Applied Vegetation Science 17 (2014) 4–5

COMMENTARY

Problems with edges: tree lines as indicators of climate change (or not)

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Abstract

Elevational tree lines are commonly seen as particularly important ecological 'ecotones' that should, according to models, respond sensitively to climate change. In this issue, Mathisen et al. report empirical analyses of two tree lines that fail to show expected upward movement. This study points up both methodological and conceptual challenges in understanding ecological edges and in connecting general expectations to specific cases.

At the 2013 meeting of the Ecological Society of America, over two dozen papers addressed tree line response to climate change; that number represents a doubling over each of the preceding 2 yrs. Climatic responsiveness of ecological boundaries is a central research priority, and tree lines seem particularly attractive, presumably because they are highly visible and are considered classic 'ecotones' – indicators of general change in community composition and ecosystem properties. Elevational tree lines may be particularly responsive to climate change because of spatial compression of climatic gradients (Beckage et al. 2008). However, assessing tree line response to climate encounters some challenges. Climate effects on elevational ranges may be masked or reversed by other drivers, particularly changes in land use or herbivory (e.g. Speed et al. 2012; Bodin et al. 2013). In addition, tree line species and their life histories vary geographically, and rates for population processes may cause lags in response (or at least detectable response) to climate change. Finally, even though tree lines are visually striking, they can be, like most ecological boundaries, empirically difficult to delineate; 'ecotones' are often conceptually slippery (e.g. Batllori et al. 2009).

Mathisen et al. (2014) assess behaviour over five decades of sub-arctic, elevational tree lines at two sites in northeast Russia. They address all of these challenges, although they do not overcome them entirely. The study area is free of historical human land use and has low grazing/browsing pressure, so may escape these confounding influences. The researchers combined tree line mapping over 50 yr using multi-temporal remote sensing, with analyses of spatial patterns and age structures of current populations to infer population status. They find only modest upward movement of tree lines – average gains of 27 and 29 m elevation are described as 'modest compared to… model-based predictions for forest advance at high latitudes' and statistically 'non-significant' – and cite similar findings from other European studies, where unresponsiveness to climate has been attributed to confounding effects of land-use history. Since human land use is not a factor here [or for similar findings of Kirdyanov et al. (2012) in Siberia], this departure from expectations under recent climate change is presented as a primary and challenging finding. The researchers suggest that this is a result of demographic lags and problems with detectability, rather than a real lack of sensitivity to warming. That is plausible; 50 yrs is still brief for assessing population dynamics of slow-growing trees where seedlings establishing above tree line may take decades to achieve the 2-m threshold used to define tree line.

Some lingering questions remain about interpretations and explanations offered by Mathisen et al. (and most other studies of tree line dynamics based on interpretation of current population distribution and age structure). Can occurrences of seedlings above existing tree line be interpreted confidently as indicating 'a clear potential for upward migration' or might they be a sink population likely to be wiped out by the next severe weather event? Without long-term survivorship data, it is difficult to differentiate an 'advance guard' of an expanding population from a dispersal-maintained sink population. Similarly, spatial 'infilling' of trees near tree line is interpreted as potentially 'priming' rapid future advances of tree line, but the inference of infilling is based on age structures of current populations. Could observed dominance of younger cohorts at tree line be a result of higher turnover rates at a stable tree line? Some of these issues might be addressable

Applied Vegetation Science
Doi: 10.1111/avsc.12077

only through even longer-term monitoring (Magnuson 1990; Bekker et al. 2007).

This study is likely to be a fertile contribution on ecological effects of climate change, but perhaps as much for questions remaining unanswered as for the specific interpretations offered. Do inconsistencies among estimates of rates of tree line change challenge the usefulness of 'global climate model-based predictions' in understanding particular systems? U.S. politician, Tip O'Neill said, 'all politics is local'. Perhaps some ecological phenomena are as individualistic as electoral constituencies, requiring projections to be conditioned on local contexts. If so, local environmental drivers may not mirror global trends; Mathisen et al. report increasing precipitation, but no temperature trend over the last 50 yrs at Murmansk (and, at 140 km from the study area, are Murmansk trends local enough?). Further, the two study areas of Mathisen et al. involve different tree line species that differ phylogenetically and in life history (a conifer, *Pinus sylvestris,* and an angiosperm, *Betula pubescens*). If species distributions along elevational gradients respond individualistically to environmental change (e.g. Bodin et al. 2013; Kopp & Cleland 2014), might it be expected that tree line dynamics, as well, will be individualistically species-dependent?

Or perhaps the relative unresponsiveness of tree line reported here and elsewhere (citations in Mathisen et al.) suggests that trees, even in marginal environments, are simply insensitive to short-term climate change, either because of demographic inertia (Jackson 2013), or because limits are not determined directly by temperature (Takahashi et al. 2012; Dubuis et al. 2013)? Yet, other studies show relatively little 'inertia' in elevational shifts of trees (Beckage et al. 2008). Could the expectation of rapid tree line change prove to be something of a straw man? Are tree lines less responsive than other elevational range limits?

Empirical studies of climate effects on local populations are still fewer than global modelling attempts. The difficulties of interpreting the kinds of evidence reported by Mathisen et al. indicate why this is so. Rigorous study of long-term change in slow systems is hard. This is not a new observation, and it has been suggested that understanding the dynamics of slow systems necessarily requires studies designed around intensive, long-term monitoring (Magnuson 1990; Bekker et al. 2007). But, unless and until more such studies are in place, we will continue to need clever, synthetic approaches combining historical data and imagery and close analysis of current populations, as done by Mathisen et al.

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Doi: 10.1111/avsc.12077