Field experiments on mechanisms influencing species boundary movement under climate change

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Abstract
Scope  Currently knowledge is weak about which plant species boundaries are determined directly by climate and soil factors, versus which are mediated by biotic interactions, such as exclusion by superior competitors or by pathogens. Under moving climate zones the difference is important. For example, will warm boundaries shrink poleward of their own accord, or only following invasion by other species? What research will most effectively strengthen our understanding of this fundamental issue in ecology?

Conclusions  Traditionally the required experiment has been transplant beyond the species boundary, together with density manipulation of putative competitors, herbivores, pathogens or facilitators. But now climate zones are being moved across species distributions, creating a different sort of experiment. In order to learn efficiently from this massive inadvertent experiment, exposure to new climate needs to be combined with experimental manipulation of other factors. Because range extensions are likely to be spatially patchy, these experiments need to be geographically extensive, to be sustained over 2–4 decades, and to be twinned with wide-area population monitoring via drones and other remote sensing. Highest priorities for experimental manipulation would be removal of competition, and provision of seedlings. Highest priorities for locations would be zones where vegetation physiognomy changes, such as woodlands into grasslands, or rainforest into fire-prone forest.

Keywords  Species boundaries · Climate change · Transplant beyond boundary · Competitive exclusion · Dispersal

The problem of geographical boundaries

Moving climate zones present a challenge for ecological research, and also an opportunity. The challenge lies in the considerable changes already under way (e.g. Bergstrom et al. 2021; Elsen et al. 2021). The opportunity lies in the potential for a new type of field experiment to clarify how future ecosystem transformations will work. This paper outlines those experiments and why they are needed.

Geographical boundaries for species distributions have long been a central question in ecology. Krebs’s textbook (first edition 1972) says it in the title – “Ecology: the experimental analysis of distribution and abundance”. Krebs’s emphasis on experimentation followed the classic field experiments of Connell (1961), transplanting barnacles up and down the tidal range. Balanus occurred lower on the shore, and transplants showed its upper boundary was set by being unable to cope with dessication. Chthamalus...
occurred higher, and transplants showed its lower boundary was set by competition from *Balanus*. Importantly, the lower limit of *Chthamalus* was well correlated with tidal height, and correlative models would have identified that physical factor as a predictor. But experimental manipulation showed that in the absence of competition from *Balanus*, the distribution of *Chthamalus* could extend much further down the shore. The chapter structure in Krebs’s textbook followed a logic diagram (Fig. 1) where the first step was to transplant a species beyond the boundary (with control transplants inside the boundary), testing for limitation by dispersal. Subsequent steps were to transplant in conjunction with suppression of competitors or predators or with amelioration of physical habitat.

Through the 1970s and 1980s manipulative field experiments became the favoured research style in ecology, the gold coin of knowledge because of their power to dispel cross-correlations. And yet, over the past 50 years the great majority of experiments on competition (or on herbivory or pathogens or mutualists) have not been conducted beyond boundaries. They have been directed at measuring the intensity of interaction within communities, more so than at understanding boundaries. Given the problems of obtaining permission to transplant beyond the current distribution, and the difficulties of executing experiments at sites distributed across hundreds of km, this is perhaps understandable. But the upshot is that our understanding about plant species boundaries remains weak.

The research community’s principal tool so far for addressing likely scenarios under climate change has been species distribution models, SDMs. However, these are intrinsically correlative. In some, other species are permitted to be predictors of the distribution of the focal species, and they “take other species into account” in this sense (e.g. Mokany et al. 2012). But if the distribution of a superior competitor coincides with isolines of the physical environment, no data analysis however sophisticated can determine which is responsible.

Paquette and Hargreaves (2021) have recently compiled the available literature about distribution boundaries. Outcomes from the portion of it that comes from transplant experiments beyond boundaries and is about vascular plants on land are summarized in Table 1. Although numbers of studies have been increasing recently, they are still rather few. More have been conducted along elevation gradients than across latitudes. A large share are for annuals or herbs, sometimes transplanted as turfs. Most have measured success via some fitness component such as growth, only a minority have followed demography through a full life cycle.

Table 1 indicates that at warm boundaries, biotic effects quite often decide the boundary location. This is expected (Louthan et al. 2015; Paquette and Hargreaves 2021) from Darwin’s hypothesis: “When we travel southward [in the northern hemisphere] and see a species decreasing in numbers, we may feel sure that the cause lies quite as much in other species being favored, as in this one being hurt” (Darwin 1859). Competition is the most common biotic effect detected, but herbivory and pathogen effects have also been found. At cool boundaries, competition effects also occur but seem less prevalent relative to direct effects of climate.

While the number of designed field experiments beyond boundaries is limited, there is considerable informal evidence. Species that have become invasive on new continents often suffer less leaf damage from herbivores and pathogens than in their native range (e.g. Leishman et al. 2014). These are transplants to different biotic environments but not usually to a different climate. When plants are grown in gardens or plantations (Booth et al. 2015; Booth 2015), they are typically protected from competition, and sometimes
watered. Under these conditions it is evident that many species can be grown at a wider range of temperatures than their observed field distribution. For example Bocsi et al (2016) found that equatorward boundaries for mid-winter daily maximum temperatures averaged more than 3 deg C warmer in gardens than in nature, with different species ranging from 0 to 11 degrees warmer.

The implication of this existing knowledge is that while some species can be expected to move in conjunction with temperature zones, for others the future movements of their distributions will depend critically on how their competitors move, or perhaps on how their pathogens or herbivores move, or on dispersal, whether natural or assisted. It needs to be a research priority to work out what to expect for particular species of importance. Ideally also, we would work out how to generalize across species that have not been individually experimented on. What traits of species or features of the situation would help us predict what controls a boundary?

### A new type of field experiment

Krebs assumed that experiments to test how boundaries were determined had to be accomplished by transplanting the species in relation to habitat. This indeed is how the experiments described in Table 1 have been done. In the 2020s, though, the habitat is being transplanted in relation to species. Since 1970 mean air surface temperatures have already increased by more than 1 °C. This corresponds roughly to 150 km polewards at mid-latitudes, or to about 100 m elevation. The process continues to accelerate, and warming of a further 2 °C seems as likely as not by 2070. So the transplants that dissociate species distributions from climate zones are now being done for us, but by relocating the climate rather than the species, and over time scales of decades.

Four possible outcomes from the movement of climate zones are outlined in Fig. 2. The schematic is simplified to the iconic case of two species (Connell 1961) with the equatorward boundary of one coinciding with the poleward boundary of the other. Either species could equally be construed as a category such as evergreen canopy plants. The moving environmental gradient shown in Fig. 2 is mean annual temperature, but equally could be precipitation, or temperature extremes of different kinds, which are not perfectly correlated with mean temperatures, or in principle any environmental factor that is moving polewards and that is decisive for species distributions.

|                      | Warm boundary | Cool boundary |
|----------------------|---------------|---------------|
| # of studies (# that were latitudinal rather than elevation) | 33 (4) | 57 (22) |
| # of taxa transplanted | 63 | 128 |
| # of taxa where particular processes were found to limit occurrence beyond the boundary | | |
| Dispersal | 14 | 46 |
| Temperature or precipitation or unspecified climate | 27 | 67 |
| Competition | 21 | 26 |
| Herbivory or seed predation | 9 | 6 |
| Pathogens, parasites | 3 | 1 |
| Pollination | 0 | 2 |
| Mutualism (ant and Rhizobium) | 2 | 0 |
| Facilitation by other plant species | 0 | 0 |
Outcomes 1, 3 and 4 represent delay or hysteresis in movement of species distributions compared to temperature zones. Biological mechanisms that can contribute to these delays (Fig. 2 column C) include slow dispersal or establishment and hence slow range extension, persistence of populations even after recruitment has fallen below replacement, and competitive advantage. The reason why manipulative experiments are important is that we need to assess which of these mechanisms are operating in particular situations. There are important consequences for future ecosystems and management. Should we be encouraging migration, by assisted colonization, or possibly via corridors? Or should we discourage it? Should we be clearing established species in order to allow others to migrate?

The movement of climate zones that dissociates habitat from species distributions in itself offers useful information. But to learn efficiently from it, experimental manipulations are also needed. So this paper’s proposal is, in brief, that the research community should get organised to conduct experimental manipulations in conjunction with the poleward travel of climate zones across species distributions. This cannot be accomplished just by individual researchers applying for 3-year research grants. It needs a more extensive coordination, and more consistency through time.

Priorities and choices

Which mechanisms to target?

There are a large number of mechanisms that could potentially be experimentally manipulated, and variations within each of those mechanisms (Box 1). Even if only one binary contrast were included to address each of the seven major categories of mechanism in Box 1, such an experiment would already be at $2^7 = 128$ treatments, which with replication is a very large experiment indeed. Yet at the same time, we need experiments to be repeated across a wide spread of locations. Choices need to be made about priorities.

Box 1 List of major possible experimental manipulations, with brief notes on variations. Each manipulation targets a different mechanism

1. Provision of dispersal for species not currently present at the site
   1.1. Variations in which species provided, in the provenance from within the range of those species, in whether provided as seeds or seedlings, and in whether symbionts such as mycorrhizas are also provided
2. Suppression of competition
2.1. Variations in whether all competitors are suppressed or only one species or a category such as canopy individuals or grasses

3. Modification of resources

3.1. Possibly the most interesting being bringing soil from elsewhere, since distributions are often restricted by soil type as well as by climate. Addition of soil nutrients, or irrigation, are also possibilities

4. Facilitation – the possibility (for example) that woody plant seedlings entering into herbaceous vegetation will be more successful under previously established woody plants

5. Mutualisms – for example symbioses with rhizobia or mycorrhizas, or interactions with ants that concentrate nutrients

6. Exclusion of herbivores

6.1. Vertebrate herbivores require fencing and invertebrates usually require pesticides

7. Suppression of plant pathogens

7.1. Requires repeated spraying of fungicide (for example)

On existing evidence (Table 1), dispersal and competition are the factors most likely to influence transitional processes while vegetation responds to moving climate zones, and consequently the factors that we most need to understand. Also, facilitation and mutualism are intrinsically less satisfactory as explanations for species boundaries. If the reason why species A does not occur beyond a boundary is absence of species B, then this simply shifts the question to being about the boundary of species B. Accordingly it is proposed that the basic core design for experiments (Table 2) should provide dispersal for species from warmer environments, and should assess the consequences of suppressing competition.

There is much scope for elaborating this base-design set of four comparisons in Table 2. For example, further experimental contrasts could be added where there was reason to expect soil or herbivory or pathogens to be important. Or tests on physiological heat tolerance for key species could be added to complement the field experiment. However, in my opinion the impulse to elaborate should usually be resisted. The highest-priority aim should be to generalize effectively, across species and situations and local-site variability, and this aim would not be well served by elaborate multi-factor experiments at a small number of sites. Experimenting in a simple way at a large number of sites is a higher priority.

Scale through time and across space

These experiments need to persist through decades, for two reasons at least. First, temperature change will be progressive, so effects across different distances will work themselves out slowly. Second, species that

| Table 2 Proposed comparisons C1-C4 in base-design experiments and the questions they answer |
|-----------------------------------------------|
| **Question** | **Comparison and experiment** |
| Is movement of species dispersal limited? | C1: Provide dispersal poleward from cool boundaries. In form of seedlings, because for perennials, mean survival from seed to seedling is commonly well under 1%, hence seed colonization experiments often produce small numbers of established seedlings. Use provenance from cool boundary. Control transplants within the range. Dispersal to current warming (1 °C distance from 1970 boundary) tests for whether dispersal has failed to keep up with temperature zone movement so far. In the event that the species has already moved in conjunction with temperature change since 1970, this experiment would not be necessary |
| Is extension at cool boundary contingent on suppression of competition? | C2: Transplant of warm-side species beyond cool-side boundary, with and without suppression of competing species. Primary treatment would be complete suppression of all competition. In vegetation where seedling establishment is mainly after fire, ashbed would be created both for treatments with and without competition. Transplant as seedlings (cf C1), but it would also be possible to introduce seeds and/or saplings in order to arrive more quickly at estimates of survival through different life stages |
| Is shrinkage of warm boundary contingent on competitors arriving? | Two comparisons here |
| | C3 Transplant of cool-side species into range of warm-side species, with and without suppression of warm-side species |
| | C4 Continuation of C2, the treatment without suppression of cool-side competitors. If the warm side species can indeed establish in face of competition, does it at a later stage competitively supersede the cool-side species? |
invade or that are experimentally introduced need time for growth and population dynamics before the answer emerges to the question whether they competitively exclude residents.

Pathways for achieving this kind of continuity will vary between different countries depending on their arrangements for supporting research. In my home continent Australia currently, the likeliest pathway is to work in conjunction with the Terrestrial Ecosystem Research Network. This is a program within the National Collaborative Research Infrastructure Strategy, and it includes vegetation plots that are to be recurrently monitored. There are (as of 2021) more than 800 Ausplots, and a smaller number of Transects and Supersites. Ausplots are for monitoring not for experimental manipulation, but experiments could be positioned near them and could be monitored within the same program.

A problem in studying advancing boundaries of species distributions is that they are likely to be very patchy in space. Experimental manipulation and boots-on-ground demographic measurement are only achievable in plots of a few m across. But the biological processes, and the management importance, operate across fronts of tens to hundreds of km. Two main steps can stretch the evidence and help with this discrepancy of scales. First, experimental manipulations such as removal of competitors can be twinned with providing seed and seedling input of prospective colonizing species. This eliminates the stochasticity associated with dispersal of propagules, one of the substantial sources of spatial patchiness. Also if at all possible, experimental plots should be distributed widely along the boundary, rather than concentrated at a single site.

Second, experimental plot work can be combined with remote sensing. Traditional satellite and air photo imagery can not provide for tracking individual species or individual plants. However recent high-altitude air photography has resolution of 5 cm or less, at a cost below $10 km\(^{-2}\) yr\(^{-1}\). Resolution and cost can be expected to continue to improve over the next decades. This is capable of picking up individual woody plants down to sapling stage, provided they are not under canopy.

In addition, new possibilities are emerging via drones. “Digital twins” – complete 3D representations of landscapes – are increasingly common, and the European Commission has a Destination-Earth (https://digital-strategy.ec.europa.eu/en/policies/destination-earth) project to develop a global digital twin by 2030. In Australia, the Research Data Commons aims to establish a scalable drone cloud (https://ardc.edu.au/project/australias-scalable-drone-cloud/) that would allow drone imagery from any source to be stitched together and converted into 3D.

Boots-on-ground identification will be needed initially. However, imagery either from high elevation or from drones may in future have potential to track year-by-year demography across tens to hundred of km, under some circumstances.

Locations and species

There are about 20,000 vascular plant species in Australia, each with different boundary mechanisms on different parts of the edges of their geographical ranges. Clearly only a few of these boundaries can be studied, and only some of the possible boundary-setting mechanisms can be tested. Priority should be species which when they move into new locations are capable of substantially changing the the physiognomy of the vegetation, for example invasion of woody plants into what was previously herbaceous vegetation. Perennial canopy plants are foundation or habitat-forming species for terrestrial ecosystems, their traits having strong influence on other species and on ecosystem processes. A large proportion of previous transplants beyond boundaries have been conducted with annuals or in herbaceous vegetation. This is understandable given they are easier to transport and their demographic fate can realistically be tracked over a shorter time. But for the future, it will be important to focus on changes with the largest ecological consequences, rather than on those easiest to study.

Where are the most important potential physiognomy changes in Australia? Treelines at higher elevation are an obvious candidate. An informal international network G-TREE (http://treelinesresearch.com/) aims for simple experiments at many locations, transplanting tree seeds beyond arctic and alpine treelines, with and without scarifying the soil surface; results have not yet been published. However, in Australia cold treelines do not account for very large areas. Much more important, in terms of area affected, is the shift from woodland or forest near the northern coastline, to grass-dominated further south.
and inland. This transition occurs between roughly 15 and 20 degrees south latitude, and is spread longitudinally across more than 2000 km. Being latitudinal it is broadly aligned with mean annual temperature, but is strongly associated also with decreasing monsoonal rainfall with distance from the coast. Change in mean temperature is almost always bound up with other factors. At the 19 Australian ecosystem types discussed by Bergstrom et al. (2021) as entering into radical change, all were experiencing at least six different pressures, including for example precipitation change, invasives, fire regime change and heatwaves as well as change of mean temperature. Some areas of north Australian grassland overlap floristically with the grass mixture under the woodlands nearer the coast, while others such as Astrebla grasslands are distinctive and influenced by soils more so than by rainfall and temperature gradients.

Another important type of transition occurs where eucalypt forest meets rainforest vegetation, since rainforest understorey tends to make fires less likely or less hot (e.g. Baker et al. 2021).

In summary, the principle for prioritizing where to position experiments is locations where movement of species from warmer environments would make a substantial difference to the physiognomic structure of the vegetation or to fire regimes or to other aspects of ecosystem behaviour.

Conclusion

Up to the present, future scenarios under climate change have relied heavily on ecophysiology, aiming to characterize drought and thermal tolerances and responses to elevated CO₂. Scenarios have used also models that draw their data from existing geographical distributions. Both these research styles have been tractable, and have attracted much research talent.

But it is clear that biotic interactions are often important. For perennial plants, existing evidence from transplants across boundaries suggests competition is especially important. To understand the role of biotic interactions in setting boundaries to distributions, manipulative field experiments are essential. They are difficult but they are the gold coin for understanding mechanisms of biotic interaction.

New experimental designs are becoming possible because of the movement of climate zones across prior species distributions. Some of the important outcomes from these experiments need to be tracked over decades, and some of the treatments need continuing maintenance.

The experiments advocated here need to extend over decades. Also they would ideally be coordinated across different ecological boundaries around Australia. They cannot happen via individual research teams seeking grants to cover 3 or 5 years of work. New forms of research organisation need to be developed that can coordinate and support such a program.

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