



Physical disturbance enhances ecological networks for heathland biota: A multiple taxa experiment



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ABSTRACT

Creation of ecological networks is advocated to increase the viability of regional populations and their resilience to climatic and land-use change with associated habitat fragmentation and loss. However, management of network elements should be appropriate for the regional biota conserved, requiring evidence from multiple taxa. We examined the response of carabids, spiders, ants and vascular plants, to six physical disturbance treatments ranging in intensity plus controls, replicated across 63 plots in a plantation trackway network of a heathland region in England. Over 2 years, 73,182 invertebrates from 256 species were identified and 23,241 observations of 222 vascular plant species made.

Abundance and richness of stenotopic carabids and plants (respectively associated with heath and dune, or unshaded physically-disturbed low-nutrient soils) increased with disturbance intensification. Ant assemblages were similar among treatments and control plots, only differing from heathland sites through addition of generalist species. Spider assemblages were less resilient; overall abundance and richness reduced with greater disturbance. Generalist spiders recovered in year two, although incompletely in the most intensely disturbed treatment. Contrasting responses among taxonomic groups likely reflect differences in dispersal ability.

Treatments that merely disrupted vegetation quickly regained plant cover and height, suggesting frequent reapplication will be required to maintain heath specialist species. Turf stripping, the most severe treatment, was quickly colonised by specialist carabid and plant species. Treatments that are more durable may allow stenotopic spider assemblages to develop in contrast to shorter-lived treatments. Effectiveness of early-successional habitat networks within regions supporting European lowland heathland will be enhanced by physical disturbance and turf stripping. Our results emphasise the importance of examining multiple taxonomic groups when assessing management outcomes.

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1. Introduction

Land-use change, with associated loss and fragmentation of habitat, provides enormous challenges to conservation biology. In addition, species adapted to narrow habitat and climate niches may struggle to keep up with predicted climate shifts in fragmented landscapes. Ecological connectivity can help mitigate such impacts by enhancing local population resilience (Gilbert-Norton et al., 2010; Haddad et al., 2003) and potentially by facilitating range shift in response to anthropogenic climate change (Heller and Zavaleta, 2009; Krosby et al., 2010; Lawson et al., 2012). Consequently, there is increasing emphasis on restoring connectivity in strategic conservation policy (Lawton et al., 2010; Mitchell

et al., 2007; Natural England, 2011). However, effective implementation requires understanding what functional groups form regional priorities for conservation (Dolman et al., 2012) and which management techniques enhance landscape permeability for these. To optimise connectivity in modern landscapes, there is a pressing need to examine how management affects network suitability for contrasting taxa of conservation concern.

Mechanisms of dispersal within ecological networks depend on the temporal and spatial scale of species' life-histories (Bennett, 2003). For relatively mobile species, facilitating individual dispersal can link discontinuous populations even if connecting elements are sub-optimal relative to the discrete habitat patches that support reproduction (Haddad and Tewksbury, 2005). In contrast, for many arthropods and plants of limited dispersal ability, percolation of resident populations requires networks of appropriate habitat quality (Bennett, 2003). Examining the occurrence of taxa among network elements that differ in habitat structure and management can therefore provide evidence to enhance network quality, without the necessity to demonstrate movement.

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European heathland assemblages are of high biodiversity value and protected under the EC Habitats Directive (EC, 1992), but over the last two centuries European lowland heathland has been reduced by 60–94%, primarily by afforestation and agricultural conversion (Farrell, 1989; Gimingham, 1972). Remnants are often small and isolated (Piessens et al., 2005; Webb, 2009). As many early-successional heathland species are dispersal-limited, isolated populations are vulnerable (Bonte et al., 2003; Piessens et al., 2005; Webb and Hopkins, 1984), consequently, efforts to reconnect heathland are important to conserve its biodiversity in the longer term (Hopkins and Webb, 1984; Lawton et al., 2010). The importance of dispersal for invertebrate populations of fragmented open-habitats is well known (de Vries et al., 1996; Turin and den Boer, 1988; Warren et al., 2001), yet we usually lack understanding of the appropriate vegetation structure or management to enhance connectivity. Many stenotopic heath species require physical disturbance that creates ruderal resources and sparse early-successional structures (Buchholz, 2010; Dolman et al., 2012). With increasing evidence that stenotopic invertebrates inhabit and percolate along trackways or road verges (Eversham and Telfer, 1994; Noordijk et al., 2011), including those within tree plantations (Bertoncelj and Dolman, in press; Pedley et al., 2013), there is potential to use disturbance treatments to enhance ecological connectivity by taking advantage of existing trackway networks. However, robust evidence across multiple taxa is first required.

The objective of this study is to determine the most effective disturbance treatment to conserve early-successional specialist heathland species by enhancing landscape connectivity. We examined the response of carabid, spider, ant and vascular plant assemblages to physical disturbance treatments in trackways within an afforested landscape in eastern England planted over lowland heathland, fallowed and marginal croplands. Within the forest 1290 km of trackways provide a network that has potential to connect both the permanent and ephemeral open habitats within the forest landscape, and to link external heathland remnants across the forest. The invertebrate and plant response to a range of treatments that differ in disturbance intensity was examined in terms of assemblage composition, richness and abundance of early-successional specialist and generalist species; invertebrate assemblages were also compared to reference heath sites.

2. Materials and methods

2.1. Study site

Thetford Forest was planted in the early 20th century and occupies 185 km² of Breckland in eastern England (0°40'E, 52°27'N). Breckland is characterised by a semi-continental climate, sandy, nutrient-poor soils and a long history of grazing and episodic cultivation (Dolman and Sutherland, 1992) supporting a regional biota that includes coastal, continental and Mediterranean elements. Physically disturbed heathland and ruderal habitats support at least 542 priority species (rare, scarce, range-restricted or UK Biodiversity Action Plan species) (Dolman et al., 2012). The forest is dominated by conifer plantations, with 80% comprised of Corsican (*Pinus nigra*) and Scots (*Pinus sylvestris*) pine, managed by clear-felling (typically at 60–80 years) and replanting of even-aged patches (planting 'coupe': mean area 9.0 ha ± 8.6 SD) creating a coarse-grained mosaic of growth stages. Coupes are subdivided by a network of forestry trackways that provide management access. Trackways comprised two elements: central wheelings with sparse vegetation and exposed substrate, flanked by vegetated verges that are cut annually to facilitate access but lack bare substrate. Trackways vary in width (mean 13.7 m ± 5.8 SD, range 5–50 m, sample size $n = 93$), substrate (sand and gravel), vegetation

and shading due to adjacent tree height. Approximately 50% of heathland associated carabid species have been recorded from this trackway network (Lin et al., 2007) as well as many characteristic heathland spider species (Pedley et al., 2013); however, some of the region's rarest and most exacting species appear absent.

2.2. Physical disturbance treatments

Six physical disturbance treatments that varied in intensity plus a set of non-managed controls, each replicated nine times across a total of 63 plots (treatment plot length 150 m, width minimum 4 m, maximum 5 m), were established within the trackway system in February 2009. Plots were distributed within the contiguous core area of Thetford Forest (comprising four management 'blocks'), and in one large southern forest block (Fig. 1). Treatments included two cutting treatments: swiping (S, sward cut with tractor mounted blades, clippings left in situ) and harvesting (H, sward cut and removed with silage harvester) and four soil disturbance treatments ranging from mild disruption by discing (D, tractor-pulled disc harrow, disrupting but not destroying vegetation with shallow soil disturbance, 10–20 cm deep), to moderate disturbance by forest ploughing (FP, soil and litter inverted in plough lines producing bare mineral substrate in the furrow, width 30–40 cm, depth 40–50 cm, alternating with 40–50 cm wide strips of intact vegetation), heavy disturbance by agricultural ploughing (AP, turf and top-soil inverted producing bare-substrate across the plot, with biomass retained and buried to 20–30 cm), and the most destructive treatment turf stripping (TS, removal of vegetation, root mat, litter and organic soil, exposing mineral subsoil at a depth of 15–30 cm).

Plots were placed within trackways at least 9 m wide, within coupes aged 10–25 years that comprise closed-canopy stands, which lack open habitat carabids (Bertoncelj and Dolman, in press), spiders (Pedley, unpublished data) or plants (Eycott et al., 2006a). To reduce shading effects plots were established in the widest verge of trackways oriented north–south, or the northern verge of trackways oriented east–west. All plots were located a minimum of 100 m away from other treatments, open areas, forest restocks and felled coupes to ensure samples were not capturing open-habitat species from adjacent habitats. The soil in each plot was initially classified as acidic (podzols and acidic brown earths), or calcareous (rendzinas, calcareous sands, and mixed calcareous–acidic periglacial complexes) from soil maps (Corbett, 1973). This was validated by sampling soil in August 2009, with four cores (4.75 cm in diameter, 5 cm deep, excluding the root mat and undecomposed litter) taken from each plot, air-dried and passed through a 2 mm sieve; 50 g from each core were mixed with 125 cm³ of distilled water and pH measured with an electronic meter.

Treatments were allocated randomly to suitable trackways, stratifying between (1) acidic soils lacking bracken *Pteridium aquilinum*, (2) acidic soils dominated by bracken, and (3) calcareous soils. Treatments were not clustered within the geographic spread of plots (latitude $F_{6,56} = 1.014$, $P = 0.426$; longitude $F_{6,56} = 1.396$, $P = 0.232$); however, to control for any geographic effects on biotic composition, forest block was examined as a categorical factor in analyses.

2.3. Invertebrate sampling in treatment plots

In both 2009 and 2010, ground-active invertebrates were sampled in each plot on three occasions: in May, June and late July/early August. In each period, six pitfall traps (each 7.5 cm deep, 6.5 cm diameter, filled with 50 ml of 70% ethylene glycol) set 15 m apart in a single transect along the centre of each plot (beginning 37.5 m from each end) were opened for seven consecutive

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