

INVITED PERSPECTIVE

Large parts of the world are brown or black: A different view on the 'Green World' hypothesis

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Abstract. Climate sets the limits to plant growth but does climate determine the global distribution of major biomes? I suggest methods for evaluating whether vegetation is largely climate or consumer-controlled, focusing on large mammal herbivores and fire as influential consumers. Large parts of the world appear not to be at equilibrium with climate. Consumer-controlled ecosystems are ancient and diverse. Their distinctive ecology warrants special attention.

Keywords: Climate-vegetation relationship; Fire ecology; Global biome; Herbivory by mammals; Trophic ecology.

Abbreviations: DGVM = Dynamic Global Vegetation Model; HSS = Hanston et al. (1960).

Introduction

What are the primary determinants of vegetation types at a regional, or global scale? Why do forests dominate in some landscapes, grasslands in others? The usual answer is climate, especially availability of moisture and energy for plant growth. Soils modify plant available moisture and vary in nutrient supply and are also important regional determinants. Hairston et al. (1960; 'HSS') proposed the radical alternative that patterns of vegetation are determined by consumption by animals. Herbivores, according to HSS, would have major impacts on vegetation but are usually prevented from doing so because they are regulated by carnivores, pests and pathogens. Without regu-

lation, herbivore impacts would explode and the world would no longer be 'green' (see Krebs 2001, for a useful summary).

It is a shock for a vegetation scientist, trained to analyse plant/soil/climate interactions as major structuring forces to accept, say, that lion predation is what is really responsible for the savanna woodland structure you are observing. It is perhaps more generally useful to ask whether vegetation is largely controlled by resources or consumers. Consumers, in this instance, mean agents that consume plants. Consumer-controlled ecosystems should have interesting properties. For example, large changes in species composition ('trophic cascades') would be expected if the controlling agent is removed.

In a review of the 'green world' hypothesis, Polis (1999) argued that terrestrial vegetation is largely determined by climate, locally modified by low-nutrient soils, with consumer-control sometimes occurring but localized in space and time. Contrary to this analysis, I believe that very large areas of the world are 'consumer-controlled'. I focus on large mammals as biotic consumers and fire as an abiotic consumer. Large mammals suffered mass extinctions in most parts of the world in the Late Pleistocene but their legacy persists (Janzen & Martin 1982; Vera 2000) and extant remnants of the fauna survive in Africa and parts of Asia. Fire has many analogies to herbivory, not least because, unlike other physical disturbances, fire consumes complex organic compounds and converts them to combustion by-products. To assess the extent of

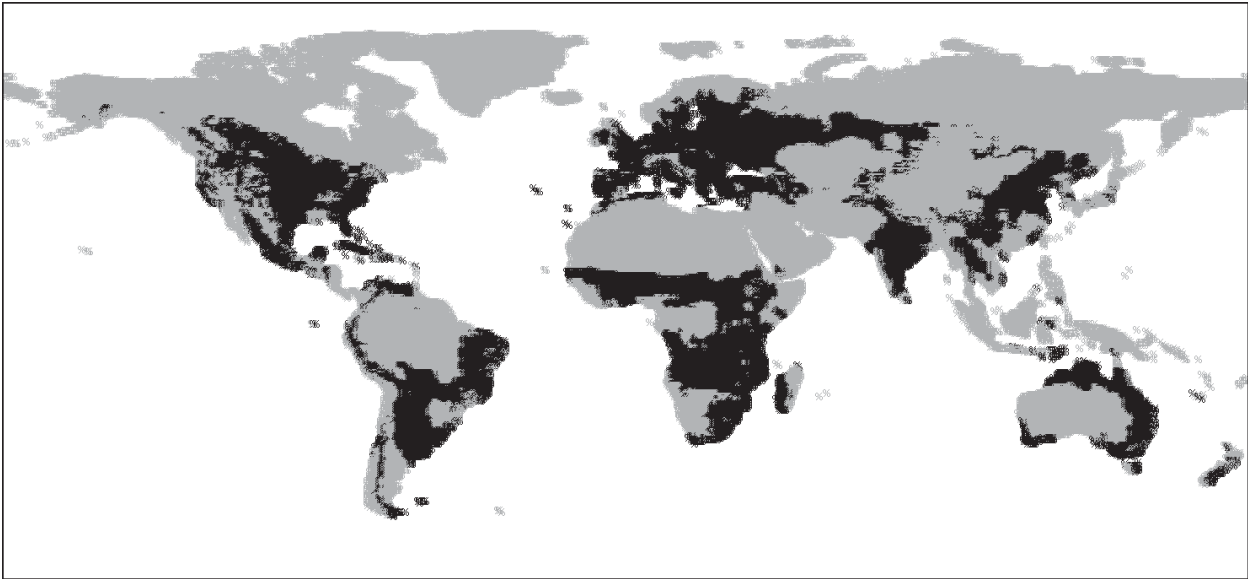


Fig. 1. Areas of the world (dark shading) falling into the ‘ecosystems uncertain’ climate envelope of Whittaker’s (1975) global biome ordination on temperature/precipitation gradients. ‘Ecosystem uncertain’ are climate zones “in which either grassland, or one of the types dominated by woody plants” occur (Whittaker 1975). Ecosystems uncertain were mapped for all pixels with $MAP > 7.143 MAT + 286$ and $MAP < -1.469 MAT^2 + 81.665 MAT + 475$; MAP = mean annual precipitation; MAT = mean annual temperature (ex Fig. 4.10, Whittaker 1975). Climate data ($10'$ grid aggregated to 0.5° squares): <http://www.cru.uea.ac.uk/cru/data/hrg.htm>

consumer-controlled ecosystems, it is useful to first assess the potential vegetation, effectively the ‘carrying capacity’ of trees for a given climate and soil type, against which actual ecosystems can be measured. I address the questions: 1. How would you measure departure from climate-potential? 2. How much of world vegetation is at its climate-limited potential biomass? 3. Which consumers are most influential in preventing ecosystems from reaching their climate-potential? 4. How might the ecology of consumer-controlled ecosystems differ from that of resource-controlled ecosystems?

Climate and global vegetation

Climate sets the limits to potential plant growth and vegetation varies depending on temperature extremes and the coincidence of energy and moisture for growth. The importance of climate in limiting vegetation has traditionally been explored by correlating the distribution of the world’s major biomes with precipitation and temperature (e.g. Holdridge 1947; Whittaker 1975; Stephenson 1998). In contrast, the importance of consumers in regulating ecosystems has been evaluated by counting the number of studies ‘for’ or ‘against’ consumer-control (Polis et al. 2000; Paine 2000). To evaluate the global importance of consumer-controlled eco-

systems we need to assess their spatial extent. One way of doing so is to look at outliers in climate/vegetation correlations. There are parts of the world where strikingly different natural vegetation occurs in the same climate. This is implied in Whittaker’s ordination of world ecosystems on a precipitation/temperature plane (Fig. 4.10 in Whittaker 1975), often reproduced in textbooks. A small region of this plane supports grasslands, shrublands, woodlands or forests – i.e. ‘ecosystems uncertain’. However its spatial extent is vast (Fig. 1). Is this the global domain of ‘consumer controlled’ ecosystems?

How should we measure departure from climate potential

To measure the global extent of consumer-controlled ecosystems, we need to agree on which properties to measure (Polis et al. 2000). Implicit in Whittaker’s (1975) system is the importance of woody biomass as a measure of vegetation structure. Large changes in woody biomass in response to experimental manipulation of an influential consumer would be clear evidence for consumer control. If, say, a grassland changed to a forest in a herbivore enclosure, few would disagree that the grassland was consumer controlled. The same experiment in a different setting may produce little effect on ecosystem structure

but significant changes in species composition. Species changes have been the more common measure of trophic ('consumer') control (Polis et al. 2000).

Species changes cannot be represented on a global scale. Instead I suggest using woody biomass as a first measure of consumer-control. The magnitude of consumer-control can, in principle, be measured by the difference between actual and climate-limited potential biomass. Experimental studies where consumers have been manipulated are an unequivocal test of actual versus potential biomass. However many years may be needed to allow trees to grow to their climate-limited potential and it is difficult to extrapolate the experimental results over space. Plantation forestry can indicate discrepancies between natural vegetation and climate-limited potential vegetation. Vast areas of grasslands and shrublands have been planted up to conifers or eucalypts, especially in the southern hemisphere (Richardson 1998) and in many areas have become invasive. Vegetation pattern is a widely used alternative or addendum to experiments. Forest patches in a grassy landscape suggest consumer-control (e.g. Bowman 2000 for fire) – or extreme forms of resource-control, such as waterlogged or nutrient-poor soils.

Observations such as these are useful indicators of consumer-controlled ecosystems (e.g. by fire) but cannot easily be extended to global scales. A promising new tool for predicting global potential woody biomass has emerged from the recent development of Dynamic Global Vegetation Models (DGVMs). These are complex models, analogous to global climate models, designed to explore global change impacts on vegetation (e.g. Woodward et al. 1995; Haxeltine & Prentice 1996; Cramer et al. 2001). The models 'grow' vegetation according to physiological principles using climate and soil texture and depth as inputs and woody biomass as one of the outputs. Model simulations have been tested against a number of measured ecosystem variables with good results (Woodward & Lomas 2004). Simulated potential biomass in grassy and shrubland ecosystems also match well with measured tree biomass in forestry plantations and long-term fire exclusion studies (Bond et al. 2003, 2005). DGVMs have their limitations, both in the input data and the modelling assumptions. Nevertheless, used with caution and with local validation, they are the most useful tools currently available for predicting anomalies between climate-limited potential biomass and natural open vegetation (Fig. 2).

We have recently simulated global vegetation using a DGVM and found large disparities between climate-limited and actual vegetation (Bond et al. 2005). One measure of the discrepancy is the global extent of forest. Closed forest vegetation currently covers some 25% of the terrestrial world (compared to about 30% before

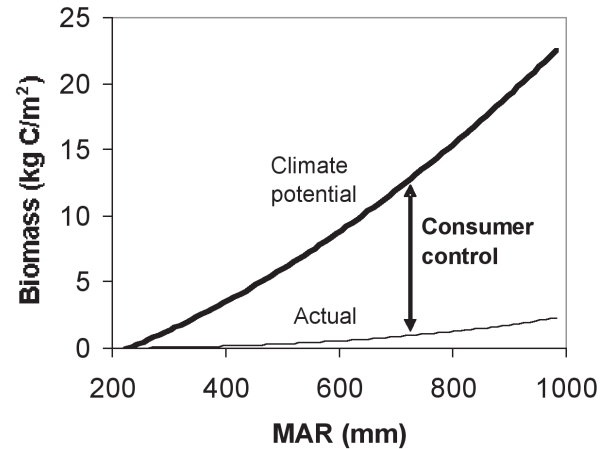


Fig. 2. Woody biomass as a measure of potential consumer-control of an ecosystem. This example is for latitude 27.25 S in South Africa. MAR = mean annual rainfall. Climate-potential was simulated using a DGVM (Bond et al. 2003). The natural vegetation is grassland and wooded grassland (biomass estimated from Rutherford 1979). Large areas at the wetter end of the gradient have been converted to forestry plantations.

deforestation, McCarthy et al. 2001). According to model simulations, the world has the climate potential to support closed forests in double this area (56%; Bond et al. 2005). The areas most at variance with climate conform quite well with the tropical grassland and savanna regions of Whittaker's 'ecosystems uncertain' (Fig. 1). The world is not as green as it should be. But which consumers are globally significant?

Which consumers are most influential in preventing ecosystems from reaching their climate-potential?

HSS emphasized predation as the central process influencing plant biomass by limiting herbivores. However the real issue is whether consumers can ever reduce plant biomass enough to significantly effect vegetation structure and composition. Critics of the hypothesis have argued that the world is green because most plants are inedible, full of indigestible components such as cellulose and lignin (Polis 1999). However food quality requirements vary with body mass and large mammals can consume low quality diets. Large animals are also difficult and dangerous prey for predators. For these reasons, Owen Smith (1988) suggested that megaherbivores (animals with body mass >1000 kg) would be particularly influential in shaping vegetation structure. Megaherbivores roamed most of the planet just a few thousand years ago. They would have been prime candidates for significant consumer-control of vegeta-

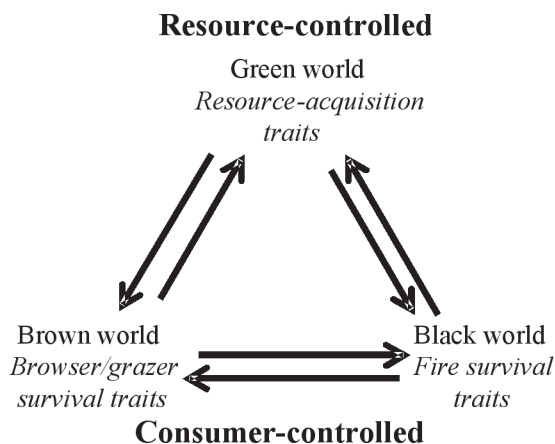


Fig. 3. A multi-coloured view of the world. Communities in any locality may have elements of all three possible ecosystem states depending on the history, magnitude, and type, of consumer-control. The resource base influences the probability of transitions from one state to another. For example, nutrient-poor soils would tend to reduce mammal herbivory, favouring fire and ‘black world’ species.

tion (Owen Smith 1988). Extant large mammal herbivores (including smaller ungulates) exert significant consumer-control in many ecosystems (Augustine & McNaughton 1998; Paine 2000).

Fire has been missing in the ecological literature as an alternate consumer of vegetation. Nevertheless it has properties, and effects, similar to those of its animal counterparts. Fire consumes large amounts of plant material in irregular ‘bites’ of varying intensity and in preferred seasons. Fire differs from mammalian herbivory in the important respect that it defoliates vegetation irrespective of quality. As Bell (1982) put it, fire ‘does not require protein for growth’. Fire thrives on just those features that make plants inedible to herbivores – high cellulose and lignin content and low nitrogen content. Indigestible plants are the ‘food’ that feeds fires.

With fire included as a consumer, the world is ‘multi-coloured’: ‘brown’ where intense mammal grazing and browsing controls vegetation; ‘black’ where vegetation is largely controlled by fire, or ‘green’ where climate, and not consumers, limit woody biomass (Fig. 3). Since fire and large mammal grazers are competing consumers of vegetation, it is intriguing to ask whether more of the world has become ‘black’ since extirpation/extinction of the megafauna. Is the current extent of fire-controlled ecosystems an artefact of megafaunal extinction (Flannery 1995)? Or is the poor forage quality and high productivity of, say, humid tropical grassy ecosystems such that fire is always the dominant consumer in higher rainfall regions? I suspect the latter but the critical studies have yet to be done.

How do community and assembly rules differ in consumer-controlled ecosystems?

Which species, or functional groups, occur together in communities and how do they respond to perturbations? The answers have generally been sought in differing abilities to compete for resources or to escape competitors by dispersal. In consumer-controlled ecosystems, HSS predicts little competition between plant species. Instead, you would expect the presence of a species to depend on its ability to persist in the face of losses to the dominant consumers. The fire literature reflects this central principle of community assembly. There are numerous studies of the mode of recovery from burning (sprouting), fire-stimulated recruitment, time to first reproduction, persistence of seedbanks to the next fire and so on (Whelan 1995; Bond & van Wilgen 1996). These life history attributes, together with the patterns of fire consumption, especially its frequency, are widely used for predicting compatible species assemblages (e.g. Bradstock & Kenny 2003; Pausas et al. 2004). Community membership in frequently burnt ecosystems is seldom attributed to interactions with other plant species, and then only if they change the disturbance regime. For example, grasses may invade a heathland promoting fires too frequent for the persistence of the original shrub species. Where competition is considered, it is usually between different functional groups, such as trees and grasses (Scholes & Archer 1997), or overstorey and understorey plants (Keith & Bradstock 1994; Vlok & Yeaton 1999), rather than members of the same group. In short, the central concerns of ecologists in consumer-controlled ecosystems (where fire is the consumer) seem to be entirely different from resource-controlled ecosystems. An obsession with competition as a structuring force is replaced by an obsession with key life history traits and their fit to the prevailing fire regime.

There are numerous studies of large mammal herbivore impacts on plant assemblages, some in the context of HSS (e.g. Paine 2000). A start has also been made in identifying key plant functional traits in ecosystems disturbed by fire or herbivory (Pausas & Lavorel 2003). However there are few studies comparing functional traits, and potential trait trade-offs, between plants growing in the ‘brown’ world of large mammal consumers versus the ‘black world’ of fire and between these and the ‘green’ world of forest. We are not yet in a position to predict the cascading consequences of fire suppression, herbivore extirpation, or the conversion of forests to open ecosystems at the global scale.

Conclusions

Where consumer-control is important, we may require a different research agenda. To identify such systems, I have suggested comparing actual woody biomass with climate-limited potential biomass. DGVMs provide a useful new tool for predicting the latter. They show that large parts of the world are open grassy or shrubby systems where the climate can support forests. Fire appears to be by far the most important 'consumer' globally, depressing biomass from its climate potential (Bond et al. 2005). It is surprising that fire has been omitted from debates on the extent of top-down control. Part of the problem is that fire has long been viewed as an anthropogenic artefact. Though people have undoubtedly altered the extent of fire-maintained ecosystems (Pyne 2001), we now know that fire, and fire-dependent ecosystems pre-date human activity by millions of years (Scott 2000; Kershaw et al. 2002). The rich flora of fire-dependent grasslands, savannas and shrublands is testimony to the long evolutionary history of 'black world' (Bond et al. 2003). Part of the problem is also one of semantics – should fire be considered a 'top-down' or 'bottom-up' control agent? In an attempt to side-step semantics, I have used the term 'consumer-control' to broaden the scope of enquiry. Fire, and fire-dependent vegetation, are so widespread, with so many analogies to herbivory, that it seems long overdue to bring these two areas of ecology together. Fire ecologists would benefit from reading the trophic ecology literature while trophic ecologists would benefit from considering fire in their conceptual thinking. For example, high cellulose and lignin content may make plants inedible for herbivores but excellent 'food' for fire. Green edible plants, by contrast, are poor fuels for fire. Where in the world can a plant get away with being green, rather than edible and eaten, or inedible and burnt? The interaction between fire and herbivory as shapers of vegetation has received remarkably little attention. It is also puzzling that large mammals, especially the megafauna, have not been more central in the trophic control literature though recent studies have re-opened the debate (Vera 2000; Svenning 2002).

So when you next step into a grassland, savanna or shrubland, I suggest asking these questions: What is the potential ecosystem here? Which consumers might prevent it from reaching climate potential? Which species exist in the assembly because of their ability to tolerate consumers? What are the key traits that enable them to do so? You may find the answers unsettling.

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References

- Augustine, D.J. & McNaughton, S.J. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *J. Wildlife Manage.* 62: 1165-1183.
- Bell, R.H.V. 1982. The effect of soil nutrient availability on community structure in African ecosystems. In: Huntley, B.J. & Walker, B.H. (eds.) *Ecology of tropical savannas*, pp. 193-216. Springer Verlag, Berlin, DE.
- Bond, W.J. & van Wilgen, B.W. 1996. *Fire and plants*. Chapman and Hall, London, UK.
- Bond, W.J., Midgley, G.F. & Woodward, F.I. 2003. What controls South African vegetation – climate or fire? *S. Afr. J. Bot.* 69: 79-91
- Bond, W.J., Woodward, F.I. & Midgley, G.F. 2005. The global distribution of ecosystems in a world without fire. *New Phyt.* 165: 525-538.
- Bowman, D.M.J.S. 2000. *Australian rainforests: islands of green in a land of fire*, Cambridge University Press, Cambridge, UK.
- Bradstock, R.A. & Kenny, B.J. 2003. An application of plant functional types to fire management in a conservation reserve in southeastern Australia. *J. Veg. Sci.* 14: 345-354.
- Cramer, W., Bondeau, A., Woodward, F.I. et al. 2001. Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biol.* 7: 357-373.
- Flannery, T.F. 1995. *The future eaters*. George Braziller, New York, NY, US.
- Hairton, N., Smith, F. & Slobodkin L. 1960. Community structure, population control and competition. *Am. Nat.* 94: 421-425.
- Haxeltine, A. & Prentice, I.C. 1996. BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Global Biogeochem. Cycles* 10: 693-709.
- Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. *Science* 105: 367-368.
- Janzen, D.H. & Martin, P.S. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. *Science* 215: 19-27.
- Keith, D.A. & Bradstock, R.A. 1994. Fire and competition in Australian heath: a conceptual model and field investigations. *J. Veg. Sci.* 5: 347-354.
- Kershaw, A.P., Clark, J.S., Gill, A.M. & D'Costa, D.M. 2002. A history of fire in Australia. In: Bradstock, R.A., Williams, J.E. & Gill, A.M. (eds.) *Flammable Australia: The fire regimes and biodiversity of a continent*, pp. 3-25. Cambridge University Press, Cambridge, UK.
- Krebs, C.J. 2001. *Ecology: The experimental analysis of distribution and abundance*. Benjamin Cummings, San Francisco, CA, US.
- McCarthy, J.J., Canziani, O.E., Leary, N.A., Dokken, D.J. &

- White, K.S. 2001. *Climate Change 2001: Impacts, adaptation and vulnerability. Contributions of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Owen-Smith, R.N. 1988. *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge, UK.
- Paine, R.T. 2000. Phycology for the mammalogist: marine rocky shores and mammal-dominated communities – how different are the structuring processes? *J. Mammal.* 81: 637-648.
- Pausas, J.G. & Lavorel, S. 2003. A hierarchical deductive approach for functional types in disturbed ecosystems. *J. Veg. Sci.* 14: 409-416.
- Pausas, J.G., Bradstock, R.A., Keith, D.A., Keeley, J.E. & the GCTE Fire Network 2004. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85: 1085-1100.
- Polis, G.A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomes. *Oikos* 86: 3-15.
- Polis, G.A., Sear, A.L.W., Huxel, G.R., Strong, D.R. & Maron, J. 2000. When is a trophic cascade a trophic cascade? *Trends Ecol. Evol.* 15: 473-475.
- Pyne, S.J. 2001. *Fire: a brief history*. University of Washington Press, Seattle, WA, US.
- Richardson, D.M. 1998. Forestry trees as invasive aliens. *Conserv. Biol.* 12: 18-26.
- Rutherford, M.C. 1979. Primary production ecology in southern Africa. In: Werger, M.J.A. (ed.) *Biogeography and ecology of Southern Africa*, pp. 621-659. Junk, The Hague, NL.
- Scholes, R.J. & Archer, S. 1997. Tree-grass interactions in savannas. *Ann. Rev. Ecol. Syst.* 28: 517-544.
- Scott, A.C. 2000. The Pre-Quaternary history of fire. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 164: 297-345.
- Stephenson, N. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *J. Biogeogr.* 25: 855-870.
- Svenning, J.-C. 2002. A review of natural vegetation openness in north-western Europe. *Biol. Conserv.* 104: 133-148.
- Vera, F.W.M. 2000. *Grazing ecology and forest history*. CABI, Oxon, UK.
- Vlok, J.H. & Yeaton, R.I. 1999. The effect of overstorey proteas on plant species richness in South African mountain fynbos. *Divers. Distrib.* 5: 213-222.
- Whelan, R.J. 1995. *The ecology of fire*. Cambridge University Press, Cambridge, UK.
- Whittaker, R.H. 1975. *Communities and ecosystems*. 2nd. ed. Collier MacMillan, London, UK.
- Woodward, F.I., Smith, T.M. & Emanuel, W.R. 1995. A global land primary productivity and phytogeography model. *Global Biogeochem. Cycles* 9: 471-490.
- Woodward, F.I. & Lomas, M.R. 2004. Vegetation dynamics – simulating responses to climatic change. *Biol. Rev.* 79: 643-670.

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