Spatial heterogeneity in the determinants of woody plant invasion of lowland heath

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Abstract

Questions: 1. What is the scale and extent of spatial variability in factors affecting Betula invasion of heaths? 2. How much effect does each factor have on within-patch patterns of invasion? 3. How can this understanding aid in managing Betula invasions?

Location: Lowland heath of southern England.

Methods: Determinants of Betula (both B. pubescens and B. pendula) invasion: biomass density, necromass density, mean vegetation height, P-availability, soil water content and total Betula seed bank density, were measured at two sites on a 5-ha sampling grid. Spatial pattern was assessed using geostatistics. Contributions of each determinant to within-site heterogeneity in predicted Betula seedling densities were estimated by varying variables over their full and interquartile ranges in a statistical model derived from experimental data.

Results: Salient spatial trends were revealed: strong autocorrelation over distances of <50 m for soil factors and more extensive autocorrelation (0 to >150 m) in vegetation variables and Betula seed bank densities. The latter resulted in single across-site gradients, the former small, distinct patches. All patterns were overlain with variance that was present at distances of <17.6 m. Variables displaying spatial pattern also accounted for within-site heterogeneity in predicted Betula seedling densities but their relative contribution to this varied between sites.

Conclusions: Identifiable spatial autocorrelation in factors controlling patch-scale invasion patterns allows managers to target invasion prone patches, potentially reducing management intensities. Furthermore, management effort may be optimised by spatially de-coupling Betula seed from safe-sites. This plan may adaptable to the management of other weeds and open-land ecosystems.

Keywords: Betula; Conservation management; Ecosystem state shift; Heathland; Kriging, Phosphorus; Safe-site limitation; Seed limitation; Variogram.


Abbreviations: P = Phosphorus.

Introduction

Invasion of native and exotic woody plants into non-forested areas generates transitions between ecosystem states differing in ecosystem function and community composition (Scheffer et al. 2001; Wardle 2002). These changes occur because woody plants provoke environmental changes that facilitate the invasion of conspecifics and associated species (Wilson & Agnew 1992). Such invasions are considered deleterious to the conservation of open-land ecosystems, e.g. grasslands and heathlands, as restoration to the non-wooded, state is often difficult, expensive and incomplete (Suding et al. 2004).

Invasion of woody plants is often patchy, implying spatial pattern in propagule availability or habitat invasability, factors which are equivalent to safe-site and seed limitations (Eriksson & Ehrlén 1992). There have been many studies of what determines the recruitment of colonising trees (e.g. Li & Wilson 1998; Terwillinger & Pastor 1999) but few (e.g. Gross et al. 1995; Jurena & Archer 2003) which consider spatial variation in invasion determinants and its effects upon colonisation patterns. There has also been little discussion of spatial heterogeneity in recruitment limitations in invasion management strategies.

The invasion of Betula spp. (both B. pubescens and B. pendula) causes transitions between heath and scrub ecosystems, with significant transformations to community and ecosystem properties occurring within as little as 25 years (Satchell 1980; Hester et al. 1991a, b). These changes are highly resistant to restoration, which is labour intensive and expensive (Auld et al. 1992; Mitchell et al. 1999). A multi-site, multi-factorial field experiment (Manning et al. 2005) found both seed and safe-site factors to limit Betula colonisation. Data from this experiment was used to fit a statistical model (hereafter the general model) describing Betula seedling densities (assumed to be indicative of invasion success) as a function of: mean vegetation height, biomass density, P-availability, necromass density, total Betula seed bank
density and soil water content. There were numerous interactions between these determinants, particularly vegetation factors and total Betula seed bank density. What remained unknown was which factors vary over critical ranges in field conditions and display spatial patterns that are identifiable by managers. Spatial pattern is expected because Betula invasion is patchy at many scales (Chapman et al. 1989a; Rose et al. 1999), including the patch scale (0-5 ha); that to which management is applied. We therefore investigated the extent, scale and pattern of variation in the determinants in typical heathland conditions at the patch scale. This was achieved by measuring the determinants on a grid at two heathland sites and employing geostatistical analysis. We then estimated the relative importance of the factors in determining within-patch heterogeneity in predicted invasion success by varying each variable over its range within the general model. These results are integrated with those of earlier studies to produce a management plan that aims to prevent Betula invasion whilst conserving characteristic heathland species. Although its detail is specific to heathlands this plan is adaptable to other open-land ecosystems undergoing woody plant invasion from surrounding habitats.

Methods

Study sites and sampling regime

Spatial heterogeneity in all general model variables was studied on two heaths, one each in the Surrey and Dorset heath regions of southern England. Sites were selected for: being representative of their region, being > 5 ha (200 m x 250 m) and lacking fragmentation. The sites and data were also used to validate the general model (Manning et al. 2005).

Each site’s sampling grid consisted of 130 regularly spaced points, with distances between points ranging from 17.6 m to 250 m (Fig. 1). The rationale for this grid is that smaller scale variation is effectively stochastic to managers while larger scales are irrelevant to many heathlands, which are often small (< 10 ha) (Webb & Haskins 1980).

The first site at Arne, Dorset, ‘Arne’ (50°42'04'' N, 2°02'45'' W) is dominated by Calluna vulgaris, Pteridium aquilinum, Erica tetralix and Molinia caerulea. Most vegetation is in the mature and degenerate phases of the dwarf shrub cycle (Watt 1947) but there is also short vegetation of mown firebreaks. The site is bordered by Betula scrub on one corner (the bottom right of Fig. 2K) and contains a few Betula trees around its perimeter. No burning has occurred for over 30 years except for a small patch in 1998. Because no seedlings were sampled using quadrat techniques Betula seedling density was estimated at 0.0/m² (standard error (SE) = ± 0.0) (Manning et al. 2005). The site is not grazed by domestic animals but Sika Deer (Cervus nippon) are often seen nearby.

The second site, at Horsett, ‘Horsett’, (51°20'24'' N, 0°32'54'' W) has undergone substantial invasion by Pinus sylvestris and Betula spp. (towards the top left and top right of Fig. 2M). The dominant species are C. vulgaris, E. tetralix and M. caerulea. Vegetation is mostly in the building and mature stages making it shorter and with less necromass than at Arne. Some areas have experienced recent scrub removal while others are overlain with young trees (e.g. the centre bottom of Fig. 2M). The site was not burnt in the 30 years prior to study. Betula seedling density was 0.11/m² (SE = ± 0.05) (Manning et al. 2005). Horsett is not grazed by domestic animals.

Data collection and analysis

Vegetation density and height were recorded using a point quadrat procedure (Manning et al. 2004) which records presence/absence of biomass and necromass for each 1 cm height interval of 60 mm diameter fibre canes. This allows estimates of biomass and necromass density and mean vegetation height. However, although quadrat size (2 m x 1 m) was the same as for Manning et al. (2004), point density was only 18 and estimates were adjusted accordingly. Vegetation surveys were conducted in July 2000 at Arne and July 2001 at Horsett. Soil sampling was conducted in November 1999. Samples were taken with a 20 mm diameter cylindrical soil borer and analysed, at 0-50 mm depth, for gravimetric soil water content (% total mass) and long term P-availability, as
measured by ammonium oxalate extractable P (P_{oa}), according to the Pote et al. (1996) method. Because ammonium oxalate dissolves iron and aluminium oxides P_{oa} represents a larger and longer-term available P-pool than that estimated by weaker extractants. Total Betula seed bank density was estimated by taking seed bank samples (five 30 mm cores with a total area of 98 cm²) in February 2000 and processing them according to the method of Manning et al. (2005). The method is based around removing emerging seedling Betula from an irrigated seed bed, covered thinly by the sample, over 4 months.

Within-patch heterogeneity in all general model variables was explored with variogram estimation and kriging interpolation (McBratney & Webster 1986; Robertson 1987). There were insufficient data to analyse Betula seedling densities. A variogram describes covariance (γ) as a function of spatial separation, or lag distance (h). The nugget, or intercept, variance, γ (0), is the combination of sampling error and autocorrelated variance on a scale below the minimum lag (17.6 m). A flat variogram therefore represents a lack of spatial structure. Two other parameters, the range (a), which represents the h where autocorrelation ceases, and the sill (C), the covariance at a, allow spatial dependency estimates; 1 – (γ (0) / C) = the proportion of autocorrelated variance. The asymptote represents average patch size.

Initial data inspection found that anisotropy was absent and so subsequent analysis assumed a constant trend of autocorrelation. Three variogram models: spherical, exponential and Gaussian, were fitted to each variable using weighted non-linear least squares and that with the minimum residual sum of squares was selected. Each lag estimate was based upon ≥ 30 distance pairs. Goodness of fit for each selected model was compared with a null model with an intercept equalling population variance. The a of some variograms exceeded the maximum lag (150 m). In such cases estimates of proportional autocorrelated variance are questionable, as much is assumed from extrapolation. Once variograms were fitted they were used in ordinary kriging. In this process interpolation weights are based upon the variogram (Robertson 1987). The end result was a grid of 900 interpolated values for each variable which allows visualisation of patterns described by the variograms.

Very low seedling densities prevented us from relating actual invasion to the measured determinants. For this reason the impact of the determinants on within-patch heterogeneity in predicted Betula seedling densities was estimated by varying each determinant over its full and interquartile range (of the original rather than kriged data) within the general model, whilst holding the others constant at their site mean. The difference between maximum and minimum predicted values was then calculated.

With this method, variables with large expected impacts on patch-scale variability are those varying over ranges with strong effects on predicted Betula densities in the general model. The potential drawbacks of this approach are that interactions between variables are ignored and that it assumes (a) the general model is correct, and (b) that relationships of the general model hold when extrapolated. The extent to which the first drawback operated was assessed using Pearson’s rank correlation. If variables are uncorrelated then their average interaction effect will equal the interaction of their site means. Discussion of second drawback can be found in Manning et al. (2005), the third in the discussion. All analysis was performed in S-Plus 6 for Windows (Venables & Ripley 2002). Some data (maximum n = 18) were absent from the Horsell analysis. This was due to points coinciding with mature Betula and footpaths and the loss of two soil samples.

**Results**

Variogram fit exceeded null model fit for all variables (explained deviance 28-96%) and autocorrelated variance (where estimable) accounted for 16-96% of the total (Table 1, Fig. 2 A-M). Although variogram fit was fairly consistent, patch size (a) and spatial dependency varied between sites and between variables within a site (Table 1). Despite this variability, soil variables (soil water content and P-availability) always displayed a values of ca. 25 m (Fig. 2A-F) while vegetation and seed bank variables had a values >150 m (Table 1, Fig. 2G-M). This resulted in identifiable gradients in vegetation properties, within which there was considerable small-scale (<17.6 m) variation. Kriged grids of total Betula seed bank density estimates were consistent with Betula distribution indicating that the spatially structured component of Betula seed bank densities declined strongly over distances of ca. 50 m from mature trees (Fig. 2J-M).

Data range manipulation demonstrated that all variables generated within-site heterogeneity in predicted Betula seedling densities but that some, such as total Betula seed bank density at Arne, lacked sufficient variation to contribute much (Table 2); the range of predicted Betula seedling densities generated by full range manipulation of this variable was 0.01/m². Other variables, particularly soil factors, generated larger within-patch differences (Table 2). Full range manipulations of P-availability for example, generated predicted Betula seedling density ranges of 0.12/m² at Arne and 0.17/m² at Horsell. Differences between interquartile and full range manipulations show that some typical variability could explain patch scale heterogeneity (e.g. vegetation height at Arne generated ranges of 0.08
over the interquartile range and 0.1 over the full range), but that extreme values may explain occasional high densities (e.g. total Betula seed bank density at Horsell generated ranges of 0.01/m$^2$ over the interquartile range but 175.3/m$^2$ over the full range).

There was little correlation between the determinants at the sites ($r$-values were typically $< \pm 0.30$). Exceptions to this were P-availability and soil water content (Horsell $r = 0.84$, Arne $r = 0.40$) and vegetation height and biomass density at Horsell ($r = 0.51$).

**Discussion**

**Spatial pattern and variation in determinants of Betula invasion**

There was considerable between-patch and between variable differences in the scale, extent and magnitude of variation in invasion determinants. Understanding the cause of these differences is difficult because patterns are probably generated by complex interactions between management history, geology and endogenous ecological processes. Despite strong variability, there were general trends; soil variables (Fig. 2A-F) displayed smaller patches than vegetation and seed variables (Fig. 2G-M), which revealed continuous within-patch gradients. Furthermore, autocorrelation was present in all determinants and was strong for many (Table 1), suggesting that spatially explicit management may be efficient and cost-effective.

> Estimated effects of invasion determinants on within site invasion

There was no single key determinant of within-patch heterogeneity in predicted Betula seedling densities as the importance assigned to each variable was site-specific. It is therefore clear that safe-site and seed limitation strengths can vary within and between patches. This is most clearly exemplified by the total Betula seed bank density results. The general absence of Betula at Arne suggests that seed limitation is an important contributor to very low seedling densities in the patches. We estimate that if mean Betula seed bank density was 200/m$^2$ then predicted Betula seedling densities would have a mean

| Table 2. Estimated within-patch heterogeneity in predicted Betula seedling density accounted for by invasion determinants at two heaths. Values given are the difference between maximum and minimum predicted Betula seedling densities (m$^{-2}$) when variables were varied over their observed interquartile (IQ) and full ranges in the general model. Other variables were held constant at their mean. |
|------------------|------------------|------------------|-------|--------|
|                  | Arne: IQ range   | Arne: Full range | Horsell: IQ range | Horsell: Full range |
| Total Betula seed bank density (m$^{-2}$) | 0.004 | 0.01 | 0.011 | 175.27 |
| Biomass (hits m$^{-2}$)                          | 0.022 | 0.25 | 0.023 | 0.10  |
| Necromass (hits m$^{-2}$)                        | 0.009 | 0.04 | 0.060 | 0.15  |
| Mean vegetation height (cm)                      | 0.080 | 0.10 | 0.019 | 0.09  |

| Table 1. Key parameter estimates for variograms fitted to data from the Horsell and Arne study sites. NA is presented where the range estimate exceeds the maximum distance lag (150 m). Explained deviance was calculated as fitted model deviance/null model deviance. |
|------------------|------------------|------------------|-------|
|                  | Selected model type | Range (a) (m) | Proportion of autocorrelated variance |
| Horsell          | Total Betula seed bank density (m$^{-2}$) | Exponential | 137 | 0.55 |
|                  | Biomass density (hits m$^{-2}$) | Exponential | >150 | NA |
|                  | Necromass density (hits m$^{-2}$) | Gaussian | >150 | NA |
|                  | Mean vegetation height (cm) | Spherical | 69 | 0.94 |
|                  | P-availability (μg-P$_{m}$g$^{-1}$(0-50 mm)) | Spherical | 36 | 0.16 |
|                  | Soil water content (% total mass) (0-50 mm) | Exponential | 22 | 0.59 |
| Arne             | Total Betula seed bank density (m$^{-2}$) | Exponential | >150 | NA |
|                  | Biomass density (hits m$^{-2}$) | Spherical | >150 | NA |
|                  | Necromass density (hits m$^{-2}$) | Exponential | 29 | 0.68 |
|                  | Mean vegetation height (cm) | Exponential | 22 | 0.26 |
|                  | P-availability (μg-P$_{m}$g$^{-1}$(0-50 mm)) | Spherical | 39 | 0.96 |
|                  | Soil water content (% total mass) (0-50 mm) | Exponential | 31 | 0.18 |
Fig. 2A-M. Spatial pattern in *Betula* invasion determinants at two heath patches as described by variograms and kriged grids. Darker areas on kriged grids indicate higher values. On variograms empty squares and dashed line is Arne site and filled circles and unbroken line is Horsell site. $\gamma$ is half the averaged squared difference between the values of the variable at points separated by distance ($h$).
of 0.48/m$^2$ with a range of 0-7.05/m$^2$ (instead of 0.07/m$^2$ with a range of 0-0.55/m$^2$). Despite this, the estimated effect of total Betula seed bank density on within-patch heterogeneity in predicted Betula seedling density was tiny because the whole site was seed limited. Horsell, in contrast had higher mean seed bank densities and strong patchiness in these resulting in huge potential contributions to within-site variation.

It is notable that natural variation in P-availability generated differences in predicted Betula seedling density of a similar magnitude to the other determinants, despite lower ranges of availability (ca. 0-100 µg-P.g$^{-1}$) than in the experimental plots that the general model was based on (ca. 40-650 µg-P.g$^{-1}$). Another consistently high ranking determinant of within-site variation in predicted seedling densities was soil water content. However, caution must be sanctioned as much of this variable’s range was absent in the data that the model was derived from.

The problem of correlation between determinants is minor as most interacting determinants were uncorrelated, therefore co-incidence of conditions favouring Betula recruitment did not occur greatly more often than expected by chance. An exception is the correlation between vegetation height and biomass density at Horsell, which may have resulted in underestimation of these factors importance in generating variation in seedling densities. Despite these limitations our results do indicate that determinants displaying spatial pattern also control patch-scale invasion patterns (e.g. Betula seed bank density at Horsell), thus providing further support for the adoption of spatially explicit management.

**Control of Betula at the patch scale**

Betula differ from many exotic invasives because they are not weeds outside heaths, thus necessitating patch-scale management. Patch-scale variation in most determinants generated heterogeneity in predicted Betula seedling densities but these amounts were often small and previous explorations of the general model (Manning et al. 2005) have found that Betula recruitment limitation can originate from a single important variable e.g. high vegetation density, even where other conditions are suitable (as exemplified by seed limitation at Arne). For this reason, management can concentrate a small number of important determinants, allowing some potentially important variables (e.g. P-availability) to remain unmanaged. Spatially extensive patterns in vegetation and seed variables suggest that they are the most manageable determinants as large invasion prone regions can be targeted. Patterns of Betula seed bank density, for example, appear coarsely estimable from mature Betula patches, as hotspots of seed bank density coincided with Betula scrub patches (Fig. 2K, M).

Here we propose a Betula management plan based upon published research and this study. The central tenet is to remove isolated trees, and where necessary to manage for short, dense vegetation in high seed rain areas. Because correlations between invasion determinants appear exceptional, management seems necessary to generate a decoupled relationship between Betula seed and vegetation structure. Perhaps the most cost-effective means of reducing invasion is removing isolated trees. These are often left during clearances to provide a bird and invertebrate habitat (Pickess et al. 1992) which does not require conservation as it is increasing rapidly and so we suggest halting this practice. Where total removal of Betula is not possible, and where Betula scrub ecotone habitats are desired, the ecotone could be stabilised by creating a barricade of safe-site limited conditions close to Betula seed sources whilst maintaining invasible vegetation phases (that support a distinct biota) away from these. Because soil variables display unidentifiable and unmanageable small-scale variability we suggest creating the barricade using low intensity and regular mows (that do not severely damage vegetation) thus preventing vegetation from entering the invasible degenerate and pioneer phases (Khoon & Gimingham 1984). Prior identification of uninvasible vegetation patches (e.g. those seen on Fig. 2F, I) would reduce mowing requirements. An additional benefit of mowing is the prevention of P-accumulation in soil organic matter (Chapman et al. 1989b). Although this plan is somewhat intuitive there has not been data to support these ideas and spatially informed heathland management is rarely mentioned in existing strategies (e.g. Anon 2002; Auld et al. 1992). The barricade plan may be better suited to smaller heaths than grazing, which is spatially unpredictable and can result in uniform short vegetation.

This plan is complicated by uncertainty over the required barricade width. We suggest making it as wide as possible with the constraint that 1-2 ha areas of all vegetation stages are retained. On small patches wide barricades are not possible but our data (Fig. 2K, M) suggest that about twice the height of the adult tree (ca. 40-50 m) may suffice. Data for the ecologically similar Betula papyrifera supports this by indicating exponential declines in seed rain within 0-100 m of the parent tree (Perala & Alm 1990) although an accurate Betula dispersal kernel needs to be derived before conclusions are drawn.

Spatially informed management will, in principle, eradicate most Betula recruitment opportunities. However, a drawback is evident in the large nugget variance of many variables (Table 1; Fig. 2) which suggests that predicting within-patch scale invasion patterns will be hindered by small (< 17.6 m) invasion prone patches that
are independent of broader spatial trends. In the case of seed bank densities this is not surprising, although most seed rain falls near the parent the maximum dispersal distance for 20 m tall trees in a 5 m/s wind was estimated at 192 m for *B. pendula* and 145 m for *B. pubescens* (Perala & Alm 1990). Estimates derived from records of post-glacial spread indicate Betula dispersal > 2000 m (Clark et al. 2001). In addition to spatially unstructured variance our results also demonstrate small-scale patchiness in soil variables (Fig. 2A-F) which results in effectively random variation. Furthermore, the general model predicts ‘stochastic’ invasion where predicted densities are low (Manning et al. 2005). All this highlights the potential for low density invasion irrespective of management and the need to monitor and remove Betula from all areas regularly (ca. 3 years). We suggest doing this before individuals reach maturity as this should prevent the seed bank and soil changes that promote Betula scrub (Atkinson 1992; Mitchell et al. 1997, 1999). Our data suggest that Betula effects on seed banks are far wider reaching than P-availability effects as there was a clear correspondence between adult trees and seed densities (Fig. 2K, M) but not P-availability (Fig. 2E, F).

Conclusions

Spatial autocorrelation in Betula invasion determinants allows for the targeting of invasion prone patches but the required amounts of seed or safe-site management will be site dependent. Our data also suggest that a reasonable proportion of the variation which generates invasion patterns is effectively random at the management scale, necessitating regular survey for low-density invasion in all regions of a heath. The management plan, in which seed and safe-sites are spatially decoupled is, in principle, widely applicable to the management of open-land ecosystems undergoing invasion from surrounding wooded habitats (e.g. *Pinus halepensis* invasion of garrigue (Lavi et al. 2005)) as most woody plant populations will experience both seed and safe-site limitations. The details however, will require refinement according to both the invader and the system under invasion, as both dispersal and the identity of manageable safe-site factors will be case-specific.

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