence suggests that many species will face migration challenges (Clark et al. 2001, 2003). For anticipating future risks, it will be important to identify when and how dispersal is likely to play a role.

Understanding processes can suggest changes in research directions. The analyses of Clark et al. (2001, 2003) indicated that recent emphasis on dispersal has overshadowed the important contribution of reproductive capacity. In fact, the two are much more synergistic than traditional models suggest. Fecundity is often overlooked, because traditional diffusion models underestimate the importance of reproduction. With rare, long-distance dispersal events, the rate of spread becomes much more sensitive to fecundity. Moreover, fecundity can be predictable, whereas specific distances traveled during extreme dispersal events that have yet occur cannot (Clark et al. 2001, 2003).

Observational and experimental research can help us understand survival and fecundity under climate and land cover settings projected for the future. How do demographic rates respond to increased temperature, moisture, and heat stress? Combinations of modeling and observational data may help us learn whether declining populations at the “back edge” of the species range can affect progress at the leading edge, as suggested by models demonstrating the importance of growth rate from the leading edge of expansion (e.g., Kot et al. 2004.). What are the environmental settings that lend themselves to effective dispersal (Nathan et al. 2000)? New environments may provide recruitment opportunities that differ from those of the current range, in which case, parameter estimates from here and now may not apply to migration in the future. What is the role of human activity and landscape fragmentation on dispersal? Spread predictions will be complicated further more by the fact that species dispersal is going to be affected by humans. Natural dispersal patterns will be shaped by landscape fragmentation, and human activity will inadvertently or purposefully contribute to some species dispersal. Despite a large literature on demographic rates of plants, there has been limited

effort to estimate rates in environments that may be important for future spread.

Such insight has direct application on contemporary climate change. For tree populations, these results indicate that species characteristic of late successional settings deserve attention. These species tend to have long generation times and limited fecundity. Fragmented habitats tend to be especially unfavorable for such species (Malanson and Carins 1997, Collingham and Huntley 2000). Such limitations are compounded by factors that have narrow connections to climate envelopes and habitat area. For example, the southeastern United States might lose its only two dominant late-successional species: Eastern hemlock (*Tsuga canadensis*), due to woolly adelgid (*Adelges tsugae*) infestations, and beech (*Fagus grandifolia*), due to beech bark disease (*Cryptococcus fagisuga*). Population growth and spread is already low for these species due to delayed maturation and limited fecundity in closed stands. Currently, these are the only long-lived species that consistently recruit in low-light forest understories. How might forests’ function change in the absence of such late successional species? Will new late successional species invade? Or will future forests simply lack this “functional group”? A preoccupation with traditional SRP models would ignore changes in ecosystem function and overlook the disappearance of slow-growing species.

Changes in biotic interactions

As already suggested in the last section, climate change leads to reorganized food webs, altering the interactions between long-lived plants and their herbivores, seed predators, and pathogens (Ayers and Lombardero 2000). Devastating consequences of pests related to global warming may already be upon us: mountain pine beetle (*Dendroctonus ponderosae*) outbreaks are moving north in British Columbia, Canada. Spruce beetles (*D. rufipennis*) have caused a record mortality, 90%, of spruce trees in the southern Kenai Peninsula of Alaska (Logan et al. 2003). New and intensified herbivore and pathogen pressures may add to the risks of already stressed plant species. Relationships between plants and associated fungal pathogens (Roy et al. 2004) and mycorrhizal mutualists (e.g., Heinemeyer et al. 2004) may also be altered and consequently affect plant populations. Clearly, we are not yet at the point where mechanistic understanding gained from experiments (e.g., Bais et al. 2003), can be used in a predictive fashion. Ultimately, limited alternates may cause us to rely more heavily on deeper understanding of mechanisms that can derive from studies that target mechanisms.

The potential complexity of climate–trophic relationships often calls for a regional perspective (e.g., Root and Schneider 1993). For example, on the basis of simple climate predictions for the southeastern United States, live and laurel oaks (*Quercus virginiana* and *Q. laurifolia*) of the Coastal Plain are potential immigrants

to the Piedmont. Their colonization of the region has been predicted under warmer climate scenarios (Iverson et al. 1999, Bachelet et al. 2001; Fig. 1). However, severe herbivore pressure may be among the factors currently limiting the regeneration of the once-dominant oaks in the Piedmont. Acorns are a preferred source of food for a large number of vertebrates (McShea and Schwede 1993). And oaks are heavily browsed by rapidly increasing deer populations (Bryant et al. 1980, Garrott et al. 1993). Herbivores and seed predators already feeding on native oaks could also adopt new hosts. Future experimental and modeling studies might address (1) how the migration patterns of predators, parasites, and microbial mutualists and pathogens can affect existing and novel prey and host species; (2) how migrating plant and animal species will respond to novel microbial communities; and (3) whether migrating species might experience a release from pathogen pressure, similar to those documented for invasive plants (Mitchell and Power 2003).

Changes in phenology

Under current trends in air temperature, species responding to changes in temperature, i.e., degree-days, are expected to alter their phenologies, the seasonal timing of biological events (fruiting, flowering, migration, reproduction). Phenological shifts may evolve in response to climate change, even at the time scale of a few decades (Berteaux et al. 2004, Davis et al. 2005). The magnitude of the response will be species specific (Woodward 1987, Bradley et al. 1999), with species having environmental cues that are weakly dependent on temperature being hardly affected. As a consequence relationships among species will be decoupled with unknown consequences that involve space, time, and trophic levels (Harrington et al. 1999, Visser and Holleman 2001).

Phenological shifts linked to climatic change have already been reported (i.e., Hughes 2000, Walther et al. 2002) and will become more significant in future decades. In Europe and North America, biological activities such as flowering, bird migrations, egg-laying, and the juvenile survival of large mammals are correlated with changes in winter climate and the earlier onset of spring (e.g., Bradley et al. 1999, Crick and Sparks 1999, Post and Stenseth 1999). Bird (Thomas and Lennon 1999) and butterfly (Parmesan et al. 1999) species are extending their ranges northwards in the northern hemisphere. Even if bird species are not directly affected by climate change, they may face redistribution of resources, nesting habitats, and migratory routes (Both and Visser 2001). Changes in bird migratory behavior will affect long-distance dispersal of some plant species and not others.

Temporal and spatial relationships among species and among trophic levels may be decoupled with unprecedented consequences (Harrington et al. 1999). For example, plant-pollinator associations will change with

flowering times (Hughes 2000). Effects on reproduction should affect migratory capability of many plant species. The important observational evidence of climate change effects highlights biotic interactions that are not captured by current SRP methods, but that clearly must be considered in projecting future ecosystem health. We see a contrast between the insight that is accumulating from these studies that target processes, and the relatively uninformative extinction predictions available from SRPs. Again, experimental and observational approaches aimed at understanding processes and variables that are vulnerable, may provide more guidance.

A "limited source" of future biodiversity

If climate change and habitat degradation make a region unfavorable for resident species, what is the source of species with the potential to colonize? A "limited source" for future biodiversity is relevant in many regions, where changing climate will select for combinations of characteristics that are not represented in the species pool that currently resides within migration reach. For example, forecasts for the end of this century in the southeastern United States include temperature increases of 5°C in winter and 5–10°C in summer and a precipitation decrease during the summer (Mearns et al. 2003). These conditions resemble current conditions in the Caribbean and Central America for January, but predicted July temperatures and precipitation that are more like deserts in southwestern North America. Where will colonizers come from if natives are unable to acclimate to this new climate?

If the available species pool is limited, we might place more emphasis on understanding adaptation potential, particularly genetic diversity within and among populations (Davis and Shaw 2001, Etterson and Shaw 2001, Davis et al. 2005). Species will encounter different soil conditions, as, for example, temperate species encounter young soils of glacial origin to the north or novel parent materials and terrain at higher elevation. Some terrestrial insect species may track a moving climate envelope, but face novel habitats (Coope 1994, Hill et al. 1999). We might also place greater emphasis on identifying the potential source of colonizing species. Transplant experiments constitute a promising line of research. Such studies move beyond the often intractable question of dispersal limitation and ask instead, if a species arrives, could it invade (Agenbad et al. 2004; I. Ibáñez, J. S. Clark, M. C. Dietze, *unpublished manuscript*). Using natural environmental gradients within a region, such as altitude, exposure, or soil types, performance of potential immigrant species can be assessed with respect to that of natives. This information is needed for models of vegetation change under future climate scenarios.

We still have only rudimentary understanding of establishment potential with climate change in human-dominated ecosystems. Questions about how to actively manage for biodiversity in the face of climate change

(Halpin 1997) will require an adaptive management approach (MacIver and Dallmeier 2000). Reclamation projects can be a source of insight (Robinson and Handel 2000), particularly if species used in reclamation anticipate potential shifts in range caused by climate change. Differences among populations in their adaptive capacity (e.g., Etterson 2004) in the face of changing conditions will play a role when determining the source of individuals used in restoration operations. The observations should inform both managers and scientists.

The limited pool of species available for colonization with climate change raises several management-relevant issues. Species with limited migration capacity or faced with barriers to dispersal may move with human assistance. Ethics and economics come into play, but they are not entirely new. Questions involving how and where to move species, in what density, and from what genetic stock, arise in restoration ecology (e.g., Maunder 1992). The proper target for restoration is not obvious if we are faced with communities that have no modern analog and are based on model predictions that are themselves uncertain. The target for restoration is itself expected to be dynamic as climate and land-cover change continues. This last concern is especially important for long-lived species, such as late successional trees, for which a 50–100 year climate scenario may be an inappropriate management timeframe, given that a viable reproductive population requires a century or more to establish.

CONCLUSIONS

The most productive efforts to understand future biodiversity will focus on emerging tools that allow us to exploit sources of information that already exist and collection of new data that target processes, species, and regions expected to be vulnerable to global change. SRPs have provided some valuable perspectives, but it is now time to go beyond predictions of extinctions based on species–area relationships and climate envelopes. Species differences related to dispersal and reproductive potential, potential shifts in biotic interactions and their timing, and the complex issues for regions having a limited source of future biodiversity all impress us as topics needing further attention.

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