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Frontiers of Biogeography

Title

update: From acorns mighty micropockets grow

Permalink

https://escholarship.org/uc/item/2rr3z0dm

Journal

Frontiers of Biogeography, 1(1)

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Publication Date

2009

DOI

10.21425/F5FBG12225

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ISSN 1948-6596 news and update

update

From acorns mighty micropockets grow

Dispersal processes may be critical in determining rates of species range shifts under future climate change. Travis Marsico, Jessica Hellman and Jeanne Romero-Severson, writing in the Journal of Biogeography, shed new light on the future by examining the past shifts in Oregon oak since the Last Glacial Maximum (LGM) (Marsico et al. 2009). They find that it doesn't take a village, it just takes a single tree. This helps support an emerging new view of how plant range shifts are realized when climate shifts rapidly.

Until recently, prevailing concepts of biological response to rapid warming in North America and Europe were of large, monolithic range shifts in which species totally vacated habitat of waning suitability, moving to new, completely disjunct range. This view began to change in 1995 when Matt McGlone and Vera Markgraf presented a starkly contrasting model of vegetation shift in the Southern Hemisphere. In New Zealand, McGlone found recolonization of the South Island to be much more rapid than could be accounted for by long-distance dispersal (McGlone 1995). In southern South America, Markgraf documented vegetation change keeping pace with extremely rapid climate 'flickers' (Markgraf and Kenny 1995). Both authors suggested that micropockets of vegetation could explain the very rapid observed changes in dominant vegetation. Such micropockets of vegetation were very plausible in these southern settings where no large continental ice sheets existed.

Evidence has since grown that micropockets may be important in Northern Hemisphere settings as well (recent literature is briefly reviewed by Marsico et al.). Tree remains very close to the boundary of the ice sheet have been found in paleorecords of both Europe and North America. Pollen signatures that were previously assumed to be from long-distance blow-in are now being reinterpreted as possible evidence of vegetation micropockets.

If the growing consensus around micropockets is correct, the implications for vegetation response to future, human-induced climate change is profound. Patches of vegetation of a few tens of meters on a side might provide source material at rapidly expanding range margins. Long-distance dispersal might establish micropockets of vegetation that would serve as stepping-stones for additional long-distance dispersal.

Marsico et al. show that in Oaks in the Pacific Northwest, dispersal was primarily from individuals on the leading edge of the range. Chloroplast DNA markers were remarkably homogenous in their samples. At 16 of 22 sites all individuals sampled shared a single chloroplast haplotype. Having identical chloroplast haplotype indicates a common maternal ancestor, so these populations were established from single colonizations or multiple colonizations by seeds from the same tree (which seems much less likely).

The implication is that single trees are critical for establishing populations in newly suitable range. Micropockets of vegetation would have ample sources of seeds for range shifts, if all it takes is a single tree. Marsico et al. found much more diversity in nuclear DNA, indicating that once single colonizations occur, populations grow and are diversified by wide pollen flow from many individuals. Colonists from micropockets and diversity from broader populations may be a key mechanism in rapid range shifts as rapid human-induced climate change gathers force.

Markgraf, V. & Kenny, R. (1995) Character of rapid vegetation and climate change during the late-glacial in southernmost South America. In Huntley, B., Cramer, W., Morgan, A.V., Prentice, H.C. and Allen, J.R.M. (eds.) Past and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota, pp. 81-102. Springer-Verlag, Berlin.

Marsico, T.D., Hellmann, J.J. & Romero-Severson, J. (2009) Patterns of seed dispersal and pollen flow in *Quercus garryana* (Fagaceae) following post-glacial climatic changes. Journal of Biogeography, 36, 929-941.

McGlone, M.S. (1995) The responses of New Zealand forest diversity to Quaternary climates. In Huntley, B., Cramer, W., Morgan, A.V., Prentice, H.C.

news and update ISSN 1948-6596

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commentary

New insights on a classic topic: The biogeography of Southeast-Asian mammals

Investigating the fauna of Malesia, the insular region between Indochina and Australia, has a long history in biogeography. In relating the distribution of animals to geographic settings of the present and the past, A.R. Wallace (1869) has not only defined our discipline but also provided data and ideas that substantially aided understanding organic evolution (e.g., Davies 2008). Given the depth of investigation of the Malesian region by Wallace and subsequent researchers until today (see references in Woodruff and Turner 2009), it is surprising that the delineation of the region towards the north-west, i.e. between 'Sundaland' and the Indochinese continental region, and the causes for this faunal transition, remained out of focus for so long.

In their recent article, Woodruff and Turner (2009) have used data on mammal distributions to investigate the faunal transition between continental Southeast Asia and the Thai-Malay peninsula (Fig. 1), building upon earlier analyses of the group (e.g. Woodruff 2003, Hughes et al. 2003). Woodruff and Turner show that there is not, in contradiction to common presumption and earlier results (e.g., Cranbrook 1981, Hughes et al. 2003, de Bruyn et al. 2005), a well-defined Indochinese-Sundaic faunal boundary, but rather a ca. 800 km gap between a southern fauna of the Malay peninsula (south of 5ºN) and the continental fauna (north of 14ºN). In this region species richness is reduced, and even many widespread species have gaps in their distributions. The authors discuss sea level changes as an agent that may explain this pattern. In the following I will first appraise two methodological and conceptual features – namely, 'simplistically' relying on raw distributional data, and the consideration of ancient shorelines during times when sea levels were higher than today. I will then raise the issue of historical versus environmental explanations in biogeography, in relation to Woodruff and Turners' fine work.

Woodruff and Turner relied on actual presence records to analyze the limits of species' distribution. The nature of their study region, with a clear north-south orientation, allowed using latitudinal range limits as a simple measure of distribution. For all but the best-sampled regions and taxa of Europe and North America, such data are surely biased by undersampling - species may occur well outside recorded limits, but have not yet been found. A large number of methods, ranging from more or less clearly defined 'expert range assessments' to numerical models of species' ecological niches (e.g., Elith et al. 2006), have been proposed to correct for such biases. However, such estimates of 'true' ranges are unable, at present, to account for the effects of dispersal barriers or local extinctions (e.g., Munguía et al. 2008), but require a priori assumptions on distributional limits caused by historical factors. Any gain by correcting for undersampling would therefore be punished by an increased circularity of arguments when the aim is to define historically caused boundaries of distribution. Decisions on using range estimates or raw data must be weighted in light of the investigated system (i.e., degree of undersampling) and the questions asked, and in Woodruff and Turner's study this is clearly in favour of the 'old-