



What drives divergence from chronosequence-based predictions of birch forest succession?

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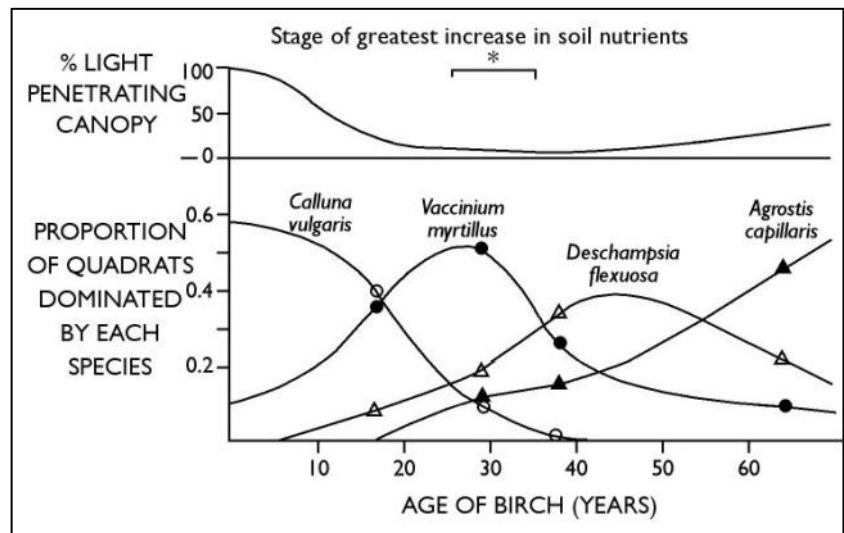
Introduction

Space-for-time substitutions in the form of chronosequences have long been used in the study of succession and have been invaluable in helping form many of the concepts and ideas which are still prevalent today. However, despite the many decades of field-based successional research, rarely have chronosequence-based studies of long-term successions (>50 years) been tested against real temporal changes at the same sites, to assess the efficacy of this approach. Most such studies have used old-field successions, which are relatively short-term. Recent reviews of these few studies have variously concluded that assumptions based on chronosequence-based sequences are at best only partially accurate, too static, or invalid. But in some cases this may be due more to inappropriate use (spatial variability compounding assumed temporal variability; insufficient replication; missing successional stages in suite of sites chosen; etc) than invalidity of the chronosequence approach *per se*.

Our approach

We use chronosequence and repeat-visit data from a 34-year study of a low diversity birch forest succession (Miles & Young 1980; Hester *et al.* 1991a, b, c) to examine: a) how well do chronosequence-based predictions reflect the reality of successional changes over the last 34 years; b) where there is divergence between predictions and real changes, what are the main drivers of divergence, and how predictable might they be? The system is a secondary succession, taking on average 100 years to change from open moorland, dominated by the dwarf shrub heather (*Calluna vulgaris*), to mature birch forest (*Betula pubescens*, *B. pendula*) which then senesces. Our basic premise is that: if successional patterns inferred from the initial single-visit chronosequence data from our study sites are indicative of true successional dynamics, then the temporal dynamics observed between the three survey dates should correspond with the single-visit static patterns. If (where) they do not correspond, we examine the main causes of divergence from predictions and assess the predictability of alternative pathways of succession.

Figure 1. Chronosequence-predictions of successional change at one of the 3 sites: Craggan, from data collected in 1986 (redrawn from Hester *et al.* 1991a).

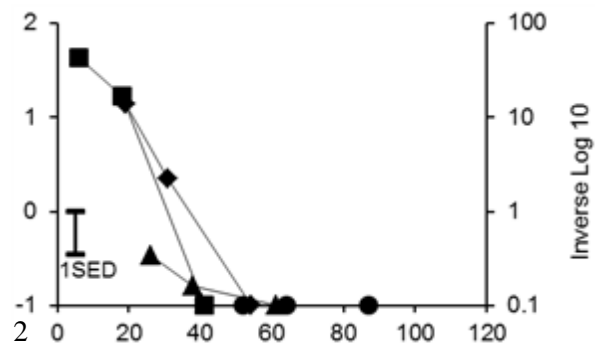


Findings

Comparison of predicted changes (from the chronosequence data) with real changes over 34 years showed good correspondence for species richness and Ellenberg indicator species data, but variable correspondence for the individual species shown in the diagram above.

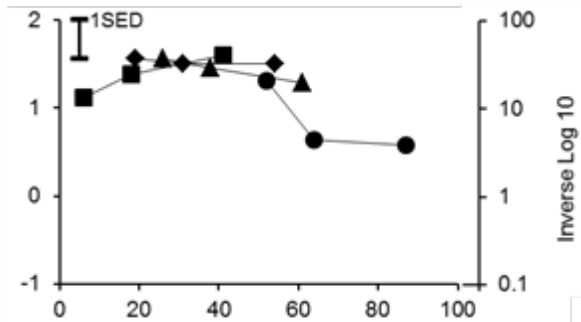
Calluna vulgaris showed good correspondence, declining in cover as predicted through the succession to mature birch woodland (Fig 2).

Figure 2. Actual changes in *Calluna vulgaris* cover through time (years) within all sample plots (individual symbols indicate replicate plots). RHS y axis shows back-transformed % cover values.



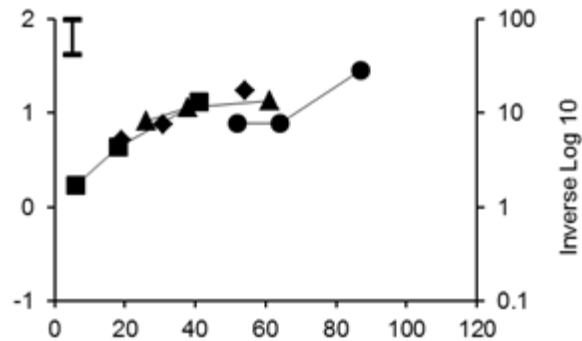
Vaccinium myrtillus was predicted to increase to maximum cover under c.25 year-old birch and then decline. The real changes showed good general correspondence with predictions but its cover remained high for much longer than predicted by the chronosequence data (Fig. 3).

Figure 3. Actual changes in *Vaccinium myrtillus* cover through time (years) within all sample plots (individual symbols indicate replicate plots). RHS y axis shows back-transformed % cover values.



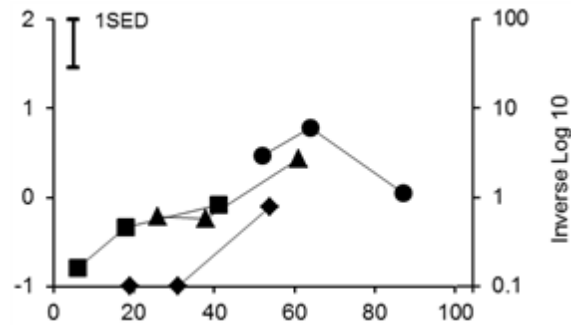
Deschampsia flexuosa was predicted to increase following the decline of *V. myrtillus* and then decline again at c. 45 year-old birch; real changes showed the expected increase but then this species persisted or even increased its cover even under the oldest birch stands (85 years) (Fig. 4).

Figure 4. Actual changes in *Deschampsia flexuosa* cover through time (years) within all sample plots (individual symbols indicate replicate plots). RHS y axis shows back-transformed % cover values.



Agrostis capillaris was predicted to increase rapidly as the birch aged from about 20 years old, becoming dominant under c.55 year-old birch. Temporal changes in *Agrostis spp* cover were highly variable and no sites followed predictions for this species: at Craggan, cover of this species changed markedly between each recording year in the oldest stand, but changed little in the other stands.

Figure 5. Actual changes in *Agrostis capillaris* cover through time within all sample plots (individual symbols indicate replicate plots). RHS y axis shows back-transformed % cover values.



Discussion

The subset of data shown here show how some successional patterns inferred from the initial single-visit chronosequence data were indeed indicative of true successional dynamics; whereas others did not follow predictions. In the latter cases, we have examined the likely causes of divergence from these static predictions, to allow us to assess the predictability of alternative pathways of succession. This focused primarily on changes in canopy cover and soil nutrients as the main drivers of this succession, but we also examined changes in grazing levels where information was available.

We found little evidence for soil-related drivers of divergence from predicted successional pathways. Light levels changed significantly in the late 1980s due to outbreaks of winter moth, *Operophtera brumata*, resulting in significant opening of the canopy in some parts of this site, but again there was no evidence of this being the main driver of the deviations from predicted changes in the main species shown above (in contrast, at two other sites, similar outbreak-driven tree deaths and increases in light were hypothesised to be the main driver of deviations from predicted successional pathways).

A major change in grazing regime at this site is hypothesised to be the main driver of the deviation from predictions for *V. myrtillus* and *D. flexuosa*. Until c. 1990 the site was winter-grazed by sheep; the timing of the cessation of this grazing use strongly correlates with the divergence from predictions for both *V. myrtillus* and *D. flexuosa*: both were predicted to decline but continued to increase in cover following sheep removal. Both are relatively grazing-sensitive.

From the data at all our sites combined, we are constructing a successional model incorporating alternative pathways to that shown in Fig. 1, with hypotheses about the conditions under which any of these pathways might be followed. From our data, the two main perturbations causing the most dramatic deviations are premature tree loss (in this case due to insect outbreaks) and changes in grazing regime, leading to knock-on effects on the direction of plant community change. Our data add support for the use of chronosequence studies as an essential part of a suite of tools for successional studies (Walker *et al.* 2010). Chronosequence studies can help unravel the processes driving vegetation change and provide a useful framework for development and testing of hypotheses about important drivers of change in different systems.

Acknowledgements

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References

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