

Novel climates, no-analog communities, and ecological surprises

John W Williams^{1*} and Stephen T Jackson²

No-analog communities (communities that are compositionally unlike any found today) occurred frequently in the past and will develop in the greenhouse world of the future. The well documented no-analog plant communities of late-glacial North America are closely linked to “novel” climates also lacking modern analogs, characterized by high seasonality of temperature. In climate simulations for the Intergovernmental Panel on Climate Change A2 and B1 emission scenarios, novel climates arise by 2100 AD, primarily in tropical and subtropical regions. These future novel climates are warmer than any present climates globally, with spatially variable shifts in precipitation, and increase the risk of species reshuffling into future no-analog communities and other ecological surprises. Most ecological models are at least partially parameterized from modern observations and so may fail to accurately predict ecological responses to these novel climates. There is an urgent need to test the robustness of ecological models to climate conditions outside modern experience.

Front Ecol Environ 2007; 5(9): 475–482, doi:10.1890/070037

How do you study an ecosystem no ecologist has ever seen? This is a problem for both paleoecologists and global-change ecologists, who seek to understand ecological systems for time periods outside the realm of modern observations. One group looks to the past and the other to the future, but both use our understanding of extant ecosystems and processes as a common starting point for scientific inference. This is familiar to paleoecologists as the principle of uniformitarianism (ie “the present is the key to the past”), whereby understanding modern processes aids interpretation of fossil records. Similarly, global-change ecologists apply a forward-projected form of uniformitarianism, using models based on present-day ecological patterns and processes to forecast ecological responses to future change. Thus, both paleoecology and global-change ecology are inextricably rooted in the current, and research into long-term ecological dynamics,

past or future, is heavily conditioned by our current observations and personal experience.

The further our explorations carry us from the present, the murkier our vision becomes. This is not just because fossil archives become sparser as we look deeper into the past, nor because the chains of future contingency become increasingly long. Rather, *the further we move from the present, the more it becomes an inadequate model for past and future system behavior*. The current state of the Earth system, and its constituent ecosystems, is just one of many possible states, and both past and future system states may differ fundamentally from the present. The more that environments, past or future, differ from the present, the more our understanding of ecological patterns and processes will be incomplete and the less accurately will our models predict key ecological phenomena such as species distributions, community composition, species interactions, and biogeochemical-process rates.

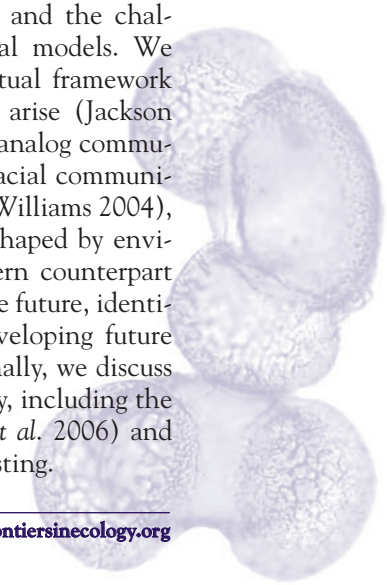
Here, we focus on “no-analog” plant communities (Panel 1), their relationship to climate, and the challenges they pose to predictive ecological models. We briefly summarize a niche-based, conceptual framework explaining how no-analog communities arise (Jackson and Overpeck 2000). We discuss past no-analog communities, using the well documented late-glacial communities as a detailed case study (Jackson and Williams 2004), and argue that these communities were shaped by environmental conditions also without modern counterpart (Williams *et al.* 2001). We then turn to the future, identifying regions of the world at risk of developing future novel climates (Williams *et al.* 2007). Finally, we discuss the implications for global-change ecology, including the risk of future novel ecosystems (Hobbs *et al.* 2006) and the challenges posed for ecological forecasting.

In a nutshell:

- Many past ecological communities were compositionally unlike modern communities
- The formation and dissolution of these past “no-analog” communities appear to be climatically driven and linked to climates that are also without modern analogs
- If anthropogenic greenhouse-gas emissions continue unabated, many future climates will probably lack modern analogs, with tropical regions at greatest risk
- Regions over much of the globe are likely to develop novel communities and other ecological surprises in a future greenhouse world

¹Department of Geography and Center for Climatic Research, University of Wisconsin, Madison, WI 53706 * (juw@geography.wisc.edu);

²Department of Botany and Program in Ecology, University of Wyoming, Laramie, WY 82071



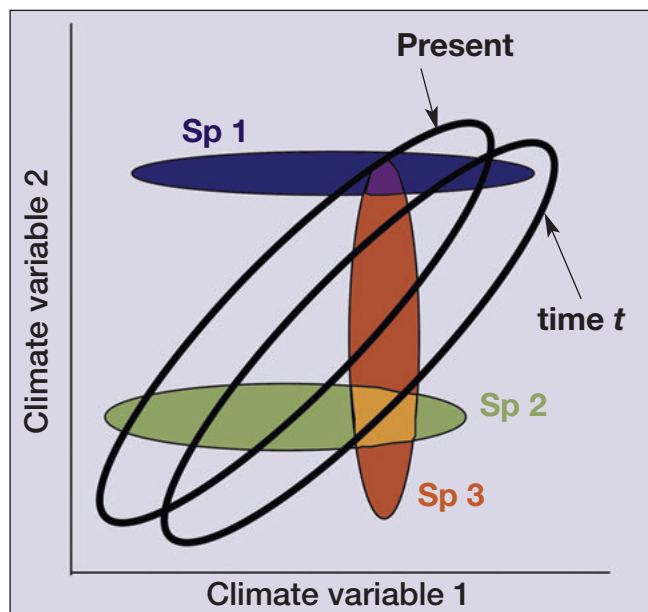


Figure 1. A conceptual diagram showing how no-analog combinations of species arise in response to novel climates. The set of climates in existence at two periods, “present” and an arbitrary “time t ”, are represented as open ellipses. The fundamental niches for three species are shown as colored ellipses. Associations between species can occur only when their fundamental niches overlap with one another and with the set of climates in existence at a particular time period. A present-day ecologist would therefore sometimes observe communities containing both Species 1 and 2, but would never observe co-occurrences of Species 2 and 3 (nor Species 1 and 3). If the right climates arise, however, Species 2 and 3 could co-occur, forming a “no-analog” community from the perspective of the present-day ecologist. Adapted from Figure 5 in Jackson and Overpeck (2000).

■ Individualistic species shifts and no-analog communities: a conceptual framework

The formation and disappearance of no-analog communities (see Panel 1 for definition) are part of a more general phenomenon: the individualistic responses of species to environmental change. Ranges and abundances of terrestrial species shifted dramatically during the last deglaciation. Species varied widely in the timing, magnitude, and direction of these responses, and communities did not migrate as intact units (Gleason 1926; Davis 1981; FAUNMAP Working Group 1996; Jackson and Overpeck 2000). Similar responses occurred during earlier periods of climate change (Wing *et al.* 2005) and individualistic behavior is documented for species responding to current climate changes (Walther *et al.* 2002).

Quaternary vegetation dynamics were driven by orbitally controlled glacial–interglacial climate cycles, as well as by sub-orbital (millennial) modes of climate variability (Overpeck *et al.* 2003). These environmental changes varied regionally, and included changes in multiple variables (eg seasonal temperature, precipitation magnitude and timing, insolation) and changes in both mean

state and variability (Clark *et al.* 1999). These complex climate changes accompanied, and were partially driven by, glacial–interglacial changes in atmospheric CO_2 and CH_4 concentrations (Siegenthaler *et al.* 2005; Spahni *et al.* 2005). Similarly complex changes are expected for this century (IPCC 2007). The richly varied trajectories of species migrations, both past (Williams *et al.* 2004) and future (Iverson *et al.* 2004) derive from these multivariate changes in climate, energy inputs, and atmospheric chemistry (Jackson and Overpeck 2000; Webb *et al.* 2004).

Individualistic species dynamics and the formation of no-analog communities can be explained by a niche-based conceptual framework (Jackson and Overpeck 2000; Figure 1). Each species has a unique, multidimensional fundamental niche, defined as the environmental envelope within which it maintains viable populations (Araújo and Guisan 2006). Not all combinations of environmental variables are realized, however, and so portions of a fundamental niche may not exist today (Jackson and Overpeck 2000; Figure 1). If climate change leads to new combinations of climate variables, species can expand into previously unrealized portions of their fundamental niche.

Depending on the environments available, groups of species may co-occur at some times but not others (Figure 1). As climate changes, shifts in the realized environmental space may drive disaggregation of some species associations and emergence of others. The formation of no-analog communities, past or future, should therefore result from the development of climates also lacking any modern counterpart (Williams *et al.* 2001; Jackson and Williams 2004).

In this conceptualization, species’ niches are static, but the environment is not. Of course, in reality, species evolve and niches are not static, so this conceptual model is best suited to time scales at which rates of environmental change are large relative to rates of evolutionary change. Paleocologists have generally assumed that adaptive responses to late-Quaternary environmental changes were small, because plant and mammalian niches appear to have been largely conserved during the late Pleistocene (Huntley *et al.* 1989; Martínez-Meyer *et al.* 2004). Adaptive responses to past climate change, however important, are still poorly understood (Davis *et al.* 2005). Because rates of evolutionary change are controlled in part by generation time and within-species genetic correlations among traits (Etterson and Shaw 2001), the importance of adaptive responses to 21st-century climate change will vary among taxa and will presumably be greatest for organisms with comparatively short (< 1 year) generation times.

■ No-analog communities of the past: a late-glacial case study

No-analog fossil assemblages are pervasive in Quaternary paleoecological records, documented for plants (eg Overpeck *et al.* 1992; Jackson and Williams 2004), mammals (eg Stafford *et al.* 1999; Graham 2005), coleopterans

(eg Morgan and Morgan 1980), mollusks (eg Kitamura 2004), and foraminifera (eg Cannariato *et al.* 1999; Mix *et al.* 1999). No-analog assemblages occur in terrestrial and marine settings and from high latitudes (Edwards *et al.* 2005) to low (Bush *et al.* 2004). The assemblages appear to represent truly anomalous communities and are not due to after-death mixing of fossils from temporally or spatially distinct communities (Jackson and Williams 2004). The best-known cases are from the most recent glacial–interglacial transition in North America (Anderson *et al.* 1989; Overpeck *et al.* 1992; FAUNMAP Working Group 1996; Williams *et al.* 2001; Edwards *et al.* 2005).

Networks of fossil pollen data collected from lake and mire sediments reveal the distribution (Figure 2a) and composition (Figure 2b,c) of late-glacial no-analog plant communities in North America. In the minimum-dissimilarity maps (Figure 2a), high dissimilarities (darker reds) indicate where fossil assemblages have no close analog in modern pollen assemblages (Williams *et al.* 2001). These communities are characterized by anomalously high abundances of some taxa (eg *Betula*; Figure 2c), co-occurrences at high abundances of taxa now nearly allopatric (eg *Picea*, *Fraxinus*; Figure 2b), and/or very low abundances of now common taxa (eg *Pinus*; Figure 2b). The no-analog plant associations in Alaska and eastern North America are broadly contemporaneous with each other (indicated by similar trends in the minimum dissimilarity between fossil pollen assemblages and their closest modern counterparts; Figure 2d), and are also apparently contemporaneous with no-analog plant assemblages in Europe (Huntley 1990; Willis *et al.* 2000) and the southwestern US (Betancourt *et al.* 1990), and with North American no-analog mammalian communities (FAUNMAP Working Group 1996; Stafford *et al.* 1999). These phenomena are very likely related. However, conclusively demonstrating that no-analog communities were contemporaneous across taxonomic groups and continents requires more systematic data integration as well as re-dating key sites (often collected decades ago) using the precise radiometric dating techniques now available (eg Stafford *et al.* 1999; Grimm and Jacobson 2004).

Several lines of evidence indicate that development of late-glacial, no-analog plant communities was linked to the occurrence of no-analog climates, characterized by higher-than-present temperature seasonality (Delcourt and Delcourt 1994; Williams *et al.* 2001; Edwards *et al.* 2005). The similar timing between the development of Alaska and eastern North American no-analog communities (Figure 2a,d), which were separated by the Laurentide and Cordilleran Ice Sheets, suggests a common atmospheric driver. Simulations from two climate models (Kutzbach *et al.* 1998; Marsiat and Valdes 2001) indicate that both regions had anomalously large annual ranges (maximum–minimum monthly mean values) of insolation and temperature (Williams *et al.* 2001; Figure 2 e, f) with the largest temperature ranges coinciding with peak vegetation dissimilarity (Figure 2 d, f).

Panel 1. What is a “no-analog” community?

No-analog communities consist of species that are extant today, but in combinations not found at present. “No-analog” is therefore shorthand for “no present analog” and can refer to both past and potential future communities. This definition casts no-analog communities as ecological, not evolutionary, phenomena, because it is assumed that the constituent species still exist today but are reshuffled into combinations not found at present. No-analog fossil assemblages also have been called “disharmonious”, “mixed”, “intermingled”, “mosaic”, or “extraprovincial” assemblages (Graham 2005), whereas future no-analog ecosystems have also been called “novel” or “emerging” (Milton 2003; Hobbs *et al.* 2006). Here, we use “no-analog” and “novel” interchangeably. Our usage is not the same as in Ohlemüller *et al.* (2006), who use “non-analogue” to mean current climates with no future analog (which we call “disappearing” climates; Williams *et al.* 2007).

In eastern North America, the high pollen abundances of temperate tree taxa (*Fraxinus*, *Ostrya/Carpinus*, *Ulmus*) in these highly seasonal climates may be explained by their position at the edge of the current North American climate envelope (Williams *et al.* 2006; Figure 3). This pattern suggests that the fundamental niches for these taxa extend beyond the set of climates observed at present (Figure 3), so that these taxa may be able to sustain more seasonal regimes than exist anywhere today (eg Figure 1), as long as winter temperatures do not fall below the -40°C mean daily freezing limit for temperate trees (Sakai and Weiser 1973).

However, the evidence for higher-than-present seasonality does not rule out effects of other environmental factors (eg lowered CO_2 concentrations, absent or sparse human populations, existence of now-extinct mega-herbivores) upon late-glacial vegetation composition and structure (Owen-Smith 1987). Lowered CO_2 concentrations, in particular, probably affected late-glacial vegetation profoundly, by limiting the amount of carbon substrate for photosynthesis and increasing sensitivity to moisture stress (Sage and Coleman 2001). These alternative mechanisms require testing (eg Robinson 2005; Wu *et al.* 2007).

In summary, many late-glacial ecosystems would appear strange to modern ecologists, even though they consisted of extant species. The observed correspondence between past no-analog communities and climate suggests a causal relationship – further evidence that no-analog communities may develop in the future if novel climates arise.

■ Risk of novel climates by 2100 AD

Although community reshuffling driven by individualistic species responses to 21st-century climate change has been discussed (Schneider and Root 1998; Stafford *et al.* 1999; Jackson and Overpeck 2000; Davis and Shaw 2001; Overpeck *et al.* 2003), there has been no attempt to quantify the magnitude or spatial distribution of risk. We review our recent work that maps risk of novel climates by 2100 AD (Williams *et al.* 2007).

Our risk maps (Figure 4) are based upon analyses of an

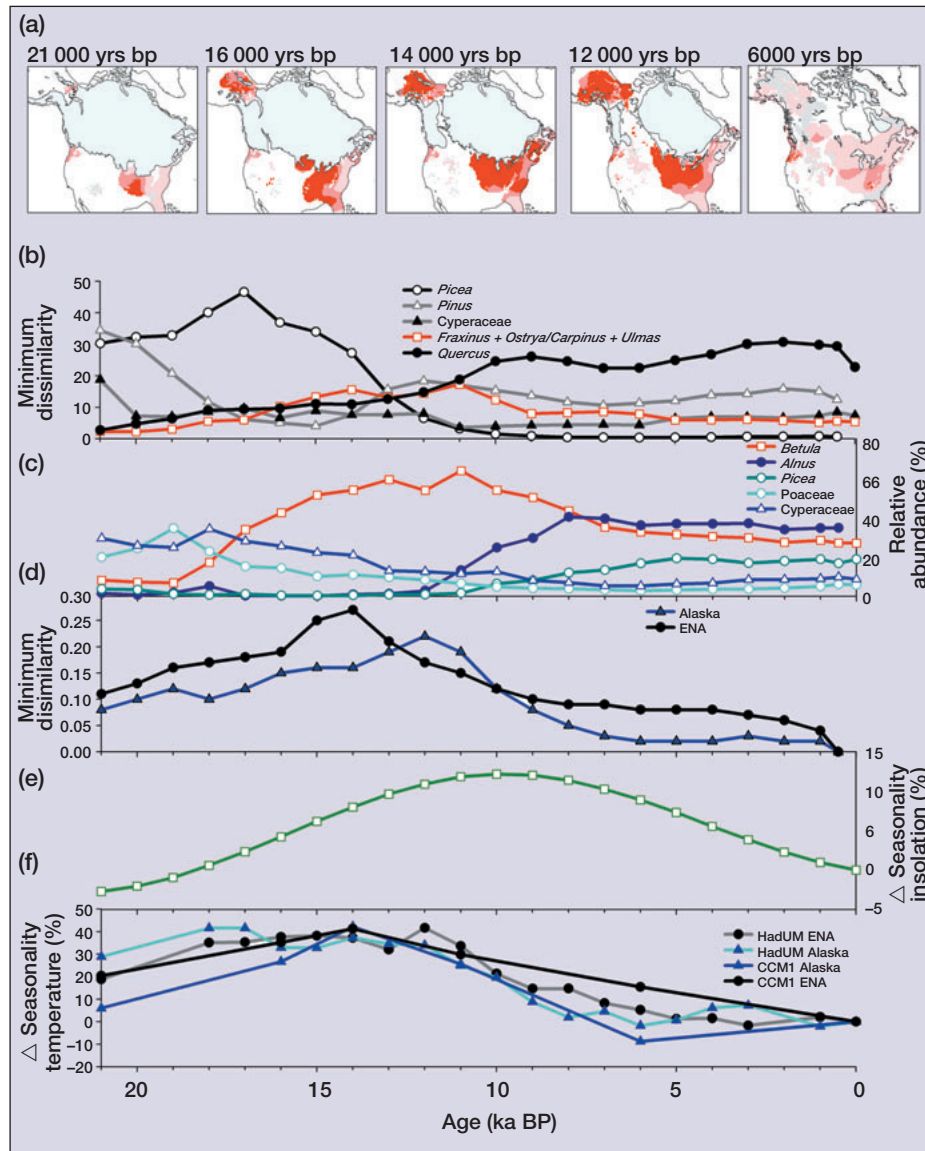


Figure 2. “No-analog” plant communities in North America were most extensive between 17 000 and 12 000 years ago and were most prevalent in Alaska and the interior of eastern North America (a; red shading is scaled to the dissimilarity between fossil pollen assemblages and their closest modern analogs). Trends in community composition between the “no-analog” pollen assemblages of (b) east-central North America (ENA) and (c) Alaska are quite different, (d) yet the timing of peak no-analog conditions is similar, suggesting a common forcing. Likely candidate forcings include seasonality of (e) insolation and (f) temperature, both of which were higher than present during the late-glacial period. Changes in temperature and insolation seasonality are expressed as $100\% \times (\text{AnnualRange}_{\text{past}} - \text{AnnualRange}_{\text{present}}) / \text{AnnualRange}_{\text{present}}$. Insolation values are for 60°N (Berger and Loutre 1991); temperature time series are based on simulations from the HadUM and CCM1 climate models (Kutzbach et al. 1998; Marsiat and Valdes 2001).

ensemble of global climate simulations performed for the IPCC 2007 report, from which we calculated the dissimilarity between mean 1980–1999 and 2080–2099 climates across all terrestrial grid-cells (in the climate model simulations analyzed here, mean grid-cell size was 2.8 degrees latitude by 2.8 degrees longitude). Climate change is represented by a dissimilarity index that integrates four variables: mean summer temperature, winter temperature, summer precipitation, and winter precipitation. A 21st-

century climate simulated for a model grid-cell is novel if its combination of seasonal temperature and precipitation differs substantially from all late 20th-century climates (Williams *et al.* 2007). More formally, we deemed a 21st-century climate grid-cell novel if its dissimilarity to its closest 20th-century match exceeded a critical threshold, here defined as the dissimilarity value that optimally discriminates whether a pair of 1980–1999 climate grid-cells were drawn from the same or different biomes (Williams *et al.* 2007). Risk is represented by the fraction of climate models simulating novel climates out of all models analyzed. We analyzed simulations for the IPCC A2 emissions scenario (where atmospheric $p\text{CO}_2$ reaches 850 ppm by 2100 AD and is not yet stabilized) and the IPCC B1 scenario ($p\text{CO}_2$ stabilized at 550 ppm by 2100 AD).

Our projected novel climates were concentrated in tropical and sub-tropical regions (Figure 4). This spatial fingerprint is the result of global warming: as the world warms, the warmest areas are the first to move outside the present climate space. Precipitation changes are important, but secondary. In the A2 simulations (Figure 4a), novel climates are likely to develop in lowland Amazonia, the southeastern US, the African Sahara and Sahel, the eastern Arabian Peninsula, southeast India and China, the IndoPacific, and northern Australia (“likely” defines cases in which over half of analyzed climate models simulate novel climates). Novel climates

might develop in the western US, central Asia, and Argentina (“might” defines cases in which fewer than half of models simulate novel climates). Temperate and upper latitudes have little apparent risk of future novel climates, at least by 2100. Risk is distributed similarly in the B1 simulations, but at lower levels (Figure 4b).

In this analysis, if a 21st-century climate grid-cell has an analog anywhere in current climates, it is not counted

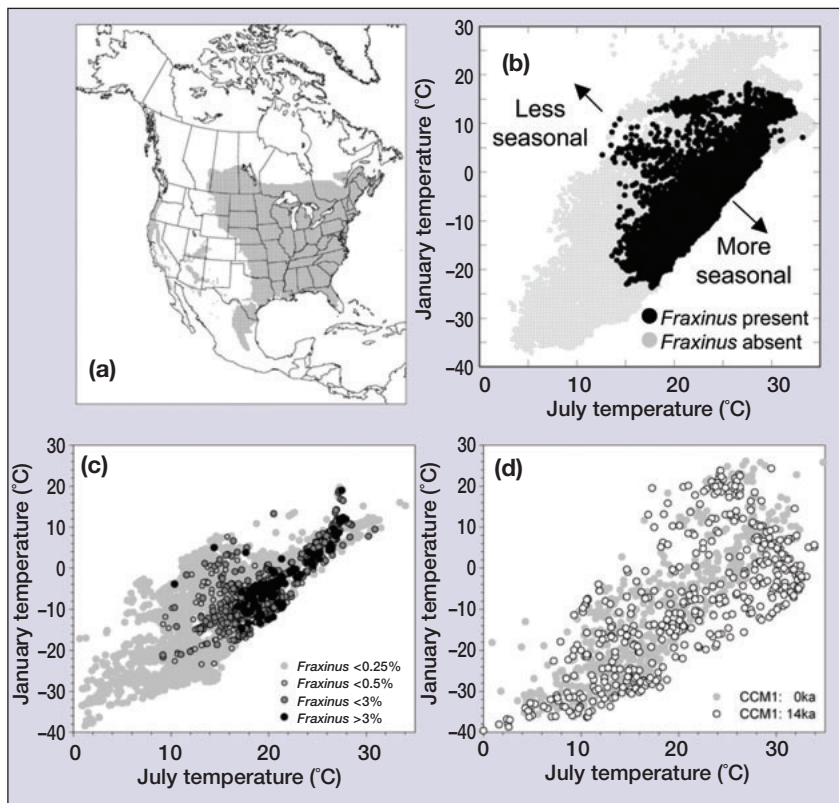


Figure 3. (a) Thanks to extensive forestry and meteorological data, the North American range of *Fraxinus* (all species) is well defined geographically and climatically, (b) except where *Fraxinus* is at the edge of the North American climate envelope (Thompson *et al.* 1999). (c) *Fraxinus* abundances in pollen samples from modern sediments show a similar distribution (Whitmore *et al.* 2005; Williams *et al.* 2006). The position of *Fraxinus* at the edge of the North American climate envelope suggests that it is poised to expand into climates more seasonal than any found at present. Climate models indicate that late-glacial (ca 14 000 years ago) climates in North America were more seasonal than modern climates, helping to explain why *Fraxinus* was apparently a major constituent of many late-glacial, no-analog plant communities (Kutzbach *et al.* 1998; Jackson and Williams 2004).

as novel, even if its 20th-century counterpart is geographically distant. Of course, most species cannot disperse globally without assistance, so they will effectively experience novel future climates if analogs are not present within their migration radius. To represent this situation, we further constrained the pool of potential 20th-century analogs to grid-cells within 500 km of the target grid-cell (Figure 4 c,d). This distance represents an extreme upper-end estimate of unassisted plant migration capabilities by 2100 AD (McLachlan *et al.* 2005) and therefore conservatively estimates the likelihood that climates will be regionally novel.

Regionally novel climates are globally pervasive in the A2 simulations (Figure 4c), particularly in South America, Africa, India, and the IndoPacific. Regions with no risk of globally novel climates are at risk of regionally novel climates. In the B1 simulations, northern hemisphere continents remain at low risk of regionally novel climates, but such climates are extensive in tropical South America and Africa.

■ Implications for ecological forecasting

Novel climates represent a serious challenge for forecasting ecological responses to climate change. Bioclimatic niche models are widely used to predict future species range shifts and extinction risks (Hannah *et al.* 2002; Iversen *et al.* 2004; Thomas *et al.* 2004; Thuiller *et al.* 2005). Such models are based on correlations between current climates and species distributions. It is widely recognized that dispersal limitations and other biotic factors prevent species from fully occupying their fundamental niches, reducing the predictive power of niche models (Araújo and Guisan 2006). It is less widely recognized that, even in the absence of biotic limitations, fundamental niches will be incompletely represented by niche models if the modeled niches are not fully circumscribed by current climates (Figures 1 and 3).

Thus, predicting species responses to novel climates is problematic, because we often lack sufficient observational data to fully determine in which climates a species can or cannot grow (Figure 3). Fortunately, the no-analog problem only affects niche modeling when (1) the envelope of observed climates truncates a fundamental niche and (2) the direction of environmental change causes currently unobserved portions of a species' fundamental niche to open up (Figure 5). Species-level uncertainties accumulate at the community level owing to ecological

interactions, so the composition and structure of communities in novel climate regimes will be difficult to predict. Increases in atmospheric CO₂ should increase the temperature optimum for photosynthesis and reduce sensitivity to moisture stress (Sage and Coleman 2001), weakening the foundation for applying present empirical plant–climate relationships to predict species' responses to future climates. At worst, we may only be able to predict that many novel communities will emerge and surprises will occur. Mechanistic ecological models, such as dynamic global vegetation models (Cramer *et al.* 2001), are in principle better suited for predicting responses to novel climates. However, in practice, most such models include only a limited number of plant functional types (and so are not designed for modeling species-level responses), or they are partially parameterized using modern ecological observations (and thus may have limited predictive power in no-analog settings).

Thus, the accuracy and precision of both empirical and mechanistic ecological models need to be assessed for environments outside the modern domain (Prentice *et al.*

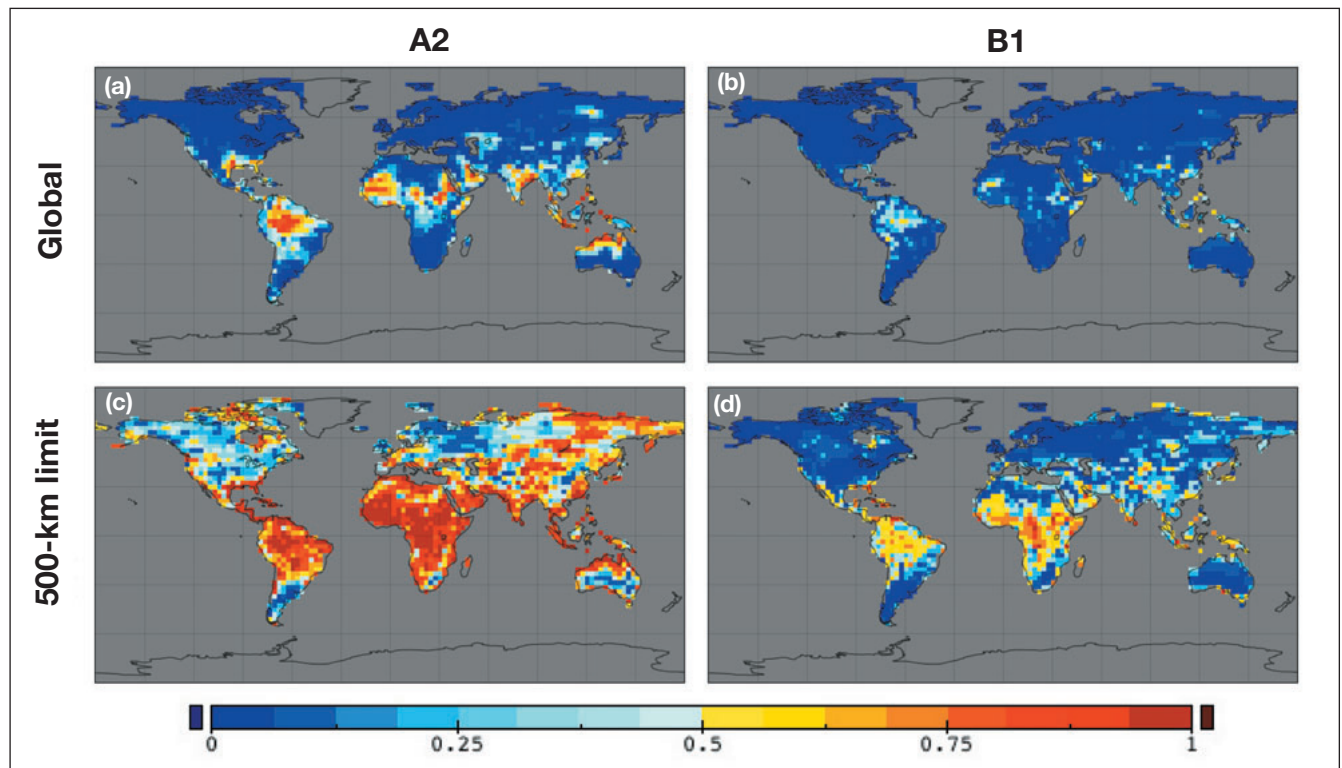


Figure 4. Analyses of IPCC climate-change scenarios (A2 and B1) suggest that climates with no modern analog may develop by the end of this century. The mapped risk estimates show for each grid-cell the fraction of climate models indicating that 2080–2099 climates will lack any close match with 1980–1999 climates. In (a and b), the search for 20th-century analogs was global, so that “novel” 21st-century climates lack analogs anywhere in global 20th-century terrestrial climate space. In (c and d), the search for 20th-century analogs was limited to < 500 km from the target grid-cell, so that in this context, “novel” 21st-century climates are novel regionally, and may or may not be novel globally. (a and c) Results for the “business-as-usual” A2 scenario, in which CO₂ concentrations reach 850 ppm by 2100 AD. (b and d) Results for the B1 scenario, in which CO₂ concentrations stabilize at 550 ppm by 2100 AD. Adapted from Figures 2 and 3 in Williams et al. (2007).

1991; Martínez-Meyer *et al.* 2004), and particularly for no-analog climates. Past no-analog climates differ from those we will encounter in the future, but they can be used to test the robustness of ecological models. Demonstrating that ecological models can accurately simulate past species distributions and community composition is necessary but not sufficient to impart confidence in future predictions.

The challenge posed by future novel climates is compounded by their apparent concentration in regions of high ecological complexity and diversity (Figure 4). This increases the likelihood of ecological surprises arising from species interactions and other emergent phenomena. Furthermore, the high rate of projected climate change means that novel communities will arise as transient responses owing to interspecific differences in climate sensitivity and migration capacity (Kirilenko and Solomon 1998). Human land use, landscape fragmentation, biological invasions, increases in atmospheric CO₂, and other biogeochemical shifts will interact with novel climates to yield yet more ecological surprises (Milton 2003; Hobbs *et al.* 2006). Shifts in species composition may lead to changes in ecosystem functioning, the nature and direction of which may be difficult to predict.

■ Conclusions: “Here there be dragons”

As we sail into the future, we need to forecast what lies ahead (Clark *et al.* 2001). However, novel climates represent uncharted portions of climate space, where we have no observational data to parameterize and validate ecological forecasts. They are the climatic equivalent of uncharted regions of the world, to which early European cartographers supposedly applied the label, “Here there be dragons”. Of course, dragons were never found, although other hazards and opportunities were encountered. While dragons may or may not lurk in our future, the problem of novel climates needs to be confronted squarely, and the adequacy of ecological models under novel climates rigorously assessed. Ecological forecasts for novel climates will always be less certain because they are inherently extrapolative. Given the risk of ecological surprises and the loss of ecological services in a greenhouse world, there is considerable societal value in keeping climate “on the map”, within the range of optimal predictive capacity.

■ Acknowledgements

The IPCC climate simulations were provided by international modeling groups, collected and archived by the

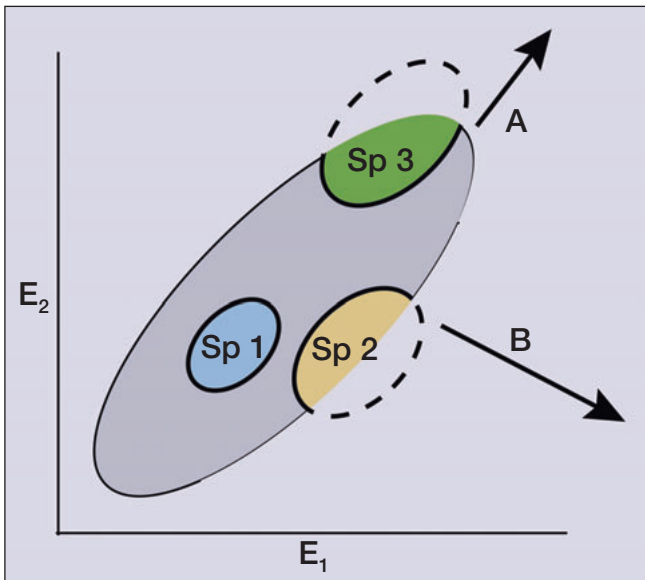


Figure 5. Conceptual diagram showing that the predictive ability of niche-based ecological models varies by species, and depends on (1) whether the present climate space (gray ellipse) encompasses species' fundamental niches (colored ellipses) and (2) the trajectory of climate change (arrows). Niche model-based forecasts for Species 1 should be fairly reliable regardless of climate-change trajectory, because its niche is entirely encompassed by the present climate space. Conversely, the fundamental niches for Species 2 and 3 are only partially described by modern climate observations, and the predictive ability of niche models for these species varies with climate-change trajectory. If trajectory A, then currently unobserved portions of the fundamental niche for Species 2 will open up (resulting in unexpected behavior by Species 2) but not for Species 3. The inverse is true if trajectory B is followed.

Program for Climate Model Diagnosis and Intercomparison (PCMDI). The Coupled Model Intercomparison Project (CMIP) and Climate Simulation Panel facilitated community analyses. P Behling (UW Center for Climatic Research) and the IPCC WGI Technical Support Unit provided technical support. The IPCC Data Archive at the Lawrence Livermore National Laboratory is supported by the US Department of Energy. J Kutzbach collaborated on the future-climate analyses and J Kaplan and L Zajac assisted with data preparations for the HadUM simulations. We thank the many contributors and maintainers of the North American Pollen Database. Comments from A Solomon and J McLachlan improved the manuscript. This work was supported in part by grants from the National Science Foundation (ATM-0507999, DEB-0716471, DEB-0613952, DEB-0345012, DEB-0716591) and the University of Wisconsin-Madison Graduate School.

References

Anderson PM, Bartlein PJ, Brubaker LB, *et al.* 1989. Modern analogs of late-Quaternary pollen spectra from the western interior of North America. *J Biogeogr* **16**: 573–96.

Araújo MB and Guisan A. 2006. Five (or so) challenges for species

- distribution modelling. *J Biogeogr* **33**: 1677–88.
- Berger A and Loutre ME. 1991. Insolation values for the climate of the last 10 million years. *Quaternary Sci Rev* **10**: 297–317.
- Betancourt JL, Van Devender TR, and Martin PS (Eds). 1990. *Packrat middens: the last 40 000 years of biotic change*. Tucson, AZ: University of Arizona Press.
- Bush MB, De Oliveira PE, Colinvaux PA, *et al.* 2004. Amazonian paleoecological histories: one hill, three watersheds. *Palaeogeogr Palaeoclimatol* **214**: 359–93.
- Cannariato KG, Kennett JP, and Behl RJ. 1999. Biotic response to late Quaternary rapid climate switches in Santa Barbara Basin: ecological and evolutionary implications. *Geology* **27**: 63–66.
- Clark JS, Carpenter SR, Barber M, *et al.* 2001. Ecological forecasts: an emerging imperative. *Science* **293**: 657–60.
- Clark PU, Webb RS, and Keigwin LD (Eds). 1999. *Mechanisms of global climate change at millennial time scales*. Washington, DC: American Geophysical Union.
- Cramer W, Bondeau A, Woodward FI, *et al.* 2001. Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Glob Change Biol* **7**: 357–73.
- Davis MB. 1981. Quaternary history and the stability of forest communities. In: West DC, Shugart HH, and Botkin DB (Eds). *Forest succession*. New York, NY: Springer-Verlag.
- Davis MB and Shaw RG. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* **292**: 673–79.
- Davis MB, Shaw RG, and Etterson JR. 2005. Evolutionary responses to changing climate. *Ecology* **86**: 1704–14.
- Delcourt HR and Delcourt PA. 1994. Postglacial rise and decline of *Ostrya virginiana* (Mill) K Koch and *Carpinus caroliniana* Walt in eastern North America: predictable responses of forest species to cyclic changes in seasonality of climates. *J Biogeogr* **21**: 137–50.
- Edwards ME, Brubaker LB, Lozhkin AV, and Anderson PM. 2005. Structurally novel biomes: a response to past warming in Beringia. *Ecology* **86**: 1696–1703.
- Etterson JR and Shaw RG. 2001. Constraint to adaptive evolution in response to global warming. *Science* **294**: 151–54.
- FAUNMAP Working Group. 1996. Spatial response of mammals to late Quaternary environmental fluctuations. *Science* **272**: 1601–06.
- Gleason HA. 1926. The individualistic concept of the plant association. *B Torrey Bot Club* **53**: 7–26.
- Graham RW. 2005. Quaternary mammal communities: relevance of the individualistic response and non-analog faunas. *Paleontol Soc Pap* **11**: 141–58.
- Grimm EC and Jacobson Jr GL. 2004. Late-Quaternary vegetation history of the eastern United States. In: Gillespie AR, Porter SC, and Atwater BR (Eds). *The Quaternary period in the United States*. Amsterdam, Netherlands: Elsevier.
- Hannah L, Midgley GF, Lovejoy T, *et al.* 2002. Conservation of biodiversity in a changing climate. *Conserv Biol* **16**: 264–68.
- Hobbs RJ, Arico S, Aronson J, *et al.* 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecol Biogeogr* **15**: 1–7.
- Huntley B. 1990. Dissimilarity mapping between fossil and contemporary pollen spectra in Europe for the past 13 000 years. *Quaternary Res* **33**: 360–76.
- Huntley B, Bartlein PJ, and Prentice IC. 1989. Climatic control of the distribution and abundance of beech (*Fagus* L) in Europe and North America. *J Biogeogr* **16**: 551–60.
- IPCC (Intergovernmental Panel on Climate Change). 2007. *Climate change 2007: the physical science basis. Summary for policymakers*. Geneva, Switzerland: Intergovernmental Panel on Climate Change.
- Iverson LR, Schwartz MW, and Prasad AM. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecol Biogeogr* **13**: 209–19.

- Jackson ST and Overpeck JT. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiol* **26S**: 194–220.
- Jackson ST and Williams JW. 2004. Modern analogs in Quaternary paleoecology: here today, gone yesterday, gone tomorrow? *Annu Rev Earth Pl Sc* **32**: 495–537.
- Kirilenko AP and Solomon AM. 1998. Modeling dynamic vegetation response to rapid climate change using bioclimatic classification. *Climatic Change* **38**: 15–49.
- Kitamura A. 2004. Effects of seasonality, forced by orbital–insolation cycles, on offshore molluscan faunal change during rapid warming in the Sea of Japan. *Palaeogeogr Palaeocl* **203**: 169–78.
- Kutzbach JE, Gallimore R, Harrison SP, et al. 1998. Climate and biome simulations for the past 21 000 years. *Quaternary Sci Rev* **17**: 473–506.
- Marsiat I and Valdes PJ. 2001. Sensitivity of the northern hemisphere climate of the last glacial maximum to sea surface temperatures. *Clim Dynam* **17**: 233–48.
- Martínez-Meyer E, Peterson AT, and Hargrove WW. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecol Biogeogr* **13**: 305–14.
- McLachlan JS, Clark JS, and Manos PS. 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* **86**: 2088–98.
- Milton SJ. 2003. “Emerging ecosystems”: a washing-stone for ecologists, economists, and sociologists? *S Afr J Sci* **99**: 404–06.
- Mix AC, Morey AE, Pisias NG, and Hostetler SW. 1999. Foraminiferal faunal estimates of paleotemperature: circumventing the no-analog problem yields cool ice age tropics. *Paleoceanography* **14**: 350–59.
- Morgan AV and Morgan A. 1980. Faunal assemblages and distributional shifts of Coleoptera during the late Pleistocene of Canada and the northern United States. *Can Entomol* **112**: 1105–28.
- Ohlemüller R, Gritti ES, Sykes MT, and Thomas CD. 2006. Towards European climate risk surfaces: the extent and distribution of analog and non-analog climates 1931–2000. *Global Ecol Biogeogr* **15**: 395–405.
- Overpeck JT, Webb RS, and Webb III T. 1992. Mapping eastern North American vegetation change of the past 18 ka: no-analogs and the future. *Geology* **20**: 1071–74.
- Overpeck JT, Whitlock C, and Huntley B. 2003. Terrestrial biosphere dynamics in the climate system: past and future. In: Bradley RS, Pedersen TF, Alverson KD, and Bergmann KF (Eds). *Paleoclimate, global change and the future*. Berlin, Germany: Springer-Verlag.
- Owen-Smith N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology* **13**: 351–62.
- Prentice IC, Bartlein PJ, and Webb III T. 1991. Vegetation and climate changes in eastern North America since the last glacial maximum: a response to continuous climatic forcing. *Ecology* **72**: 2038–56.
- Robinson GS. 2005. Landscape paleoecology and megafaunal extinction in southeastern New York State. *Ecol Monogr* **75**: 295–315.
- Sage RF and Coleman JR. 2001. Effects of low atmospheric CO₂ on plants: more than a thing of the past. *Trends Plant Sci* **6**: 18–24.
- Sakai A and Weiser CJ. 1973. Freezing resistance of trees in North America with reference to tree regions. *Ecology* **54**: 118–26.
- Schneider SH and Root TL. 1998. Climate change. In: Mac MJ, Opler PA, Puckett Haeker CE, and Doran PD (Eds). *Status and trends of the nation's biological resources*. Reston, VA: US Geological Survey.
- Siegenthaler U, Stocker TF, Monnin E, et al. 2005. Stable carbon cycle–climate relationship during the late Pleistocene. *Science* **310**: 1313–17.
- Spahni R, Chappellaz J, Stocker TF, et al. 2005. Atmospheric methane and nitrous oxide of the late Pleistocene from Antarctic ice cores. *Science* **310**: 1317–21.
- Stafford Jr TW, Semken Jr HA, Graham RW, et al. 1999. First accelerator mass spectrometry ¹⁴C dates documenting contemporaneity of non-analog species in late Pleistocene mammal communities. *Geology* **27**: 903–06.
- Thomas CD, Cameron A, Green RE, et al. 2004. Extinction risk from climate change. *Nature* **427**: 145–48.
- Thompson RS, Anderson KH, and Bartlein PJ. 1999. Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America: hardwoods. Denver, CO: US Geological Survey. Professional paper 1650-B.
- Thuiller W, Lavorel S, Araújo MB, et al. 2005. Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci USA* **102**: 8245–50.
- Walther G-R, Post E, Convey P, et al. 2002. Ecological responses to recent climate change. *Nature* **416**: 389–95.
- Webb III T, Shuman BN, and Williams JW. 2004. Climatically forced vegetation dynamics in North America during the late Quaternary period. In: Gillespie AR, Porter SC, and Atwater BF (Eds). *The Quaternary period in the United States*. Amsterdam, Netherlands: Elsevier.
- Whitmore J, Gajewski K, Sawada M, et al. 2005. North American and Greenland modern pollen data for multi-scale paleoecological and paleoclimatic applications. *Quaternary Sci Rev* **24**: 1828–48.
- Williams JW, Jackson ST, and Kutzbach JE. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proc Natl Acad Sci USA* **104**: 5738–42.
- Williams JW, Shuman B, Bartlein PJ, et al. 2006. An atlas of pollen–vegetation–climate relationships for the United States and Canada. Dallas, TX: American Association of Stratigraphic Palynologists Foundation.
- Williams JW, Shuman BN, and Webb III T. 2001. Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology* **82**: 3346–62.
- Williams JW, Shuman BN, Webb III T, et al. 2004. Late Quaternary vegetation dynamics in North America: scaling from taxa to biomes. *Ecol Monogr* **74**: 309–34.
- Willis KJ, Rudner E, and Sümegi P. 2000. The full-glacial forests of central and southeastern Europe. *Quaternary Res* **53**: 203–13.
- Wing SL, Harrington GJ, Smith FA, et al. 2005. Transient floral change and rapid global warming at the Paleocene–Eocene boundary. *Science* **310**: 993–96.
- Wu H, Guiot J, Brewer S, et al. 2007. Dominant factors controlling glacial and interglacial variations in the treeline elevation in tropical Africa. *Proc Natl Acad Sci USA* **104**: 9720–24.

