Effects of experimental disturbance on multi-taxa assemblages and traits: conservation implication in a forest-open landscape mosaic

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Abstract

Overcoming fragmentation and isolation requires innovative solutions if cohesive biodiversity networks are to be created in modernised landscapes. Within Europe much of the biodiversity interest is in semi-natural habitats that exist as isolated reserves. This thesis aimed to test the connectivity potential of open habitat for lowland heathland biodiversity within a mosaic forest landscape. A range of experimental management treatments were implemented covering a gradient of disturbance intensity intended to enhance connectivity through plantation forest for early-successional biodiversity. Both species composition and life history traits were investigated enabling a comprehensive interpretation of response across multiple species. Sampling programs identified over 87000 invertebrates, comprising 38188 spiders from 183 species, 41531 ants from 20 species and 7564 carabids from 93 species, and recorded 23241 observations of 222 vascular plant species. Initial investigations revealed forestry trackways contained a component of the regional heathland spider assemblage, but this was significantly degraded as adjacent forest matured. Experiments to augment heathland biodiversity in trackways resulted in contrasting responses between taxa. Specialist carabids and vascular plants (associated with heathland or early-successional habitats), increased in abundance and richness with high intensity disturbance. Spider assemblages were left depauperate and did not completely recover after two seasons; ants did not respond at any disturbance level. Trait-based analysis showed that the abundance of aerial dispersers increased and size decreased with disturbance intensity for carabids and plants. In contrast, spider body size increased with greater disturbance and aerial dispersal was not significant. For spiders, ephemeral stepping stones, in the form young restock coupes, support the majority of the heath assemblage, whereas open linear habitat in the form of trackways, suffer from edge effects and are dominated by generalist and woodland spiders. Network cohesion will benefit from intensive disturbance management and a combination of connectivity elements to incorporate contrasting dispersal abilities.

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Chapter 1

Introduction

1.1 Landscape connectivity

Extensive landscape modification has resulted in widespread fragmentation and loss of terrestrial natural habitat across the globe (Fischer and Lindenmayer 2007). Increased agricultural production and new crop markets continue the disintegration of natural areas and threaten species loss (Fitzherbert et al. 2008; Tilman et al. 2001). Effects of fragmentation are intensified further with recent reports of climate induced range shift, as species that are adapted to narrow habitat and climate niches are unlikely to track predicted climate shifts in fragmented landscapes (Honnay et al. 2002; Warren et al. 2001). Isolated remnants are susceptible to reduced rates of immigration and gene flow that can leave populations vulnerable to deleterious mutations and stochastic extinction events (Saunders et al. 1991). Mitigation against these effects necessitates improved network connectivity to enhance local population resilience (Krosby et al. 2010; Lawson et al. 2012).

Restoring network connectivity in fragmented landscape is a challenging problem when targeting multiple species and taxa (Chetkiewicz et al. 2006). Calls for network enhancement are now at the forefront of policy and planning (DEFRA 2011; Lawton et al. 2010; Mitchell et al. 2007). Conservation biologists need to provide solutions so that funds and efforts can be directed appropriately. Over the past three decades there has been mounting evidence for the use of habitat corridors to facilitate species movement for a range of taxa including butterflies (Haddad 1999; Haddad and Tewksbury 2005; Sutcliffe and Thomas 1996), carabids (Eggers et al. 2010; Noordijk et al. 2011), crickets (Berggren et al. 2002), planthoppers (Baum et al. 2004), birds (Castellon and Sieving 2006; Haas 1995), and small mammals (Andreassen et al. 1996; Bennett 1990; Coffman et al. 2001). However, there is a lack of alternative solutions for those species that are not supported by conduits or that require high quality connective habitat. Furthermore, most evidence comes from behavioural studies using only a very few species, which do not allow predictions beyond the study animals. Improvements in the functional understanding of species will help target conservation efforts and may provide generalised responses patterns for certain groups, enabling predictions of ecosystem functions (Hooper et al. 2005; McGill et al. 2006).

Network connectivity needs to take account of the temporal and spatial scale of species life-history. For large mammals and relatively mobile species that do not require connectivity as breeding habitat, connective elements can involve low quality habitat facilitating movement of individuals between discrete patches (Beier and Noss 1998; Haddad and Tewksbury 2005). For animals that are scarce in the environment and disperse rapidly, evidence for corridor use mostly concerns individual movement behaviour. In contrast, for habitat specialists with poor dispersal abilities or sedentary life histories, connecting elements may require high quality habitat that allows breeding and dispersal over generations (Bennett 2003). Evidence of species occurrence in connecting elements may be sufficient for percolation over generations, rather than data on individual movement behaviour.

There is sufficient evidence, and policy motivation, to include connective elements in restoration plans. Furthermore, in severely fragmented landscapes where options for increased patch size and number are not available, connectivity via linear strips, stepping stones and habitat mosaics may provide the only viable options for increasing connectivity (Fig. 1.1). However, policy and planning requires the evidence base for relevant species and taxa before conservation funds are diverted.

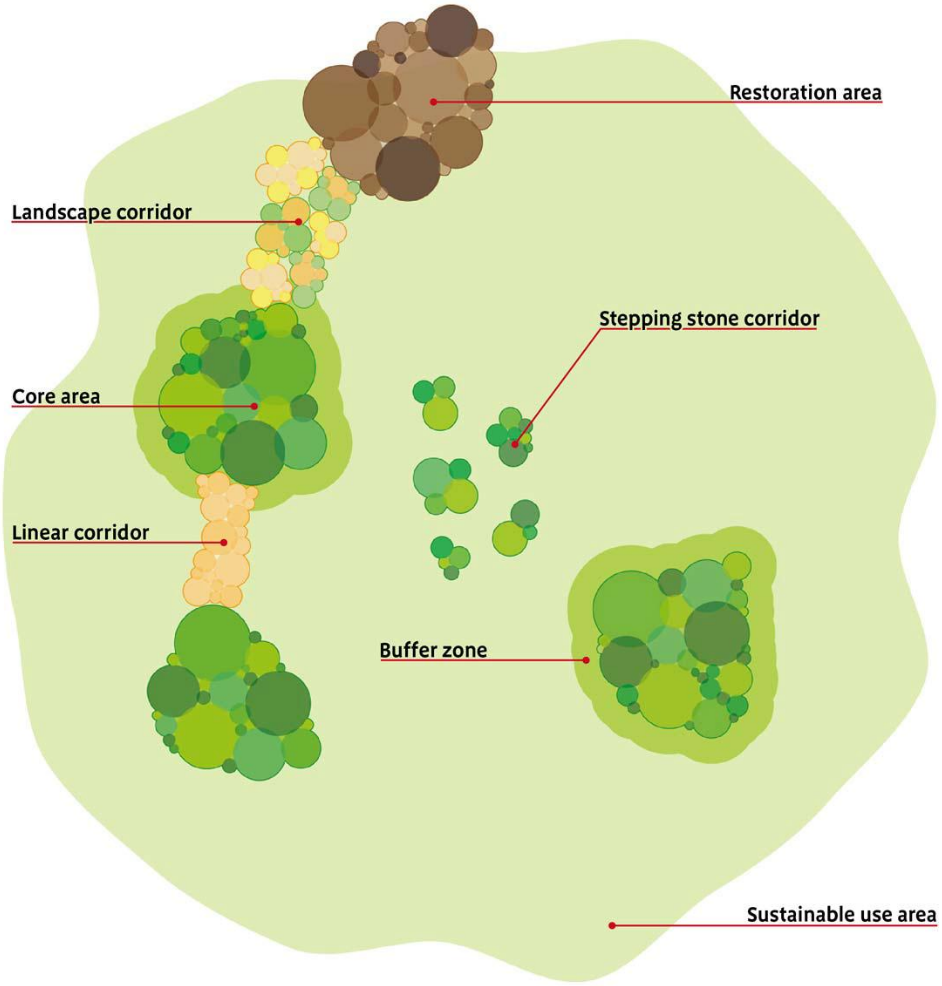

Fig. 1.1. Connectivity elements of ecological networks. Source: Lawton et al. (2010)

1.2 Plantation forestry

Global deforestation continues to fragment and reduce natural forest in the face of increased afforestation of plantation forest (FAO 2001). Globally, over 29% of land area is forest, of which 3% is plantation. However, in some countries much greater percentages of the total forest land comprises plantation; for example, in the UK 69%, Japan 44% and India 51%. As plantation forest increases, so does the importance of management to ensure regional biodiversity needs are met. There have often been concerns associated with plantation forest (Brockerhoff et al. 2008; Hartley 2002). When compared to natural forest, plantations can lack specialist species associated with mature forest (Finch 2005; Helle 1986; Niemela et al. 1993). In areas where afforestation has occurred on non-forest habitat, as is often the case in Western Europe, plantations may also have negative effects on the open habitat biodiversity (Brockerhoff et al. 2008; Butterfield et al. 1995).

Conservation within plantation forest has often focused on species richness with comparisons being made to either natural forest or pre-plantation habitat. General consensus indicates that clear-fell plantations in temperate regions, due to the heterogeneous mixture of forested stands of different ages and open areas, provide species-rich landscapes (Fahy and Gormally 1998; Mullen et al. 2008; Niemela 1997). However, comparisons should not be based solely on species richness or diversity indices but should examine assemblage composition (Lindenmayer 1999; Oxbrough et al. 2005; Taboada et al. 2011), as managing habitats for maximum biodiversity reduces efficacy, resulting in over simplification of community structure and loss of biological information. Furthermore, plantation landscapes need to focus on providing habitat for regionally important taxa rather than maximising total species richness.

In areas where plantation forests provide a significant portion of the landscape, the necessity to incorporate forestry land in conservation strategies is greater. Currently, open space within plantation forest is limited; policy states that only 10% of UK plantation area needs to comprise open habitat (Forestry Commission 2011; UKWAS 2008). The majority of open habitat management is not aimed at biodiversity enhancement but is designed to facilitating forest access for felling, thinning and planting operations and recreational purposes. Evidence of the biodiversity value of plantation forest for regionally important forest species (Berndt et al. 2008; Brockerhoff et al. 2003; Humphrey et al. 2000) and open habitat species (Bertoncelj 2010; Lin et al. 2007; Noordijk et al. 2011) highlights the conservation potential even under current management regimes. With improved and targeted management, plantation forests could provide important habitat for threatened and vulnerable species playing a significant role in conservation networks.

1.3 Study system

1.3.1 Habitat

In Western Europe, much of the conservation concern is for the biodiversity in semi-natural habitats formed by centuries of human land use. Large areas of lowland heathland, developed on unproductive soils, were maintained by low intensity grazing and episodic cultivation. With the improvement of agricultural techniques large areas of heathland were lost to intensive croplands and forestry. Over the last two centuries 60-94% of lowland heath has been lost across Europe (Farrell 1989; Gimingham 1972). Heathland often remains in isolated fragments (Piessens et al. 2005; Webb 2009).

Heathland assemblages are of high biodiversity value, recognised in inclusion of heathland biotopes in Annexes of the EC Habitats Directive (EC 1992), such that member states have an obligation to designate and ensure favourable conservation status of examples of the habitat (as Special Areas of Conservation). As many specialist heathland species are dispersal-limited, and remnant heathland often comprises isolated reserves, populations are vulnerable (Bonte et al. 2003; Piessens et al. 2005; Webb and Hopkins 1984). Heathland biodiversity is further threatened by increased nutrient levels which accelerate successional processes (Barker et al. 2004; Hardtle et al. 2006). Efforts to reconnect heathland are important to conserve its biodiversity in the longer term (Hopkins and Webb 1984; Lawton et al. 2010).

Due to the difficulty of creating new habitat patches on ex-arable land caused by fertiliser inputs and unfavourable seed banks (Bakker and Berendse 1999; Mortimer et al. 2002; Perner and Malt 2003), efforts to recreate heathland have often focussed on the removal of plantation forest as soils under agroforestry remain nutrient poor with viable seed banks (Pywell et al. 2002; Walker et al. 2004). However, in fragmented landscapes, there is increasing evidence that stenotopic invertebrates occur widely within plantation landscapes (Bertoncelj 2010; Lin et al. 2007) and can inhabit and percolate along road verges or trackways within tree plantations (Eversham and Telfer 1994; Lin et al. 2007; Noordijk et al. 2011). Thus appropriate management of open habitat networks within a plantation landscape may have potential to sustain regional heathland fauna without the necessity for land-use change and reversion.n Western Europe, much of the conservation concern is for the biodiversity in semi-natural habitats formed by centuries of human land use. Large areas of lowland heathland, developed on unproductive soils, were maintained by low intensity grazing and episodic cultivation. With the improvement of agricultural techniques large areas of heathland were lost to intensive croplands and forestry. Over the last two centuries 60-94% of lowland heath has been lost across Europe (Farrell 1989; Gimingham 1972). Heathland often remains in isolated fragments (Piessens et al. 2005; Webb 2009).

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1.3.2 Species

The choice of what to monitor in conservation biology is frequently a decision based on the amount of available time and funding. Often the use of indicator species is advocated in monitoring programs due to the enormity of exhaustive methods. Appropriate indicators may include ‘keystone’ species (that provide important functions on which ecosystem composition and structure depend) or ‘umbrella’ species, for example those that require large expanses of habitat such that their conservation will bring along associated biodiversity. However, serious questions regarding the ability of indicators to protect species beneath the umbrella exist (Andelman and Fagan 2000; Simberloff 1998). Conservation monitoring which incorporates multiple species and taxa as a surrogate for biodiversity is widely seen as a better alternative (Larsen et al. 2012; Manley et al. 2004).

The use of terrestrial arthropods as surrogate indicators for diversity and biotic and abiotic conditions is well documented (Kremen et al. 1993; Lawes et al. 2005; Pearson and Cassola 1992), particularly carabids (Rainio and Niemela 2003) and spiders (Cardoso et al. 2004; Scott et al. 2006). Epigeic arthropods are thought to be effective indicators for conservation studies as they are relatively short lived, have high reproductive rates, are found in abundance in most habitats and include habitat-specific or specialist species. Furthermore, sampling terrestrial arthropods is relatively quick and simple to perform, providing abundant information on assemblage changes, even over short time periods.

Both spiders and carabids are species-rich groups considered important predators of crop pests (Schmidt et al. 2005; Thomas et al. 1992), and spiders, being one of the top macro-invertebrate predators, have strong influences on food webs (Halaj and Wise 2001; Schmitz et al. 2000; Wise 1993). The spider community is greatly affected by changes in habitat structure (Duffey 1968; Robinson 1981). Carabids, having both predatory and herbivorous species, and comprising a wide diversity of species with differing microhabitat requirements, provide insight on vegetation structure and richness (Lovei and Sunderland 1996; Rainio and Niemela 2003). Spider communities also respond quickly to brief or sudden changes in environmental conditions, such as variations in prey density, pesticides, or pollution (Marc et al. 1999).

Although species distribution patterns are often assumed to be ordered by abiotic factors, such as those mentioned above, interspecific competition has also been proposed as an alternative mechanism shaping population dynamics and distributions (Connell 1983). Interactions between competitors can take place directly through interference competition and indirectly through resource competition, and the effects of competition are thought to be greater between closely related species that have overlapping resource use. Spiders, being generalist predators, are thought to have overlapping resources where they share space and activity periods (Marshall and Rypstra 1999). Controlled field experiments examining community organisation with closely related species of spiders have provided evidence both for and against interspecific competition. Using density manipulation studies of orb web spiders in old-field habitats, Horton and Wise (1983) have shown that interspecific competition appears to have no, or very little influence, and some responses were correlated with seasonal changes in weather and variation in vegetation composition and structure. In contrast, Spiller (1984) found evidence of exploitative and interference competition with two common orb-weaving spiders, *Cyclosa turbinata* and *Metepeira grinnelli*. In plots where the smaller *C. turbinata* was removed, *M. grinnelli* increased in body size and fecundity. In plots where *M. grinnelli* was removed, *C. turbinata* was more abundant and their web positions were higher in the vegetation.

Although competition has been shown in specific systems, the importance of interspecific competition and the magnitude of the effects in field situations have been disputed (Gurevitch et al. 1992; Schoener 1982; Shorrocks et al. 1984; Simberloff 1983). Often, interspecific competition is suggested as an *ad hoc* means to describe field observations and community patterns. For example, Petillon et al. (2005) describe wolf spider distribution on saltmarsh invaded by the grass *Elymus athericus,* suggesting that interspecific competition (especially from *Pardosa prativaga*, *P. proxima* and *P. pullata*) in areas invaded by *E. athericus* will diminish populations of the normally dominant halophilic species *P. purbeckensis*. To test interspecific competition concepts, observational and distributional studies need to be followed by experimental field studies with appropriate parameter(s) relevant to the interaction measured (Niemela 1993). Furthermore, manipulation experiments that use unrealistic demographics and/or proxies for resource overlap such as body size, instead of mandible size or gut content, may misrepresent the appearance or scale of interactions.

Due to the species- and system-specific methodology required to examine interspecific competition in shaping distribution patterns, this thesis will not be directly testing competition. Instead it will focus on community and life history trait responses to habitat manipulations and landscape elements for species rich taxonomic groups. Information on life history and habitat association has proved valuable in understanding the response of terrestrial arthropods to landscape change and disturbance (Desender et al. 2010; Ribera et al. 2001; Vandewalle et al. 2010). Furthermore, the development of trait-based approaches to understand species response to environmental stressors can provide general response patterns which allow predictive statements (McGill et al. 2006).

1.3.3 Invertebrate surveying

Pitfall trapping is used extensively to examine ground dwelling invertebrate dispersal, individual species abundance, relative abundance and community composition. However, issues regarding trapping bias are well documented. Pitfall trapping does not necessarily give accurate estimates of species relative abundance (Lang 2000; Topping and Sunderland 1992; Uetz and Unzicker 1976). Topping and Sunderland (1992) suggest pitfalls would only represent relative abundance correctly if activity were constant between species. It is also likely that changes in abundance of different species over time could be a result of a change in activity such as mate searching, food availability or post-copulatory dispersal of females. Oxbrough et al. (2006) state that pitfall trap catches are a function of species density, activity and behaviour, not a complete inventory of all the ground-dwelling species in a given habitat. Furthermore, they suggest that pitfall data should be considered a representation of the active ground-dwelling spider fauna that are susceptible to this trapping method

Changes in pitfall trap abundance, both between sample areas and over time, could reflect changes in vegetation structure (Greenslade 1964; Melbourne 1999). Dense vegetation could affect movement rates and direction of ground dwelling invertebrates, hence recorded differences in pitfall catches between sites may not reflect the actual abundances of species present. Melbourne (1999) found that ant species richness and composition were biased by habitat structure in his experiments of manipulated grassland blocks. However, ant populations were only significantly affected when groundcover was very dense, suggesting a threshold effect of habitat structure.

Other recognised biases of pitfall trapping include trap size and shape (Luff 1975; Spence and Niemela 1994), and the length of the trapping period (Niemela et al. 1990). Differences in catchability according to invertebrate body size have also been reported (Greenslade 1964; Lang 2000; Standen 2000). Comparing pitfall trapping to a combination of D-Vac and swish net sampling in limestone grasslands, Standen (2000) reported that pitfall trapping more frequently caught larger bodied spiders and beetles, but it was possible to estimate species richness from pitfall trapping alone by using species richness curves for both taxon groups. Uetz and Unzicker (1976) examined quadrat sampling compared to pitfall trapping of wandering spiders and found that due to the cursorial habits of this guild and the likelihood of temporal stratification, a continuous sampling method is more successful than quadrat sampling. Also, by comparing the two methods with other studies in the literature, Uetz and Unzicker (1976) found pitfall trapping provided a closer estimate of the number of species in a community and concluded that limiting pitfall trapping to cursorial species may help eliminate the effect of differences in activity among species in relative abundance estimates.

Topping and Sunderland (1992) compared pitfall catches to absolute density sampling (D-Vac 0.5 m^2 area followed by immediate hand searching of the area). Although they concluded that determining relative abundance was only partially successful using pitfalls, they found more individuals from pitfall trapping (5069 compared to 4116), more species (41 compared to 35) and a greater percentage of adults (95% compared to 33%). Luff and Eyre (1988) suggests that pitfall trapping is successful for creating pitfall catch indexes to interpret ecological differences between areas. They state that classifying sites by pitfall data is meaningful as long as it is remembered that the classification is not based on population density but on the actual catch.

Interpreting results derived from invertebrate sampling depends on; a) the direction and magnitude of trapping biases, and b) the purpose of the study. If estimates of absolute density or complete inventories of species richness are required then pitfall trapping alone is not suitable. Like all non-exhaustive animal surveys, sampling bias and problems surrounding animal detectability through survey timings, habitat differences, weather and sampling effort will affect recording. Efforts need to be taken to minimise these and results should indicate potential directions and magnitude of the bias. Standardising the trapping procedures, such as the number of traps, trap design and timings will help alleviate some of the sampling issues. Within this thesis, standardised pitfall trap catches are referred to as ‘abundance’ although others authors have termed these measures ‘activity density’ or ‘capture rates’. This type of abundance data reflects an aggregate of the population density and relative activity of individuals, which reveals aspects of habitat utilisation by species and is the most commonly used method for collecting invertebrate data over large temporal and spatial scales.

1.4 Thesis background

1.4.1 Thesis aims

This thesis examines the function of a plantation forest landscape for multiple invertebrate species. The plantation forest, set within a heathland region, provides a highly fragmented landscape of scarce open habitats juxtaposed within a hostile matrix of forest patches. Using data for multiple species and taxa, this study answers practical conservation questions while having robust data enabling the exploration of wider conceptual ecology theories. The study uses pitfall trap catches to sample diverse groups of ground-active invertebrates from semi-natural, agroforestry and experimental sites.

This study first explores the potential of forestry trackways to support open habitat assemblages, comparing communities against those in heathland sites outside the plantation. The potential to use disturbance treatments to maintain or enhance nationally important invertebrate and plant assemblages is explored with mechanical manipulations within the forest. This can provide an evidence base relevant both to management of biodiversity within heathland remnants, and increasing the quality and functional utility of connecting elements across the landscape. Functional traits are examined to explore predictive responses to disturbance that have greater transferability to other species, systems and taxa. In addition, different landscape elements comprising linear strips and ephemeral stepping stone patches are examined for their ability to provide connectivity for spider assemblages.

1.4.2 Contributions to the thesis

The first data section of the thesis (Chapter 2) comprises analysis conducted as part of this PhD, but uses spider by-catch from material originally collected from forestry trackways sampled in 2005 as part of a previous PhD study (Bertoncelj 2010). From this material, spiders from a single month of samples were identified prior to the current thesis (Pedley undergraduate dissertation). This was greatly augmented, with two additional months of spider material from the 2005 samples identified during the current

PhD study and all analysis conducted within the current study. Chapter 2 also makes use of additional sampling of heathland sites conducted within the current PhD study, to provide reference samples against which the composition of open habitat elements within the forest could be compared. All other aspects of the thesis were conducted during the four year study period (2008-2012).

All experiment design, initial site surveys and selection, invertebrate sampling, and collection of structural vegetation data, were conducted by S Pedley. Identification of all spider material was conducted by S. Pedley. Carabids were identified by Jake Stone and Martin Collier (Norfolk beetle recorder) and ants by Doreen Wells (Norfolk ant recorder), from invertebrate material collected by S. Pedley. Vascular plant data from experimental treatments were collected by Tim Pankhurst (Plantlife UK) and Dr Paul Dolman. All analysis was conducted by S Pedley.

1.4.3 Thesis structure

The four main data chapters (Chapters 2-5) of the thesis are written in the format of manuscripts for peer-reviewed journals. At the time of thesis submission, Chapter 2 and Chapter 3 have been published (Pedley et al. 2013a; Pedley et al. 2013b). Chapter 2 compares spider assemblages of forestry rides to open reference heathland in the study region. In doing so, this chapter assess the current potential of linear open trackway networks within the forest to provide connectivity for open-habitat spiders, in contrast to assemblages found in extant heathland remnants. Furthermore, it enables the distinction of different assemblages based on shading effects of adjacent forested compartments, to understand factors influencing trackway suitability. Chapter 3 evaluates the potential of physical disturbance treatments to enhance habitat quality of trackway networks for stenotopic fauna and open habitat plants, by examining the multi-taxa assemblage response to experimental treatments applied within forestry rides. Compositions are compared over two years to determine the appropriate level of disturbance that would facilitate connectivity through the plantation landscape for regionally important species. In Chapter 4 the experimental manipulations in the previous chapter are used as a gradient of disturbance to examine functional responses and trait shifts. Two diverse arthropod groups, carabids and spiders, are used as well as vascular plants. The predictability and consistency of trait responses across the disturbance gradient are explored. In Chapter 5 arachnid assemblages are compared among open habitats of contrasting configuration within the forest. Trait characteristics are compared to address the relative importance of body size, dispersal, environmental tolerance and life history among ‘corridors’ and ‘stepping stones’, represented by linear trackway elements and ephemeral open patches (comprising a chronosequence of forestry coupes). Chapter 6 draws together some of the implications and conclusions of the thesis, and suggests directions for future work.

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Chapter 2

The value of the trackway system within a lowland plantation forest for ground-active spiders

Abstract

European forest management guidelines include conservation and enhancement of biodiversity. Within plantation forestry, trackways provide contiguous permanent open-habitat with potential to enhance biodiversity. We examined the ground-active spider assemblage in the trackway network of Thetford Forest, Eastern England, the largest lowland conifer forest in the UK, created by afforestation of heathland and farmland. Results are relevant to other forests in heath regions across Europe. We used pitfall trapping to sample the spider assemblage of trackways within thicket-aged stands (n=17), mature stands (n=13) and heathland reference sites (n=9). A total of 9314 individuals of 71 species were recorded. Spider assemblages of the trackway network were distinct from those of the heathland reference sites; however trackways were found to support specialist species associated with grass-heath habitats, including nationally scarce species. Richness of grass-heath species was similar for trackways in thicket-aged forest and heathland reference sites, although the abundance of individuals was three times greater in the reference sites. Trackways in mature stands had lower grass-heath species richness and abundance than both thicket trackways and heath reference sites. Wide trackways within thicket stands contained greater richness and abundance of specialist xeric species than narrower trackways. However, fewer xeric individuals were found in trackways compared to heathland reference sites. Either inferior habitat quality in trackways or poor dispersal ability of specialist xeric species may largely restrict these to relict areas of heathland. Targeted widening of trackways to allow permanent unshaded habitat and creating early successional stages by mechanical disturbance regimes could improve trackway suitability for specialist species, helping to restore connectivity networks for grass-heath biodiversity.

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2.1 Introduction

Heathland ecosystems in Western Europe support important biodiversity (EC 1992; Webb 1998, 2009) but have been considerably reduced in extent through changing land-use, particularly afforestation and agriculture (Farrell 1993; Gimingham 1972; Granstrom 1988). Remaining heathland is highly fragmented and efforts to recreate, buffer and connect heathland are key to conserving its biodiversity in the longer term (Aerts et al. 1995; Hopkins and Webb 1984; Lawton et al. 2010). Restoration programmes have often focussed on the removal of plantation forest in former heathland regions as soils under coniferous plantations have not been modified by agricultural fertiliser and may contain viable heathland seed-banks (Eycott et al. 2006; Granstrom 1988; Pywell et al. 2002). However, permanent open space within a plantation landscape, such as that provided by extensive trackway networks, may already have potential to support open habitat species (Greatorex-Davies et al. 1994; Warren 1985) including elements of heathland biodiversity (Bertoncelj 2010; Eycott et al. 2006; Lin et al. 2007).

Furthermore, open space can greatly enhance the biodiversity within plantations (Butterfield et al. 1995; Day et al. 1993), the need for which is increasingly recognised (Kuusipalo and Kangas 1994; Spellerberg and Sawyer 1996). Previous studies have focussed on increased species richness to enhance forest biodiversity (Greatorex-Davies et al. 1993; Oxbrough et al. 2006; Warren 1985). However, for heathland assemblages, species richness is generally lower than the surrounding areas and is therefore not an appropriate criterion for assessment (Webb and Hopkins 1984). In addition to enhancing heterogeneity, complexity and overall richness, conservation goals should aim to assess the suitability of forested landscapes for species of relevant pre-plantation habitats, such as lowland heathland, dune, or upland moorland, as well as rare and threatened species that are a focus of regional conservation priority.

Within plantation forests managed by clearfelling and replanting of even-aged stands, the temporal dynamics of the mosaic growth stages may make individual trackways ephemeral in their suitability to shade intolerant open-habitat species. Therefore, dispersal will be essential for population survival. Previous invertebrate research within the open space of plantation forests has often focussed on the influence of shade on Lepidoptera species richness in trackways (Greatorex-Davies et al. 1993; Sparks et al.

1996; Warren 1985). The ability of butterflies to disperse aeronautically enables them to bypass unsuitable or low quality habitat in search of mates, food plants and nectar sources, described as stepping stone dispersal (Haddad and Tewksbury 2005; Schultz 1998). Management guidelines lack an understanding of less mobile ground-active invertebrate community in the open space within a plantation.

This study examined the ground-active spider community in the trackway network of a large lowland coniferous forest planted on a heathland region of Breckland, East Anglia, UK. The region is of high biodiversity importance for assemblages of continental heath, steppe, coastal and Mediterranean species not found elsewhere in Britain, that require open heathland or ruderal habitats (Dolman et al. 2010). Within the forest (185 km^2) there are approximately 1290 km of trackways (average width 14 m) providing a potential open habitat resource of 18 km^2, equivalent to a fifth (21 %) of the designated extent of grass-heath remaining in the region (83 km^2). Much of the remaining grass-heath is in close proximity to the forest with some sites bordering the forest. This extensive trackway network has potential to contribute greatly to the available grass-heath habitats in the region and also to provide connectivity, among permanent open and ephemeral areas within the forest landscape and also linking across the forest to connect between external heathland patches.

Heathland and disturbed ruderal sites within the region support over 600 nationally rare and/or restricted species (Dolman et al. 2010). Spiders are among the top macroinvertebrate predators, occupying an important position in terrestrial food webs (Wise 1993). Changes in spider assemblages reflect changes in environmental conditions such as habitat structure (Duffey 1968; Robinson 1981) and fragmentation (Hopkins and Webb 1984), making spiders an effective group to examine open habitat networks. Furthermore, dry grass-heath in the region contains a very distinct spider community which includes stenotopic species adapted to living in arid places including coastal dune species rarely found inland in the UK (Duffey et al. 1957). The majority of this specially adapted community are ground hunting spiders.

The aim of this study was to assess the ground-active spider assemblage in the forest trackway network; firstly by comparing the forest trackway assemblages to those of reference grass-heaths in the region, and secondly by examining different trackway types and elements in terms of age structure of the surrounding forest, width of the trackway and track component (verge and vehicle tracks). Finally, we discuss the trackway network in terms of its ability to provide connectivity through the forest for open habitat spider communities.

2.2 Methodology

2.2.1 Study site

Thetford Forest is the largest lowland coniferous plantation forest in the United Kingdom; planted in the early 20th century on heathland and marginal agricultural land it occupies 185 km^2 of the Breckland region in eastern England (0°40'E, 52°27'N). Breckland is characterised by a semi-continental climate, sandy, nutrient-poor soil and a long history of human land-use that has included extensive and intensive grazing and episodic cultivation (Dolman and Sutherland 1992). This historic anthropogenic disturbance enabled specialist xerophilic invertebrates to persist in open-sand habitats in the region. Many of these species are now rare and threatened at national or European scales, due to both habitat degradation and destruction (Dolman et al. 2010). The Breckland Forest Site of Special Scientific Interest (SSSI) is notified under UK conservation legislation, imposing a requirement to maintain populations of nationally scarce and rare invertebrates in favourable condition (English Nature 2004).

The forest is dominated by conifer plantations, of which approximately 80% comprise Corsican (*Pinus nigra*) and Scots pine (*P. sylvestris*). The plantation is managed by clear-felling and replanting of large, even-aged stands (range 2-16 ha) which create a mosaic of even-aged growth stages (Eycott et al. 2006). Stands are typically harvested 60-80 years after planting. Stands are subdivided by a network of forestry trackways that enable access for management operations. Trackways consisted of two elements: a central vehicle track with disturbed wheelings, sparse vegetation and exposed substrate, flanked on either side by vegetated verges, which include elements of heathland vegetation, but generally lack bare substrate (Eycott et al. 2006). Trackways are currently cut or forage-harvested approximately once a year to maintain vehicle access and facilitate deer management. Trackways vary in width (mean 13.7 m ± 5.8 SD, range 5-50 m, from a sample of n=93), surface structure (sand, gravel), vegetation and amount of shade due to varying age of adjacent forest stands.

2.2.2 Spider sampling in trackways

Thirty forestry trackways (the basic unit of replication) were sampled, 13 with mature trees (>30 years) adjacent (subsequently referred to as mature trackways) and 17 with thicket stands (11-20 years following Hemami *et al.* (2004)) adjacent (subsequently referred to as thicket trackways) (Table 2.1). Trackways within clear-felled, recently restocked (0-5yr) or pre-thicket (5-10yr) stands were not sampled as trackways assemblages will not be distinct from those of adjacent open forest habitat. Of the 17 thicket trackways, seven were wider than the remainder (Table 2.1) and consequently experience less shading. To reduce confounding variation, only trackways located on predominantly acidic soil types (brown earths and podzols) within central blocks of Thetford Forest (covering 99.8 km^2; Fig. 2.1) were sampled. Analysis of variance on easting and northing confirmed the age classes of sampled trackways were not aggregated within the sampled landscape (Northing; $F_{1,29}$=1.526 P=0.231, Easting; $F_{1,29}$=0.848 P=0.480). Each trackway was sampled by two pitfall transects, one on the vehicle track and the other in the least shaded trackway verge. Of the 30 trackways, 16 were oriented approximately north-south and 14 were east-west. In trackways oriented north-south the widest of both verges was sampled (four west and 12 east verges) and on trackways oriented east-west the northern (insolated) verge was sampled. Transects were set a minimum of 50 m away from the corners of trackways and away from any open areas or cleared tree stands, hence each sample represented the spider community of that trackway and not other open habitat.

Each trackway was sampled on three occasions, to span the phenology of ground-active invertebrates, with pitfall traps set in mid-May, end of July and the end of August 2005. At each site, paired transects were set along the centre of the verge (‘verge’ transect) and between the central vehicle wheelings (‘track’ transects). Transects comprised five traps (each 7.5cm deep, 6.5cm in diameter, filled with 50ml of 70% ethylene glycol), with traps being open for five consecutive days in each sampling period. Traps in each transect were set approximately 22 m apart and were staggered alternately between track and verge leaving at least 11 m between adjacent traps in the paired transects. The five traps in each transect were combined to give one sample for the track and one sample for the verge for each trackway site; these were subsequently combined in analysis that considered the trackway as the basic unit of replication (see below). All analyses were conducted on aggregate samples that pooled across the three trapping periods. During the trapping season many females Lycosids (wolf spiders) were observed with eggsac and also carrying spiderling, indicating breeding populations within the forestry trackways.

Table 2.1. Characteristics of four trackway categories showing mean (± standard deviation) age of adjacent trees and trackway width

	Number of sites	Average tree age on southern side (years)	Average tree height on southern side (m)	Average width (m)
Mature tracks	13	53.2 ± 23.3	17.3 ± 4.1	9.8 ± 2.1
Thicket tracks	17	17.8 ± 4.7	8.4 ± 3.0	17.3 ± 10.6
Narrow	10	15.7 ± 4.3	7.2 ± 2.6	10.7 ± 2.7
Wide	7	20.7 ± 3.6	10.0 ± 3.0	26.9 ± 10.4

Fig. 2.1. Central Thetford Forest blocks (99.8 km^2) showing the mosaic of open space, mature (planted before 1986) and younger (planted after 1985) tree stands. Trackways are shown as thick black lines

2.2.3 Heathland sampling

The ground-active spider assemblage was also sampled from nine heathland and ruderal reference sites considered important for specialist and rare invertebrates (Table 2.2), of which eight were designated SSSIs (including two National Nature Reserves). Within each of these, three transects were set, at least 50 m apart, providing a total of 27 sampling locations. Each comprised six pitfall traps (of the same dimensions as those used in forest trackways) and remained open for seven consecutive days over three trapping periods in 2009; mid-May, mid-June and the beginning of August. Pitfall traps where placed 15 m apart, similar to the 11 m spacing in the paired forest trackway transects. Again, aggregate samples pooled across the three trapping periods were used in analyses.

Both the 2005 forest trapping and the 2009 heathland trapping were elements of larger experiments taking place at the respective times and hence the differences in methodology. We acknowledge that sampling of reference transects may have differed slightly in effectiveness compared to forest trackways, due to the use of six not ten traps that were open for seven not five days during each trapping period (total 42 versus 50 trap-days per trapping period, respectively). In analysis of abundance we control for trapping effort (see below). Furthermore, activity and trapability may have been influenced by inter-annual differences in weather. However, the major differences in composition between forest trackway classes and heath reference sites are unlikely to have been an artefact of differences in weather between sampling years.

2.2.4 Identification

Adult spiders were identified to species using a 50x magnification microscope following Roberts (1987, 1996); juvenile and sub-adult specimens were not identified due to the lack of developed reproductive structures.

Table 2.2. Heathland and ruderal reference sites sampled for ground-active spiders, giving grid references (UK Ordnance Survey) of transect locations

Site	Notes
Deadman's Graves SSSI TL 775744, TL 776743, TL 776742	All three transects were located in short sparse vegetation with large areas of exposed sand on a heavily disturbed rabbit warren.
Eriswell Low Warren SSSI TL 739793, TL 740793, TL 739793	A sheep grazed site with a series of old plough cleaning lines, that are re-ploughed as needed to create disturbance for rare vegetation, most recently in 2003. Rabbit grazing and burrows along the lines has maintained exposed substrate. Transects were placed along the ridge of the plough lines in broken short vegetation.
Icklingham Plains SSSI TL 759734, TL 759735, TL 758735	All three transects were positioned in lichen dominated grass-heath affected by heavy rabbit activity that has maintained short vegetation and exposed sand.
Maidscross Hill SSSI TL 729825, TL 730825, TL 726823	One transect was placed along the south facing slope of former gravel-pit with sparse vegetation and exposed substrate, the remaining two were on short rabbit-grazed turf.
Wangford Warren SSSI TL 757840, TL 758841, TL 757842	Mechanically disturbed areas at the site are ploughed approximately annually to maintain open sand. One transect was positioned in ploughed unvegetated open sand, the remaining two in lichen dominated grass-heath.
Runway Field (adjacent to Wangford Warren) TL 757840, TL 757839, TL 756837	Reverted from arable after inundation by windblown sand, the site includes areas of heavy rabbit activity and one annually ploughed strip bordering Wangford Warren. One transect was positioned along the ploughed strip and the other two within areas of short rabbit-grazed turf.
Thetford Heath SSSI TL 854795, TL 849795, TL 846795	All transects were placed in closely sheep and rabbit grazed grass-heath, with short and in places broken sward.
Brettenham Heath NNR TL 916861, TL 915860, TL 916859	The area is cut annually to reduce bracken dominance. The area sampled was vegetated by a dense grass sward with substantial amounts of bracken and no exposed substrate.
Weeting Heath NNR TL 757883, TL 758882, TL 757880	Two transect were placed in a rabbit grazed area of deep sand and the third along the fence line of a rabbit grazed area of lichen dominated grass-heath. Both areas have short rabbit grazed swards with patches of exposed substrate.

2.2.5 Analysis

Species were assigned to one of five habitat associations (Table 2.3), with reference to habitat descriptions in Harvey *et al.* (2002) and Roberts (1996). Habitat associations were defined hierarchically so that upper broader categories contain any species associated with woodland and or mesic habitats irrespective of whether they may also be found in open habitat types lower in the classification, while the lowest categories solely comprise specialist (stenotopic) species restricted to a narrow range of dry open habitats. Conservation status of species followed Harvey *et al.* (2002): Notable A (Na; nationally scarce, occurring in 30 or fewer UK 10 km squares) and Notable B (Nb; nationally scarce, occurring in 31-100 of the UK 10km squares). Linyphiidae spiders where not used in the analysis due to the scarcity of heathland spiders in the assemblage. Only one species associated with xeric habitats and two associated with grass-heath were recorded. The assemblage strongly consisted of eurytopic and mesic species.

For most habitat association groups, abundance and species richness was similar between the paired track and verge samples (paired t-tests: $P > 0.1$), with the exception of xeric species (richness: track > verge, $t_{29}=1.989$ $P=0.056$; abundance: track > verge, $t_{29}=1.964$ $P=0.059$) and eurytopic species richness (track > verge, $t_{28}=1.814$ $P=0.080$). Track and verge samples were pooled and aggregate samples for each trackway site were used in all subsequent analyses.

Species accumulation with increasing sampling effort was examined separately for trackway and heathland reference samples, using sample based rarefaction performed in EstimateS (Colwell 2009) and also rescaled to examine the number of individuals sampled (to control for differential trapping effort).

Assemblage composition across samples was examined using Multidimensional Scaling (MDS) performed on a similarity matrix of Bray-Curtis coefficients of spider abundance data (standardised per trap-days and square root transformed) using PRIMER 5 (Clarke and Gorley 2001). Stress values for MDS ordinations indicate the level of accuracy in representation; < 0.05 excellent, < 0.1 good, < 0.2 potentially useful, > 0.3 points close to being arbitrarily placed (Clarke and Warwick 1994).

Species richness and abundance of each habitat association group was compared among site categories (e.g. heathland reference transect, thicket trackway, mature trackway) using generalised linear models (GLM), with abundance data standardised by the number of trap-days per sample. The error term (normal, poisson, negative binomial) for each analysis was selected by examining the deviance/degree of freedom ratio. Differences among group means were examined by sequential sidak pairwise comparisons.

For thicket trackways alone, species richness and abundance of each habitat association group, and the abundance of each of the three most numerous species, were compared between trackways of different widths using T-tests. Statistical analyses were performed in SPSS v.16 (SPSS Inc, Chicago, IL, U.S.A).

Table 2.3. Classification of habitat associations of spider species, based on species accounts in Harvey et al (2002) and Roberts (1996)

Habitat	Description
Eurytopic	Species described as eurytopic (living in most habitats), or that are associated with most of the habitats considered below.
Woodland	All species (other than eurytopic species) associated with woodland, including those also associated with open-mesic, grass-heath or xeric habitats.
Open-mesic	Species associated with grassland, moorland (upland dwarf shrub heath on peat soils), and/or marshy damp habitats; long and short vegetation; may be damp or dry but not associated with woodland.
Grass-heath	Species associated with dry lowland calcareous and/or acidic grassland, lowland heathland, sparse and/or short vegetation and not also associated with the habitats above.
Xeric	Dry heathland; sandy or dune habitats; sand or gravel pits, bare ground, lichen, coastal, scree and shingle

2.3 Results

We collected and identified 3746 spiders from 54 species in the 30 forestry trackways, while from the 27 heathland reference transects 5568 spiders from 50 species were identified. Overall, a total of 71 species were recorded, of which 21 were unique to the trackways and 17 were unique to the heathland reference sites. Pitfall trapping of ground-active spiders in this study effectively captured the assemblage composition in both the forest trackways and heathland reference sites, as sample based rarefaction approached the asymptote in each case (Fig. 2.2).

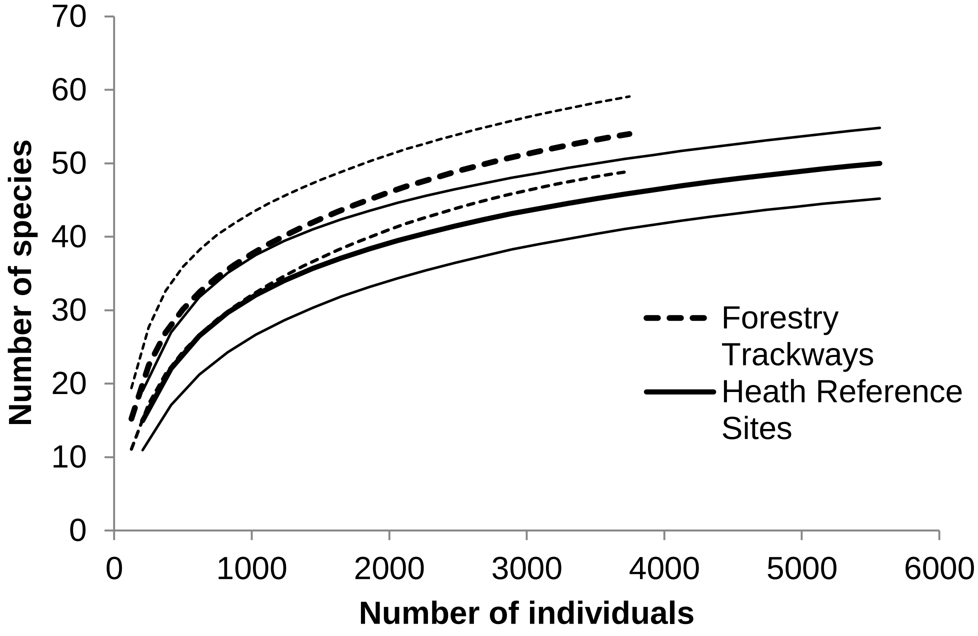

Fig. 2.2. Sample-based rarefaction curves (Mao Tau function) with 95% confidence interval lines of spider species collected from 30 trackways sampled in Thetford Forest and 27 heath reference sites

2.3.1 Ground-active spider composition in Thetford Forest trackways

The majority of spiders captured in trackways were eurytopic species (41% of the total). The family Lycosidae (wolf spiders) were the most numerous, with 2725 individuals (73% of the total sample) from eleven species. The three most numerous species caught were all Lycosidae, *Pirata hygrophilus* Thorell (n = 1012, woodland associated), *Pardosa pullata* (Clerck) (n = 900, eurytopic associated) and *Pardosa monticola* (Clerck) (n = 540, grass-heath associated).

Of the 54 species, thirteen were associated with grass-heath habitats and three with xeric habitats, comprising 26% and 1% of the total individuals found in the trackways respectively. Of the 54 species recorded, four were Nationally Scarce (Nb), including three grass-heath species: *Trachyzelotes pedestris* (C.L. Koch), *Xerolycosa nemoralis* (Westring), and *Aelurillus v-insignitus* (Clerck) and a woodland species *Micaria subopaca* (Westring).

2.3.2 Ground spider composition in heathland reference sites

In contrast to the forest trackways sampled, the majority of individuals sampled on heathland reference sites were grass-heath species (73%), while xeric species made up 3% of the total catch. The most numerous species caught were *P. monticola* (Clerck) (n = 3490, grass-heath associated), *Pardosa palustris* (Linnaeus) (n = 417, open-mesic associated) and *Steatoda phalerata* (Panzer) (n = 250, grass-heath associated).

Eight of the species recorded were Nb including two grass-heath species recorded in forest trackways *T. pedestris* and *X. nemoralis*, one additional grass-heath species *Micaria silesiaca* L. Koch, and a further three xeric species: *Ozyptila scabricula* (Westring)*; Sitticus saltator* (O.P.-Cambridge) and *Steatoda albomaculata* (Degeer), as well as one woodland and one open-mesic species, *Marpissa muscosa* (Clerck) and *Pardosa agrestis* (Westring) respectively.

2.3.3 Community composition of trackway and heathland reference assemblages

MDS successfully represented the assemblage structure with a low stress value (Fig. 2.3) (Clarke and Warwick 1994). Spider assemblages differed among the mature trackways, thicket trackways and heathland reference transects with strong separation along axis one of the ordination, mature trackways and heathland transects showed the greatest separation (Fig. 2.3a, Table 2.4). Of the outliers, three transects from a single heathland reference site with closed sward vegetation were grouped together at the top of the plot. The heathland reference transects located lowest in the ordination were obtained from the most physically disturbed sites, including heavily rabbit-grazed warrens and recently ploughed areas.

The relative abundance of the three most frequently recorded species within the ordination *Pardosa monticola* (grass-heath), *Pardosa pullata* (eurytopic) and *Pirata hygrophilus* (woodland), indicated a moisture gradient across the site classes (Fig. 2.3). *P. monticola* was most abundant in the heathland transects, scarcer in thicket trackways and was almost absent in the mature trackways (Fig. 2.3b). *P. pullata* was most numerous in the thicket trackways and closed sward heaths but was also abundant in the mature trackways (Fig. 2.3c), while small numbers of *P. pullata* were also present in approximately half of the heathland reference transects. *P. hygrophilus* is dominant in the mature trackways with smaller numbers in some of the thicket trackways (Fig. 2.3d) but was absent from the heathland transects.

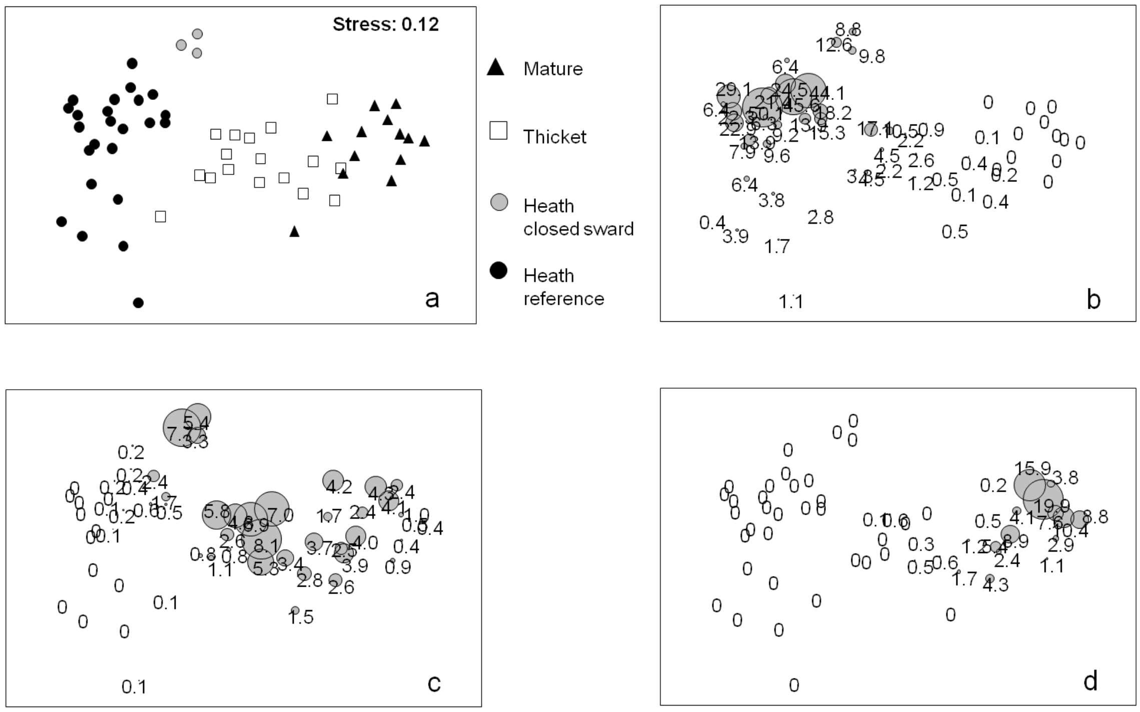

Fig. 2.3. MDS ordination plots of spider assemblages showing the two forestry trackway categories (mature and thicket) and the heathland reference transects. Plot a) shows the forest trackway samples (pooled track and verge samples) and the heathland reference transects. Bubble plots show the abundance of the three most dominant species recorded; b) *Pardosa monticola*, a grass-heath species, c) *Pardosa pullata,* a eurytopic species and d) *Pirata hygrophilus*, a damp habitat/woodland species. Numbers in bubble plots indicate the abundance of each species per site (corrected for trap/day)

2.3.4 Community comparison: habitat association

Trackways adjacent to mature stands were dominated by eurytopic and woodland spiders, both in terms of species richness and relative abundance (Fig. 2.4). Very few species restricted to xeric and grass-heath habitats were found in the mature trackways. In contrast, trackway samples in thicket stands contained significantly fewer woodland species and individuals, although were similar in richness and relative abundance of eurytopic species (Fig. 2.4, Table 2.4). Thicket trackways provided more individuals associated with xeric and grass-heath habitats than were trapped in mature trackways (Fig. 2.4, Table 2.4).

Heathland reference transects were strongly dominated by individuals of species associated with grass-heath habitats, comprising approximately three quarters of the total catch (Fig. 2.4, Table 2.4). Heathland transects contained significantly fewer woodland and eurytopic spiders than forest trackways of either class (Table 2.4). Although the abundance of grass-heath species was significantly greater in heathland reference transects than in thicket trackways, the species richness of xeric, grass-heath and open-mesic species was similar (Table 2.4).

2.3.5 Influence of trackway width

Within thicket stands, narrow trackways had significantly greater abundances of eurytopic and open-mesic spiders and also a greater species richness of woodland spiders (Table 2.5). Conversely, the species richness and abundance of spiders restricted to xeric habitats was greater in wider thicket trackways.

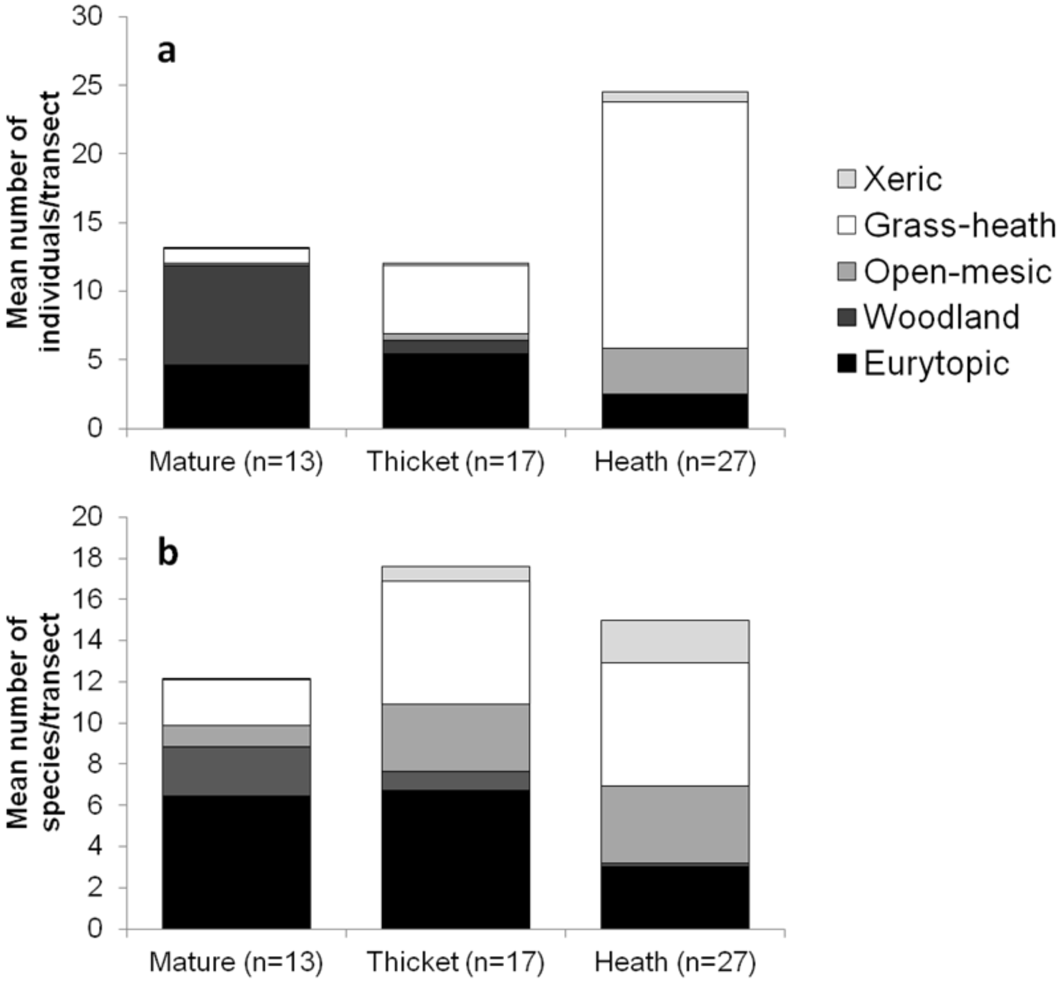

Fig. 2.4. Mean numbers of a) individual spiders (standardised for trap-days), b) species for each habitat association category compared among the three site types; mature forestry tracks, thicket forestry tracks and transects from heathland reference sites

Table 2.4. Means, standard errors and results of General Linear Models (χ^2 and p-value) comparing MDS axis scores, species abundance (standardised for number of trap days) and species richness of the spider habitat association groups among the mature tracks, thicket tracks and heathland reference sites. Sequential Sidak pairwise comparisons were used to define homogenous sub-sets (a-c ranked highest to lowest); means that share a superscript do not differ significantly (P<0.05).

	Variable	Mature n = 13 Mean ± s.e	Thicket n = 17 Mean ± s.e	Heath/ruderal n = 27 Mean ± s.e	Chi square	P-value	Mature	Thicket	Heath
Individual abundance	MDS axis 1^1	-1.27 ± 0.08	-0.33 ± 0.10	0.82 ± 0.06	352.041	<0.001	c	b	a
	MDS axis 2^1	0.00 ± 0.08	-0.14 ± 0.06	0.09 ± 0.10	3.515	0.172	a	a	a
	Grass-heath^2	1.02 ± 0.44	4.98 ± 1.26	17.90 ± 2.77	57.326	<0.001	c	b	a
	Xeric^2	0.01 ± 0.01	0.15 ± 0.04	0.78 ± 0.15	34.871	<0.001	b	b	a
	Open mesic^2	0.15 ± 0.06	0.51 ± 0.07	3.37 ± 0.98	32.120	<0.001	b	b	a
	Woodland^2	7.32 ± 1.72	0.93 ± 0.39	0.02 ± 0.01	107.175	<0.001	a	b	c
	Eurytopic^2	4.58 ± 0.62	5.45 ± 0.70	2.49 ± 0.85	20.169	<0.001	a	a	b
Species richness	Grass-heath^2	2.23 ± 0.47	6.00 ± 0.35	6.00 ± 0.36	11.396	0.003	b	a	a
	Xeric^2	0.08 ± 0.08	0.71 ± 0.17	2.04 ± 0.29	12.123	0.002	b	a/b	a
	Open mesic^2	1.00 ± 0.30	3.24 ± 0.29	3.74 ± 0.36	12.075	0.002	b	a	a
	Woodland^3	2.38 ± 0.24	0.94 ± 0.18	0.15 ± 0.07	31.467	<0.001	a	b	c
	Eurytopic^2	6.46 ± 0.43	6.71 ± 0.33	3.04 ± 0.34	11.269	0.004	a	a	b

Variable superscript indicates which model type used; 1 = linear normal, 2 = square root linear, 3 = poisson

Table 2.5. Mean ± S.E of spider abundance and species richness of spider habitat groups in thicket tracks. Differences from T-tests between the narrow and wide tracks for each spider habitat group are shown, p values < 0.05 are shown in bold.

	Species variable	Thicket narrow n = 10 mean ± s.e	Thicket wide n = 7 mean ± s.e	T statistic; DF	p-value
Abundance	Grass-heath	55.90 ± 20.76	41.00 ± 9.00	0.570, 15	0.577
	Xeric	0.50 ± 0.31	3.00 ± 0.62	-3.626, 9	**0.006**
	Open mesic	6.40 ± 0.90	3.29 ± 0.42	3.144, 13	**0.008**
	Woodland	13.50 ± 6.26	3.29 ± 2.39	1.525, 15	0.154
	Eurytopic	66.10 ± 7.42	38.00 ± 11.18	2.187, 15	**0.045**
	P. monticola	38.20 ± 17.92	21.43 ± 5.76	0.757, 15	0.461
	P. pullata	44.60 ± 6.11	25.57 ± 9.96	1.723, 15	0.105
	P. hygrophilus	12.70 ± 6.13	3.14 ± 2.41	1.247, 15	0.231
Species richness	Grass-heath	5.90 ± 0.55	6.14 ± 0.40	-0.329, 15	0.747
	Xeric	0.40 ± 0.22	1.14 ± 0.14	-2.546, 15	**0.022**
	Open mesic	3.60 ± 0.43	2.71 ± 0.29	1.563, 15	0.139
	Woodland	1.30 ± 0.21	0.43 ± 0.20	2.840, 15	**0.012**
	Eurytopic	7.20 ± 0.47	6.00 ± 0.31	1.941, 15	0.071

2.4 Discussion

2.4.1 Heathland spider communities in forestry trackways

The trackway network supported important elements of open habitat assemblages, particularly heathland species of which a number were nationally scarce. Trackways in thicket-aged stands supported similar numbers of grass-heath and xeric species as heathland sites. These results show that trackway elements within the forest landscape can be important for open habitat species and can contribute to the overall biodiversity of the landscape. Furthermore, wide trackways (those greater than 25m) in thicket stands supported greater numbers of xeric species than narrow trackways and lower abundances of woodland and eurytopic species; thus increasing the width of forestry trackways would benefit open habitat assemblages.

2.4.2 Effects of forest growth stage on trackway assemblage

Although trackways supported characteristic and rare heathland spider species, the trackway assemblage still differed considerably from that found in heathland sites; heathland reference sites were dominated by grass-heath species, whereas trackways in thicket stands contained far more eurytopic species. Furthermore, only the trackways in thicket-aged stands showed any resemblance to the assemblage found in heathland sites; trackways in mature stands were dominated by woodland and eurytopic species.

Shading by mature trees in trackways is likely to increase moisture and decrease temperature and light availability, creating unsuitable habitat for grass-heath and xeric species. This is shown by the relative distribution of the dominant Lycosidae species; the damp habitat species, *P. hygrophilus*, was confined to the mature trackways whereas the grass-heath species, *P. monticola*, dominant in the heathland reference sites was also present in thicket trackways. *P. monticola* in this study shows similar patterns of shade intolerance as open habitat butterfly species reported in other studies (Greatorex-Davies et al. 1993; Warren 1985).

2.4.3 Influence of trackway width on the spider community

Increased trackway width in the thicket stands had significant effects on the assemblage composition. Wide trackways contained fewer eurytopic individuals and woodland species and more xeric species and individuals than narrow thicket trackways, likely due to reduced shading causing changes in the microhabitat and soil moisture. Although other studies have advocated trackway widening for open habitat species (Greatorex-Davies et al. 1994; Mullen et al. 2003; Warren 1985), this study provides direct evidence that increasing trackway width can benefit specialist ground-active invertebrate species associated with xeric habitats. For example, *Arctosa perita*, a specialist species of frontal dune and dry heathland habitats was only found in the wide trackways (where it was represented by five individuals).

As well as changes in microhabitat, competition from eurytopic and woodland species from the surrounding forest may potentially also restrict xeric species in trackways. Hopkins and Web (1984) speculate that this may occur on small heathland fragments where vagrant species may outcompete heathland species. The current study showed wide trackways have lower densities of eurytopic individuals and fewer woodland species, which could alleviate competition pressures to benefit persistence of xeric species in the forested landscape.

Wide trackways sampled were two to three times the width of the average trackway in the forest. This corresponds with current conservation guidelines that suggest that to maintain open habitat communities, forest trackways need to be at least as wide, and preferably 1.5 times as wide as the height of the surrounding trees (Warren and Fuller 1993). For thicket stands where trees are approximately 10 metres tall, trackways need to be 10-15 m wide. However, to allow unshaded open habitat conditions to persist throughout the forest growth cycle would require trackway widths of 30-45 m within mature stands, where trees are 20-30 m in height. Whether connectivity requires a permanent network of unshaded trackways or can be achieved by a shifting pattern of more short lived elements, dependent on the forest management and growth cycle, depends on the relative mobility and vagility of the ground-active invertebrate fauna that forms the conservation concern.

2.4.4 Connectivity and dispersal

Given that the forest is planted in a patchwork of growth stages, trackway suitability will be both spatially and temporally sporadic. Open habitat species with relatively good cursorial dispersal abilities, such as reported for various *Pardosa* species (Bonte et al.

2007; Kiss and Samu 2000; Morse 1997), may be able to sustain metapopulations in this changing environment. However, the restricted distribution of many specialist heathland invertebrates has in part been attributed to their poor dispersal ability (Bonte et al. 2003; Hopkins and Webb 1984). For less mobile specialist xeric species a patchy mosaic of suitable habitat may not be sufficient to allow colonisation and persistence in the forested landscape.

2.4.5 Management implications

To create and maintain grass-heath biodiversity in the trackway network of plantation forests established on former heathland areas, management needs to focus on: widening existing trackways, reducing the dominance of dense grass-swards in track verges and increasing the patchiness of growth stages within the forest.

Widening trackways to create permanently unshaded habitat could facilitate dispersal and colonisation from adjacent grass-heath into the forest trackway network, linking fragmented remnants of heath across the forest and providing movement pathways through the forest for specialist xeric invertebrates. Many specialist species with poor dispersal abilities will benefit from having connectivity of wide permanently unshaded trackways that could support persistent resident populations as well as being used as dispersal corridors.

Where ground vegetation is dominated by thick-dense swards in the trackways, some form of physical disturbance may also be required to created early successional habitats with exposed substrates and reduced vegetation density. The need for disturbance to enhance grass-heath biodiversity is well known (Dolman and Sutherland 1992, 1994; Romermann et al. 2009), but little work has been carried out to compare the benefits of different techniques. Early successional stages in many heathland reference sites are maintained by large rabbit populations, but as this is incompatible with forestry management, similar vegetation structures in the trackways may require physical mechanical disturbance.

Large-congregated restocks may impede dispersal along trackways for less mobile habitat specialist when trees mature. Although trackway widening may not be feasible throughout the forest to alleviate this, we advocate an increase in patchiness of growth stages (by reducing coupe area), allowing greater proximity between ephemeral patches of open habitat to be as close as possible for dispersal limited species.

2.4.6 Conclusion

Trackways support a significant amount of the heathland spider composition. However, management in trackways may further increase the abundance of grass-heath species while reducing the influence of woodland and eurytopic species. Restoring open habitat networks would enhance the biodiversity of the forest as well as support specialist xeric species. Management options should be tested to find cost effective methods. There is great potential for trackways to enhance the biodiversity of plantation forests whilst also improving the cohesion of fragmented grass-heath habitats in the region.

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Chapter 3

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

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 two 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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3.1 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-history's (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.

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.

3.2 Methodology

3.2.1 Study site

Thetford Forest was planted in the early 20th century and occupies 185 km^2 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 (*P. 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, 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.

3.2.2 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 (see Appendix A3.1 for treatment photographs). Plots were distributed within the contiguous core area of Thetford Forest (comprising four management ‘blocks’), and in one large southern forest block (Fig. 3.1). 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 strips 40-50 cm 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).

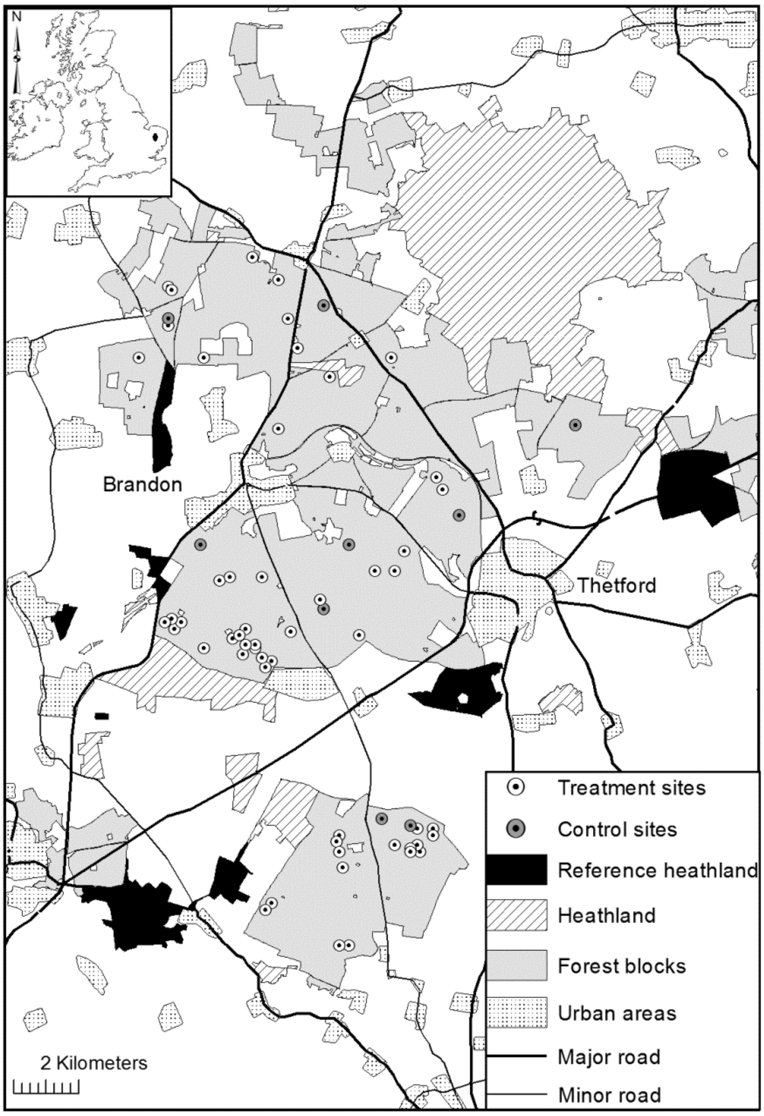

Fig. 3.1. Sample locations within Thetford Forest showing the distribution of treatment and control transects and sampled reference heathlands.

Plots were placed within trackways at least 9 m wide, within coupes aged 10-25 years that comprise closed-canopy stands lacking 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 grams from each core were mixed with 125 cm^3 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.

3.2.3 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 days. Traps in each transect were combined giving one composite sample per plot-year. Taxonomic references for subsequent species identification of carabids, ants and spiders are detailed in Appendix Table A3.2.

3.2.4 Invertebrate sampling in heath reference sites

Ground-active invertebrates were also sampled on eight heath reference sites located within 8 km of treatment plots, of which seven were designated under EU and or UK conservation legislation. All were subject to conservation management, predominantly rabbit and sheep grazing, with some mechanical disturbance (for site details see Appendix Table A3.3). Within each site, three transects were set (each of six pitfall traps of the same dimensions used in experimental plots) at least 50 m apart, open for seven consecutive days over three trapping periods (May, June and August) in 2009.

3.2.5 Plant species composition and vegetation structure

In each treatment plot, incidence of vascular plant species was recorded from 20 1 m x 1 m quadrats placed regularly along the centre, between May to August of both 2009 and 2010. In August of both years, vegetation height in each plot was assessed at 40 points using a sward stick (diameter 90 mm, weight 250 g, following Dolman and Sutherland 1992), and percentage of bare substrate visually estimated in 20 cm x 20 cm at each point. Due to protected nesting birds it was not possible to survey vegetation structure or vascular plant composition on heathland reference sites.

3.2.6 Classification of species

For each taxonomic group, we classified species as those likely to be ubiquitous in the forest (eurytopic and or woodland species: hereafter ‘generalist shade-tolerant’), and stenotopic species of regional conservation interest, for which treatments may enhance connectivity (hereafter ‘specialists’). Specialist invertebrates were defined as species associated with dry grassland, lowland heathland, dunes, chalk or gravel pits. Effects of treatments were contrasted between generalists and specialists; less exacting species of open mesic habitats (such as moorland) were not considered further but generally maintained an even abundance across treatments.

Vascular plants were classified as those that are shade tolerant and or occur in mesic (damp or nutrient-enriched) habitats (‘generalist shade-tolerant’), and specialist species restricted to oligotrophic (low nutrient) open-habitats that also require physical disturbance (i.e. ruderals, annuals, or species intolerant of competition in closed swards); these are a conservation priority in the region (Dolman et al. 2012). Vascular plant species capable of persisting in open nutrient-poor habitats without regular disturbance are ubiquitous throughout the trackway network and were not considered further. Species lists, sources for habitat classification and protection status are shown in Appendix Table A3.2.

3.2.7 Data analysis

Abundance measures comprised: frequency of each vascular plant species (per plot; range 0-20), and numbers of individuals per plot-year for invertebrates, pooled across pitfalls and sampling periods.

Sampling effort and species richness were compared among treatments and reference sites with sample-based rarefaction using the EstimateS software package (Colwell 2009).

For each taxonomic group, assemblage composition across treatments and heath reference sites was examined using non-Metric Multidimensional Scaling (NMDS) performed on a matrix of Bray-Curtis dissimilarities of abundance data (square root transformed and Wisconsin double standardization) using the vegan package (Oksanen et al. 2010) in the statistical software R (R Development Core Team 2012). Centroids for heath reference samples and treatments were plotted to visualise assemblage differences. Stress values were examined to assess the accuracy in representation: < 0.05 excellent; < 0.1 good; < 0.2 potentially useful; > 0.3 close to arbitrary (Clarke and Warwick 1994). The influence of soil pH on plant assemblage NMDS axis scores was examined by Spearman’s correlation.

To examine the stability of sampled communities between years, NMDS was also performed simultaneously on data from both years of treatment sampling and heath reference sites sampled in year one only. Paired t-tests were used to investigate differences in the ordination scores of control plots between each sampled year. NMDS axis one scores of control plots indicated stable invertebrate and plant compositions between years (paired t tests: $P > 0.05$). The large differences between years in ordination of treatments relative to reference sites are therefore unlikely to be an artefact of inter-annual variation in weather.

Species richness and abundance of specialists and generalist shade-tolerant species were compared among treatments and heath reference transects using generalised linear models (GLMs) in R. The appropriate error term (normal, Poisson, negative binomial) for each analysis was selected by comparing Akaike's Information Criterion (AIC) and examining the ratio of deviance/residual degrees of freedom. Differences among site category means (treatments and controls) were examined by Tukey pairwise comparisons. GLMs retained soil type (categorical: acidic, calcareous and mixed) and forest block when significant ($P < 0.05$). Spatial autocorrelation of GLM residuals was examined by Moran's I in the ape package v.3.0-6 (Paradis et al. 2004) in R. In all instances Moran's I was not significant ($P > 0.05$).

Sward height and the extent of bare substrate were also compared among site types (treatments, heath references and controls) over the two years using GLMs. Only those site types that contain more than one percentage bare substrate and sward heights greater than zero were included in the analysis.

3.3 Results

A total of 73 182 invertebrates from 256 species were identified over the two years, comprising 7564 carabids from 94 species, 24 087 spiders from 142 species and 41 531 ants from 20 species. In addition, 23 241 observations of vascular plants from 222 species were recorded. Sampling of ground-active invertebrates and vascular plants effectively captured the assemblage composition, as sample-based rarefactions approached their asymptote (Fig. 3.2). Species richness was lower for all invertebrate groups in heath reference transects than in treatment plots (Fig. 3.2). Fourteen species were unique to heathlands, eleven of which were specialists including six nationally scarce species, three ground spiders and three carabids.

3.3.1 Vegetation structure

Control and cutting treatments provided very little bare substrate over the duration of the experiment (Fig. 3.3). As expected, the four soil disturbance treatments provided a significantly greater extent of bare substrate compared to controls in the first year. However, by year two the extent of exposed substrate in disced plots was similar to that in control and cutting treatments, while turf-stripped sites retained more bare substrate than any other treatment in the second year. Sward-height was reduced in the three most destructive treatments (FP, AP, and TS) in year one compared to control and cutting treatments (Fig. 3.3). However, by year two sward-heights only remained significantly lower in turf stripped plots. Sward-height and percentage of exposed substrate was variable in samples from heath reference sites due to differing levels of physical disturbance (Fig. 3.3).

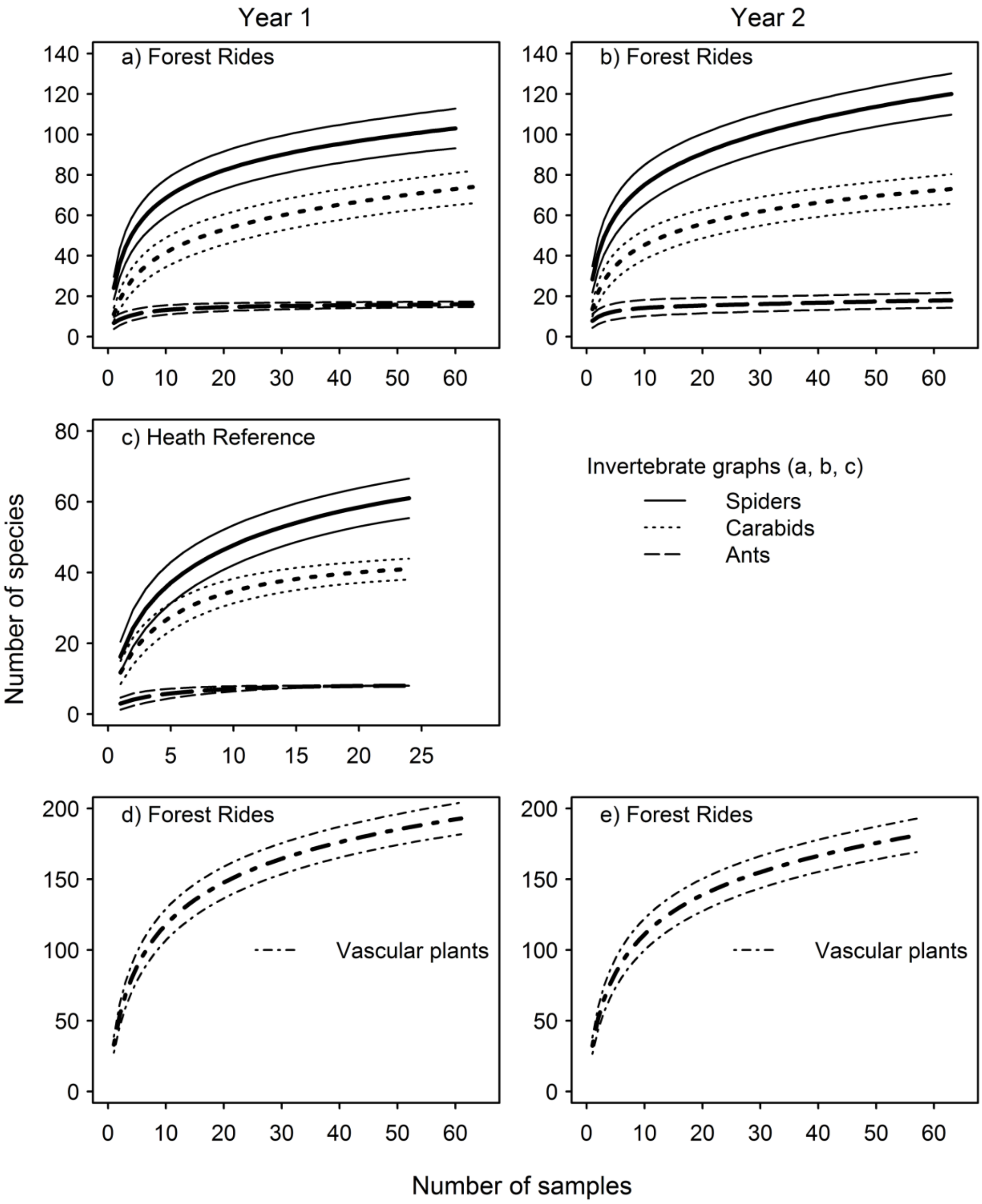

Fig. 3.2. Sample-based rarefaction curves with 95% confidence intervals for pitfall catches of ground active invertebrates and quadrat sampling for vascular plants, shown separately for each year of sampling. a-b) pitfall trap sampling from treatment and control plots of invertebrate taxa; spiders, carabids and ants; c) invertebrate sampling of heath reference sites (in year one only); d-e) vascular plant sampling from treatment and control plots.

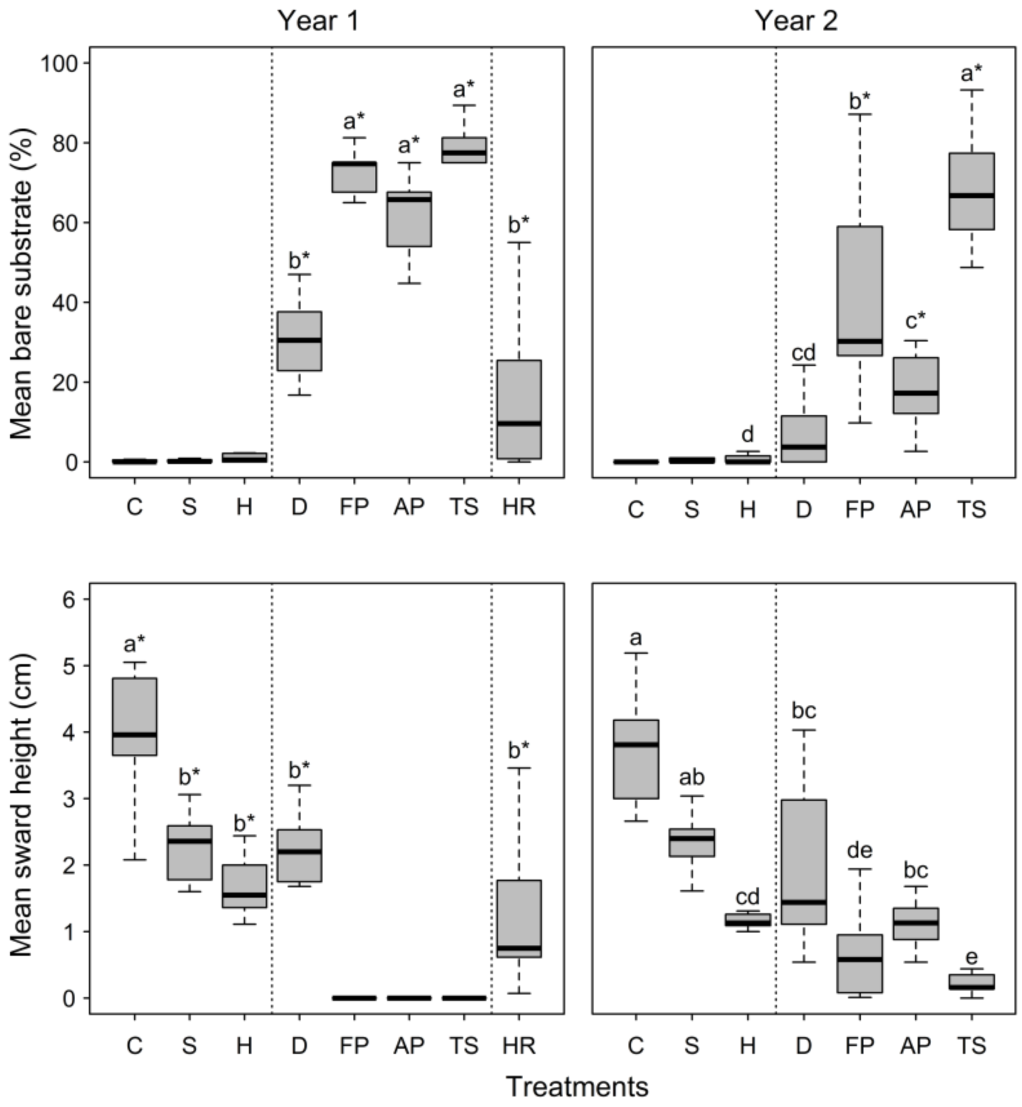

Fig. 3.3. Response of sward height and extent of bare ground to disturbance treatments: C=control, S=swipe, H=silage harvest, D=discing, FP=forest plough, AP=agricultural plough, TS=turf strip, and in HR=heath reference. Vertical dotted lines separate control and cutting treatments from soil disturbance treatments and heath reference sites. Results of Generalised Linear Models (χ^2 and p-value) comparing site types are presented; means that share a superscript (homogenous subsets, a-e, ranked highest to lowest) do not differ significantly (Tukey pairwise comparisons $P < 0.05$). Treatments with negligible bare substrate (< 1 %) or mean sward height of zero were excluded from GLMs due to heteroscedasticity; means marked with an asterisk have confidence interval that does not overlap with these zero reference classes.

3.3.2 Composition of carabid assemblages

NMDS ordination showed carabid assemblages in treatment plots differed from heath reference assemblages in year one, but in year two many of the turf stripped and agricultural plough plots were located in a similar part of the ordination space to heath transects (Fig. 3.4). Pooled abundance of specialist species increased with increasing intensity of disturbance; only turf stripped plots did not continue this upward trend in the first year but still contained twice the abundance of control plots (Fig. 3.5). This pattern of response continued in the second year, turf stripped plots had accumulated significantly greater abundance and richness of specialist species than controls (Fig. 3.5 and Fig. 3.6). Although single records of a species should be considered quasi-anecdotal observations, it is notable that the two specialist Red Data Book (RDB) species recorded in the experiment (RDB1 endangered *Amara fusca*, RDB2 vulnerable *Harpalus froelichii*) were found in turf stripped plots in year two.

3.3.3 Composition of spider assemblages

Composition of ground spider assemblages differed between treatment plots and heath reference transects, with substantial differences along axis one of the NMDS in both years (Fig. 3.4). Pooled abundance of specialist species was one or two orders of magnitude greater in heath reference transects than in treatment plots (Fig. 3.5). In addition, heath transects had lower richness and abundance of generalist shade-tolerant species. Compared to controls, the three most destructive treatments (FP, AP, TS) had reduced richness of specialist species and reduced abundance and richness of generalist shade-tolerant species in year one (Fig. 3.5 and Fig. 3.6). However, in the second year all intensely disturbed treatments, except turf stripping, had recovered in abundance of generalist shade-tolerant species and all treatments had similar species richness of both specialists and generalists.

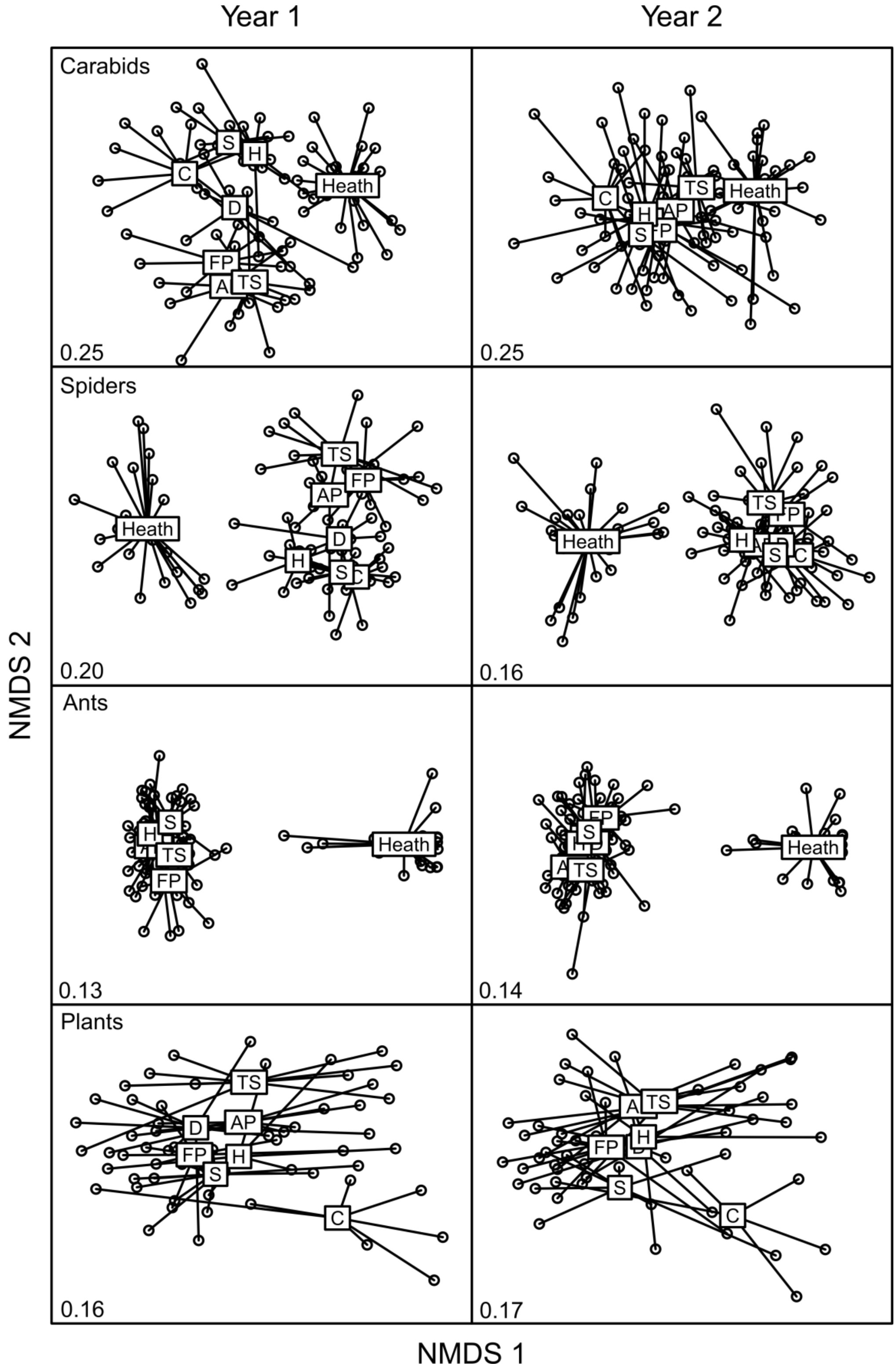

Fig. 3.4. Non-Metric Multidimensional Scaling (NMDS) ordination comparing assemblage composition of three invertebrate groups and vascular plants among seven disturbance treatments and heath reference transects. Points are sampled transects with lines connecting to habitat centroids (C=control, S=swipe, H=silage harvest, D=discing, FP=forest plough, AP=agricultural plough, TS=turf strip, Heath=heath reference). Stress values for each ordination are show at the bottom of each plot.

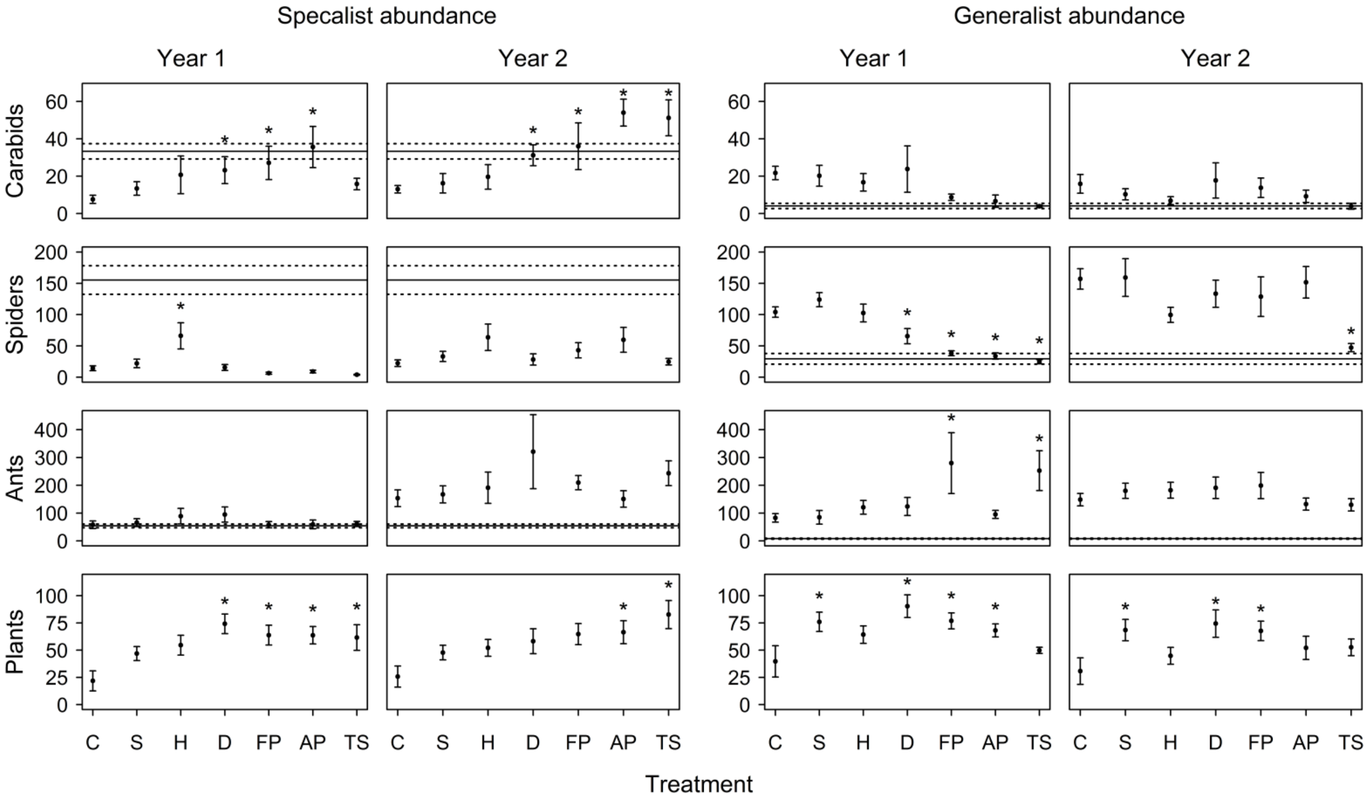

Fig. 3.5. Mean and standard error of species abundance across disturbance treatments and controls for specialist (left) and generalist shade-tolerant species (right). Mean (horizontal line) and standard error (dotted line) of invertebrate groups sampled in heathland reference sites in 2009 are also shown. Generalised Linear Models (χ^2 and p-values are shown in Appendix Table A3.4) were used to compare among treatments and controls. Tukey pairwise comparisons were used to define homogenous sub-sets; treatments that are significantly different from controls ($P < 0.05$) are shown with an asterisk.

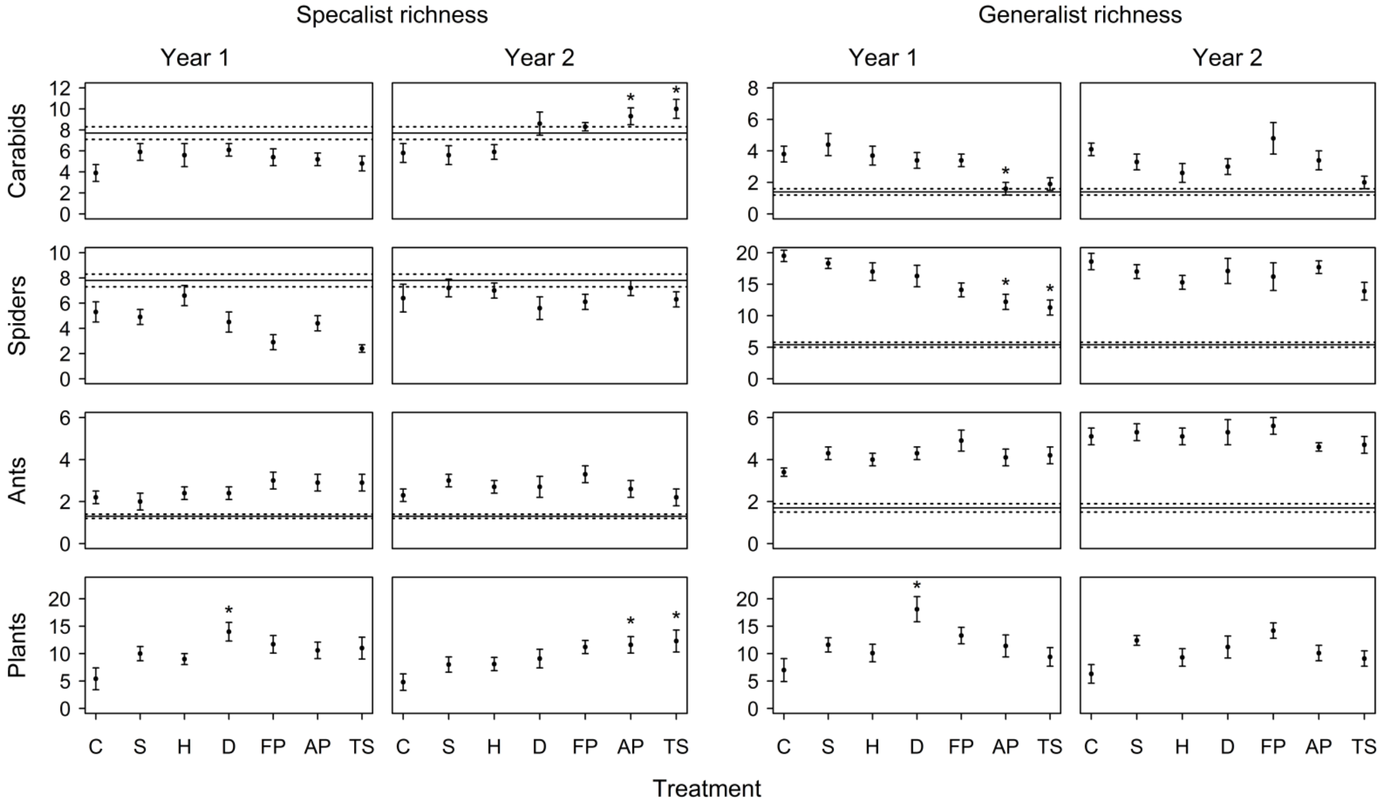

Fig. 3.6. Mean and standard error of species richness across disturbance treatments and controls for specialist (left) and generalist shade-tolerant species (right). Mean (horizontal line) and standard error (dotted line) of invertebrate groups sampled in heathland reference sites in 2009 are also shown. Generalised Linear Models (χ^2 and p-values are shown in Appendix Table A3.4) were used to compare among treatments and controls. Tukey pairwise comparisons were used to define homogenous sub-sets; treatments that are significantly different from controls ($P < 0.05$) are shown with an asterisk.

3.3.4 Composition of ant assemblages

Ant species composition of heath reference transects differed to that of treatment plots in both years along axis one of the ordinations (Fig. 3.4). Species richness of heath transects was low compared to treatment plots (Fig. 3.2 and Fig. 3.6) and all species found in heaths were also recorded in treatment plots. Species composition among all treatments was similar (Fig. 3.4) and no significant differences in species richness were recorded between treatments in either year (Fig. 3.6 and Appendix Table A3.4).

3.3.5 Composition of vascular plants

Composition of vascular plant assemblages in the NMDS was strongly influenced by soil pH, with calcareous plots located to the right on the first axis (Fig. 3.4: year 1 r_s=-0.86, $p < 0.001$; year 2 r_s=-0.76, $p < 0.001$). Species composition differed markedly among treatments with the more intensely disturbed treatments located towards the top of the ordination (Fig. 3.4). In both years the greatest separation was between turf stripped plots and the controls on axis two.

The pooled abundance of specialist plants increased with intensification of disturbance (Fig. 3.5). In year one, richness of specialist plants was greater in all soil disturbance treatments than in control and cutting treatments (Fig. 3.6), with disced treatments having the greatest species richness. However, in year two disced plots had reduced in both richness and abundance of specialist species and were similar to controls. In year two turf stripped and agricultural ploughed treatments contained similarly high abundance and richness of specialist species, both being significantly greater than controls.

3.4 Discussion

3.4.1 Enhancing quality

We examined assemblage responses to management techniques applied in a well-replicated experiment on a network of open-habitat trackways using intensive multi-taxa sampling, recording over 70 000 invertebrates and 23 000 vascular plant observations.

Mechanical disturbance treatments enhanced stenotopic early-successional carabid and vascular plant assemblages, with the most intensive disturbance, turf stripping, supporting greater richness and abundance of specialist species. Turf stripping removed the vegetation and organic matter from forest trackways, creating the exposed sparsely-vegetated substrate required by arenicolous (sand inhabiting) and thermophilous species. However, not all taxa responded positively to disturbance; spiders were less resilient while ants were unaffected by treatments at this scale. Invertebrate assemblages in heath reference sites differed from those in treatment plots, but primarily through the lack of generalists and greater abundance of specialists from heath assemblages rather than the absence of specialist species from treatment plots. Where early-successional biota represent a conservation priority, ecological networks could be enhanced through the use of severe physical disturbance.

3.4.2 Contrasting taxonomic responses

Both richness and abundance of specialist carabids and vascular plants increased with disturbance intensity, contrasting to the abundance and richness of specialist spiders and ants in disturbance plots. The positive responses to disturbance of specialist carabids and vascular plants may in part be due to local dispersal from relictual populations in the trackway network (Bertoncelj and Dolman in press), for plants supplemented by regeneration from persistent seedbanks (Eycott et al. 2006b) and endozoochorous dispersal by abundant deer (Eycott et al. 2007). These could enable specialist individuals to rapidly take advantage of newly disturbed habitat. However, the presence of rare carabids not previously recorded from the forest landscape indicates that longer distance dispersal may also have contributed to observed responses for this group.

Soil disturbance and vegetation removal alter ground microclimate and reduce soil moisture making habitats less humid, a central habitat characteristic affecting arthropod composition (Entling et al. 2007; Schirmel and Buchholz 2011). Schirmel and Buchholz (2011) suggested that greater vegetation density and the amelioration of microclimate and soil humidity were the main drivers of successional change in the arthropod assemblage, with a reduction of rare stenotopic species from grey dunes to young birch forest. In this study, turf stripped and agriculturally ploughed sites, characterised by exposed substrate and reduced vegetation density, contained the greatest numbers of specialist carabid species.

Like carabids and vascular plants, source populations of specialist ground spiders also inhabit the forestry trackways (Pedley et al. 2013). The greater vulnerability and slower recovery of ground spider assemblages compared to carabids may therefore reflect differences in both direct mortality from treatment application and differences in dispersal ability. Spider assemblages are known to be vulnerable to grassland management techniques that alter habitat structure (Bell et al. 2001; Morris 2000). In crop fields, Thorbek and Bilde (2004) showed spiders were more vulnerable through direct mortality from mechanical soil disturbance than were carabid or staphylinid beetles. It is likely that direct mortality explains the large difference in abundance of generalist shade-tolerant spiders found in low, compared to high disturbance plots in the first year.

As well as their vulnerability to physical disturbance, specialist spiders may also be dispersal limited. Although many spiders have the notorious ability to disperse by ‘ballooning’, using silk threads to catch wind currents, potentially travelling many kilometres (Bell et al. 2005; Thomas et al. 2003), compared to active flight this passive mode of dispersal gives less control over direction and, crucially, where and when to land. This may not be a problem for generalist species. However, in fragmented landscapes, species with specialist requirements may have a low probability of landing in suitable habitat. It is notable that, while ballooning is particularly common among Linyphiids (Bonte et al. 2003), of 286 Linyphiidae species known in Britain only 15 (5%) are associated with inland xeric habitats (Harvey et al. 2002). Similarly, of the 68 Linyphiidae species recorded in this study, only four could be classified as specialists (Appendix Table A3.2, see also Duffey et al. (1957)); the remainder were regarded as generalists. In addition, stenotopic spiders from grey dunes in Belgium exhibited low ballooning propensity when tested in laboratory studies (Bonte et al. 2003). Poor dispersal ability of specialist spiders was also suggested by Hopkins and Webb (1984) who found fewer specialist spiders in more isolated heathland fragments in Dorset.

In contrast to spiders, carabids are less reliant on wind currents in flight. Although overall direction may be wind dependent (As 1984), winged flight permits decisions on elevation, distance and greater control over landing sites. Effective aerial dispersal over many kilometres has been reported for both brachypterous (rudimentary or small winged) and macropterous (large winged) species that colonised islands in the Baltic

(As 1984; Kotze 2008). For the carabid *Amara plebeja*, van Huizen (1977) reported distinct flight periods with a spring dispersal to grassland reproduction sites that may use wind currents, and an autumn flight to forested hibernation sites. Effective dispersal over kilometres and appropriate seasonal site selection suggests a greater ability to find appropriate habitat.

3.4.3 Durability of treatment

Responses over two years gave some indication of the relative durability of treatments. Bare substrate and short swards are required by much of the threatened biodiversity in dry heathland and low intensity arable regions (Buchholz 2010; Dolman et al. 2012). In this study, low-impact cutting treatments maintained a relatively short sward but did not provide exposed substrate and provided little benefit to specialist species.

Although the mild soil disturbance provided by discing increased the abundance and richness of specialist plants in the first year, by year two disced plots did not differ from controls and sward height and the extent of bare substrate was similar to that of cutting treatments. Like discing, forestry and agriculture ploughing disrupted but did not remove the vegetation and soil biomass; recovery was again rapid, the extent of bare substrate quickly reduced as sward cover and height increased. To maintain bare substrate and early successional assemblages, such treatments would need repeating at intervals (estimated repetition, for discing every two to three years, for ploughing three to five years). The depletion of spiders caused by discing and ploughing makes regular reapplication on the same plot less desirable, though adjacent plots could be treated.

In contrast, turf stripped plots retained extensive bare substrate after two growing seasons. Turf removal has been used to create and restore other nutrient-poor early-successional habitats including meadows (Tallowin and Smith 2001), lowland heath (Allison and Ausden 2004) and coastal dunes (Grootjans et al. 2002) where mechanical removal of vegetation has been recommended to recharge early-successional arthropod assemblages (Buchholz 2010; Maes and Bonte 2006). Although treatment longevity for turf stripping is unknown and will depend on soil fertility (Kondoh 2001; Noordijk et al. 2010) the effects will outlast less intensive treatments allowing greater recovery time for less resilient populations.

3.4.4 Conservation implications

To support specialist species of conservation concern we advocate management of connecting elements in early-successional networks using high intensity, long lasting disturbance treatments such as turf stripping, or periodic ploughing of plots in close proximity. Applied within existing heathlands, such treatments could provide valuable heterogeneity augmenting assemblages by providing niches for early-successional specialists. For enhancement of trackways in an agricultural context, intense disturbance may require perennial buffers providing refugia for overwintering and disturbance-sensitive invertebrates. It is likely that treatments with long-lasting benefits will allow recovery of negatively affected spider communities in contrast to comparatively rapid results achieved for specialist carabids and vascular plants. A strength of this study lay in examining responses for contrasting speciose groups of invertebrates and vascular plants; nevertheless, we advise caution in applying results to other taxa, particularly vertebrates. While heathland reptiles may benefit from the creation of basking or oviposition sites through physical disturbance (Dolman and Land 1995), treatments risk harming overwintering populations and should be applied heterogeneously and at a local scale. Physical disturbance can provide habitat for priority bird species utilising ruderal seed resources or that forage in sparse open vegetation, including characteristic heathland species such as woodlark *Lullula arborea* (Mallord et al. 2007).

Conservation outcomes of physical management have often been examined for just one or a few taxonomic groups (Pywell et al. 2007; Vandvik et al. 2005); however, the contrasting responses in this study demonstrate the importance of studying multiple taxa from diverse trophic levels with differing foraging and social strategies. Extending this approach to understand responses in terms of life history traits and functional attributes of diverse taxa would enhance the understanding of conservation management options and provide greater transferability and generality of outcomes.

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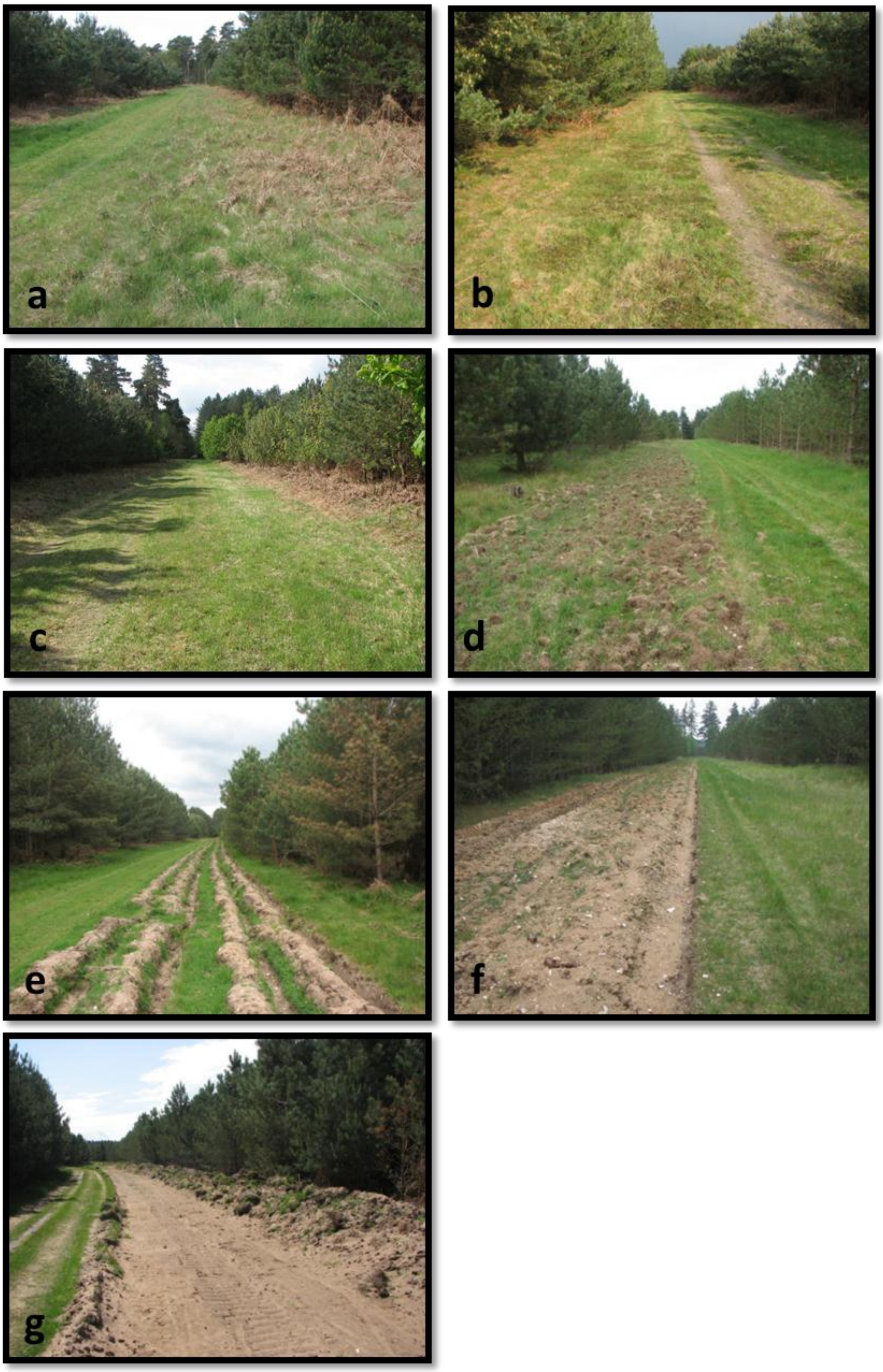
Appendices

Appendix A3.1 Forest trackway disturbance treatments a) control, b) swipe, c) harvest, d) disc, e) forest plough, f) agricultural plough and g) turf strip



Appendix A3.2. Species identified in the sampling programme together with their habitat association, species status in the UK and sampled abundance.

Family	Species	Status	Abundance	Habitat Association
Ground beetles				
Carabidae	Agonum muelleri	.	3	Eurytopic
Carabidae	Amara aenea	.	492	Dry grass-heath
Carabidae	Amara apricaria	.	10	Open-mesic
Carabidae	Amara bifrons	.	38	Open-mesic
Carabidae	Amara communis	.	81	Open-mesic
Carabidae	Amara Consularis	Nb	1	Xeric
Carabidae	Amara convexior	.	171	Dry grass-heath
Carabidae	Amara equestris	Nb	138	Xeric
Carabidae	Amara eurynota	.	2	Dry grass-heath
Carabidae	Amara familiaris	.	12	Dry grass-heath
Carabidae	Amara fulva	Nb	99	Xeric
Carabidae	Amara fusca	RDB1, RDB2, BAP	1	Xeric
Carabidae	Amara lucida	Nb	13	Xeric
Carabidae	Amara lunicollis	.	224	Eurytopic
Carabidae	Amara montivaga	.	7	Xeric
Carabidae	Amara ovata	.	106	Open-mesic
Carabidae	Amara plebeja	.	2	Open-mesic
Carabidae	Amara similata	.	66	Open-mesic
Carabidae	Amara tibialis	.	129	Xeric
Carabidae	Asaphidion stierlini	.	1	Open-mesic
Carabidae	Badister bullatus	.	31	Dry grass-heath
Carabidae	Badister sodalis	.	1	Woodland
Carabidae	Bembidion articulatum	.	1	Xeric
Carabidae	Bembidion femoratum	.	2	Xeric
Carabidae	Bembidion lampros	.	686	Dry grass-heath
Carabidae	Bembidion obtusum	.	3	Open-mesic
Carabidae	Bembidion properans	.	49	Open-mesic
Carabidae	Bembidion quadrimaculatum	.	2	Open-mesic
Carabidae	Bembidion tetracolum	.	17	Open-mesic
Carabidae	Bradycellus harpalinus	.	9	Eurytopic
Carabidae	Broschus cephalotes	.	5	Xeric
Carabidae	Calathus ambiguus	Nb	6	Xeric
Carabidae	Calathus cinctus	.	17	Xeric
Carabidae	Calathus erratus	.	47	Xeric
Carabidae	Calathus fuscipes	.	637	Open-mesic
Carabidae	Calathus melanocephalus	.	29	Open-mesic
Carabidae	Carabus nemoralis	.	68	Open-mesic
Carabidae	Carabus problematicus	.	13	Woodland
Carabidae	Carabus violaceus	.	113	Eurytopic

Carabidae	Cicindela campestris	.	30	Open-mesic
Carabidae	Curtonotus aulicus	.	9	Open-mesic
Carabidae	Curtonotus convexiusculus	.	1	Xeric
Carabidae	Cychrus caraboides	.	13	Woodland
Carabidae	Demetrias atricapillus	.	1	Dry grass-heath
Carabidae	Dyschirius politus	.	11	Xeric
Carabidae	Harpalus affinis	.	104	Dry grass-heath
Carabidae	Harpalus anxius	.	205	Xeric
Carabidae	Harpalus attenuatus	.	14	Xeric
Carabidae	Harpalus froelichii	RDB2, BAP	2	Xeric
Carabidae	Harpalus latus	.	155	Open-mesic
Carabidae	Harpalus pumilus	Na	44	Xeric
Carabidae	Harpalus rubripes	.	185	Xeric
Carabidae	Harpalus rufipalpis	.	453	Xeric
Carabidae	Harpalus rufipes	.	287	Dry grass-heath
Carabidae	Harpalus serripes	Nb	1	Xeric
Carabidae	Harpalus servus	Nb	2	Xeric
Carabidae	Harpalus smaragdinus	Nb	221	Xeric
Carabidae	Harpalus tardus	.	314	Dry grass-heath
Carabidae	Lebia chlorocephala	Nb	1	Eurytopic
Carabidae	Leistus ferrugineus	.	3	Open-mesic
Carabidae	Leistus fulvibarbis	.	1	Woodland
Carabidae	Leistus terminatus	.	4	Woodland
Carabidae	Licinus depressus	Nb	23	Woodland
Carabidae	Loricera pilicornis	.	3	Woodland
Carabidae	Masoreus wetterhallii	Na	28	Xeric
Carabidae	Microlestes maurus	.	26	Woodland
Carabidae	Nebria brevicollis	.	115	Eurytopic
Carabidae	Nebria salina	.	10	Xeric
Carabidae	Notiophilus aquaticus	.	5	Open-mesic
Carabidae	Notiophilus biguttatus	.	24	Woodland
Carabidae	Notiophilus germinyi	.	14	Open-mesic
Carabidae	Notiophilus palustris	.	16	Woodland
Carabidae	Olisthopus rotundatus	.	0	Xeric
Carabidae	Ophonus laticollis	BAP, Na	1	Xeric
Carabidae	Ophonus melletii	BAP, Na	4	Open-mesic
Carabidae	Ophonus rufibarbis	.	2	Open-mesic
Carabidae	Ophonus schaubergerianus	Nb	1	Woodland
Carabidae	Panagaeus bipustulatus	Nb	4	Xeric
Carabidae	Paradromius linearis	.	10	Xeric
Carabidae	Philorhizus melanocephalus	.	2	Xeric
Carabidae	Platyderus depressus	Nb	8	Dry grass-heath
Carabidae	Poecilus cupreus	.	145	Dry grass-heath
Carabidae	Poecilus versicolor	.	118	Open-mesic
Carabidae	Pterostichus cristatus	Nb	2	Woodland
Carabidae	Pterostichus madidus	.	852	Woodland

Carabidae	Pterostichus melanarius	.	20	Open-mesic
Carabidae	Pterostichus niger	.	60	Woodland
Carabidae	Pterostichus nigrita	.	2	Eurytopic
Carabidae	Pterostichus oblongopunctatus	Nb	1	Woodland
Carabidae	Pterostichus strenuus	.	9	Eurytopic
Carabidae	Stomis pumicatus	.	14	Woodland
Carabidae	Syntomus foveatus	.	427	Xeric
Carabidae	Syntomus truncatellus	.	216	Woodland
Carabidae	Synuchus vivalis	.	8	Eurytopic
Carabidae	Trechus quadristriatus	.	1	Eurytopic
Family	**Species**	**Status**	**Abundance**	**Habitat Association**
Ground spiders				
Anyphaenidae	Anyphaena accentuata	.	2	Woodland
Clubionidae	Cheiracanthium virescens	.	1	Xeric
Clubionidae	Clubiona comta	.	16	Woodland
Clubionidae	Clubiona diversa	.	45	Open Mesic
Clubionidae	Clubiona lutescens	.	1	Eurytopic
Clubionidae	Clubiona neglecta	.	7	Dry grass-heath
Clubionidae	Clubiona reclusa	.	30	Eurytopic
Clubionidae	Clubiona terrestris	.	5	Eurytopic
Dysderidae	Harpactea hombergi	.	1	Woodland
Gnaphosidae	Drassodes cupreus	.	306	Dry grass-heath
Gnaphosidae	Drassodes lapidosus	.	6	Dry grass-heath
Gnaphosidae	Drassodes pubescens	.	172	Open Mesic
Gnaphosidae	Drassyllus pusillus	.	350	Dry grass-heath
Gnaphosidae	Haplodrassus signifer	.	202	Dry grass-heath
Gnaphosidae	Micaria pulicaria	.	170	Eurytopic
Gnaphosidae	Micaria silesiaca	Nb	25	Dry grass-heath
Gnaphosidae	Micaria subopaca	Nb	1	Woodland
Gnaphosidae	Trachyzelotes pedestris	Nb	472	Dry grass-heath
Gnaphosidae	Zelotes electus	.	103	Xeric
Gnaphosidae	Zelotes latreillei	.	134	Dry grass-heath
Liocranidae	Agroeca cuprea	Na	1	Xeric
Liocranidae	Agroeca inopina	.	9	Woodland
Liocranidae	Phrurolithus festivus	.	846	Eurytopic
Liocranidae	Phrurolithus minimus	Na	2	Dry grass-heath
Lycosidae	Alopecosa barbipes	.	37	Dry grass-heath
Lycosidae	Alopecosa cuneata	.	105	Dry grass-heath
Lycosidae	Alopecosa pulverulenta	.	828	Open Mesic
Lycosidae	Arctosa perita	.	71	Xeric
Lycosidae	Pardosa agrestis	Nb	5	Open Mesic
Lycosidae	Pardosa amentata	.	26	Eurytopic
Lycosidae	Pardosa monticola	.	5780	Dry grass-heath
Lycosidae	Pardosa nigriceps	.	373	Eurytopic
Lycosidae	Pardosa palustris	.	463	Open Mesic

Lycosidae	Pardosa prativaga	.	59	Eurytopic
Lycosidae	Pardosa pullata	.	5618	Eurytopic
Lycosidae	Pardosa saltans	.	71	Woodland
Lycosidae	Pirata hygrophilus	.	662	Woodland
Lycosidae	Pirata latitans	.	3	Open Mesic
Lycosidae	Trochosa ruricola	.	5	Open Mesic
Lycosidae	Trochosa terricola	.	1149	Eurytopic
Lycosidae	Xerolycosa nemoralis	Nb	145	Dry grass-heath
Mimetidae	Ero cambridgei	.	1	Eurytopic
Mimetidae	Ero furcata	.	8	Eurytopic
Philodromidae	Philodromus dispar	.	2	Woodland
Philodromidae	Thanatus striatus	.	4	Open Mesic
Pisauridae	Pisaura mirabilis	.	48	Open Mesic
Salticidae	Aelurillus v-insignitus	Nb	12	Dry grass-heath
Salticidae	Euophrys frontalis	.	63	Open Mesic
Salticidae	Evarcha falcata	.	4	Woodland
Salticidae	Heliophanus flavipes	.	32	Eurytopic
Salticidae	Marpissa muscosa	Nb	2	Woodland
Salticidae	Neon reticulatus	.	4	Woodland
Salticidae	Sitticus saltator	Nb	12	Xeric
Salticidae	Talavera aequipes	.	11	Xeric
Tetragnathidae	Pachygnatha degeeri	.	1563	Eurytopic
Tetragnathidae	Pachygnatha listeri	.	1	Woodland
Theridiidae	Robertus lividus	.	95	Eurytopic
Theridiidae	Steatoda albomaculata	Nb	42	Xeric
Theridiidae	Steatoda phalerata	.	405	Xeric
Thomisidae	Ozyptila atomaria	.	38	Open Mesic
Thomisidae	Ozyptila practicola	.	2	Woodland
Thomisidae	Ozyptila scabricula	Nb	13	Xeric
Thomisidae	Ozyptila trux	.	39	Eurytopic
Thomisidae	Philodromus cespitum	.	1	Eurytopic
Thomisidae	Philodromus collinus	Nb	16	Woodland
Thomisidae	Philodromus longipalpis	.	1	Woodland
Thomisidae	Tibellus oblongus	.	12	Eurytopic
Thomisidae	Xysticus audax	.	2	Open Mesic
Thomisidae	Xysticus bifasciatus	.	1	Dry grass-heath
Thomisidae	Xysticus cristatus	.	374	Eurytopic
Thomisidae	Xysticus erraticus	.	139	Open Mesic
Thomisidae	Xysticus kochi	.	137	Open Mesic
Thomisidae	Xysticus ulmi	.	1	Woodland
Zoridae	Zora spinimana	.	240	Eurytopic

Family	**Species**	**Status**	**Abundance**	**Habitat Association**
Linyphiid spiders				
Linyphiidae	Agyneta cauta	.	4	Open Mesic
Linyphiidae	Agyneta conigera	.	25	Eurytopic

Linyphiidae	Agyneta decora	.	5	Eurytopic
Linyphiidae	Agyneta ramosa	.	1	Woodland
Linyphiidae	Agyneta subtilis	.	88	Woodland
Linyphiidae	Araeoncus humilis	.	1	Eurytopic
Linyphiidae	Bathyphantes gracilis	.	8	Eurytopic
Linyphiidae	Bathyphantes parvulus	.	190	Open Mesic
Linyphiidae	Centromerita concinna	.	2	Eurytopic
Linyphiidae	Centromerus dilutus	.	1	Eurytopic
Linyphiidae	Centromerus incilium	Nb	12	Xeric
Linyphiidae	Centromerus sylvaticus	.	2	Eurytopic
Linyphiidae	Ceratinella brevipes	.	13	Eurytopic
Linyphiidae	Ceratinella brevis	.	17	Eurytopic
Linyphiidae	Ceratinella scabrosa	.	9	Woodland
Linyphiidae	Ceratinopsis stativa	.	26	Open Mesic
Linyphiidae	Cnephalocotes obscurus	.	80	Eurytopic
Linyphiidae	Diplocephalus cristatus	.	1	Open Mesic
Linyphiidae	Diplostyla concolor	.	71	Eurytopic
Linyphiidae	Dismodicus bifrons	.	9	Open Mesic
Linyphiidae	Entelecara congenera	Nb	1	Woodland
Linyphiidae	Erigone atra	.	73	Eurytopic
Linyphiidae	Erigone dentipalpis	.	84	Eurytopic
Linyphiidae	Erigonella hiemalis	.	54	Eurytopic
Linyphiidae	Evansia merens	.	1	Open Mesic
Linyphiidae	Gonatium rubens	.	12	Eurytopic
Linyphiidae	Gongylidiellum vivum	.	11	Open Mesic
Linyphiidae	Lepthyphantes alacris	.	1	Woodland
Linyphiidae	Lepthyphantes flavipes	.	1	Woodland
Linyphiidae	Lepthyphantes insignis	Nb	2	Dry grass-heath
Linyphiidae	Lepthyphantes mengei	.	130	Woodland
Linyphiidae	Lepthyphantes pallidus	.	4	Eurytopic
Linyphiidae	Lepthyphantes tenuis	.	288	Eurytopic
Linyphiidae	Linyphia hortensis	.	3	Woodland
Linyphiidae	Linyphia triangularis	.	2	Eurytopic
Linyphiidae	Macrargus rufus	.	1	Woodland
Linyphiidae	Maro sublestus	Na	1	Woodland
Linyphiidae	Meioneta beata	.	281	Eurytopic
Linyphiidae	Meioneta rurestris	.	15	Open Mesic
Linyphiidae	Meioneta saxatilis	.	14	Eurytopic
Linyphiidae	Metopobactrus prominulus	.	12	Eurytopic
Linyphiidae	Micrargus herbigradus	.	84	Eurytopic
Linyphiidae	Micrargus subaequalis	.	1	Eurytopic
Linyphiidae	Microlinyphia pusilla	.	28	Eurytopic
Linyphiidae	Microneta viaria	.	4	Woodland
Linyphiidae	Minyriolus pusillus	.	9	Woodland
Linyphiidae	Monocephalus fuscipes	.	1	Woodland
Linyphiidae	Neriene clathrata	.	27	Eurytopic

Linyphiidae	Neriene montana	.	2	Woodland
Linyphiidae	Oedothorax retusus	.	0	Eurytopic
Linyphiidae	Ostearius melanopygius	.	5	Eurytopic
Linyphiidae	Pelecopsis parallela	.	26	Eurytopic
Linyphiidae	Peponocranium ludicrum	.	20	Open Mesic
Linyphiidae	Pocadicnemis juncea	.	144	Open Mesic
Linyphiidae	Porrhomma pallidum	.	0	Woodland
Linyphiidae	Saaristoa abnormis	.	17	Eurytopic
Linyphiidae	Saaristoa firma	.	7	Woodland
Linyphiidae	Stemonyphantes lineatus	.	6	Eurytopic
Linyphiidae	Syedra gracilis	Nb	2	Open Mesic
Linyphiidae	Tapinocyba praecox	.	1	Open Mesic
Linyphiidae	Tiso vagans	.	49	Eurytopic
Linyphiidae	Typhochrestus digitatus	.	5	Xeric
Linyphiidae	Walckenaeria acuminata	.	45	Eurytopic
Linyphiidae	Walckenaeria antica	.	34	Woodland
Linyphiidae	Walckenaeria atrotibialis	.	252	Eurytopic
Linyphiidae	Walckenaeria cucullata	.	4	Woodland
Linyphiidae	Walckenaeria dysderoides	.	117	Woodland
Linyphiidae	Walckenaeria monoceros	.	3	Dry grass-heath
Linyphiidae	Walckenaeria nudipalpis	.	3	Woodland
Linyphiidae	Walckenaeria obtusa	.	3	Woodland
Family	**Species**	**Status**	**Abundance**	**Habitat Association**
Ants				
Formicidae	Formica fusca	.	8207	Woodland
Formicidae	Formica lemani	.	1	Woodland
Formicidae	Lasius flavus	.	491	Open
Formicidae	Lasius fuliginosus	.	125	Woodland
Formicidae	Lasius meridionalis	.	57	Thermophilic
Formicidae	Lasius mixtus	.	1	Thermophilic
Formicidae	Lasius niger	.	16663	Thermophilic
Formicidae	Lasius platythorax	.	6	Woodland
Formicidae	Lasius psammophilus	.	1674	Thermophilic
Formicidae	Lasius umbratus	.	303	Woodland
Formicidae	Leptothorax acervorum	.	89	Woodland
Formicidae	Myrmica karavajevi	RDB3, RDBK	22	Open
Formicidae	Myrmica lobicornis	.	2	Thermophilic
Formicidae	Myrmica rubra	.	5	Open
Formicidae	Myrmica ruginodis	.	3527	Woodland
Formicidae	Myrmica sabuleti	.	1049	Thermophilic
Formicidae	Myrmica scabrinodis	.	9010	Open
Formicidae	Myrmica schencki	Nb	134	Thermophilic
Formicidae	Stenamma debile	.	4	Woodland
Formicidae	Tetramorium caespitum	.	161	Thermophilic
Family	**Species**	**Status**	**Frequency**	**Guild**

Vascular plants				
Aceraceae	Acer pseudoplatanus	.	3	Shade Tolerant
Apiaceae	Anthriscus caucalis	.	4	Shade Tolerant
Apiaceae	Chaerophyllum temulum	.	5	Shade Tolerant
Apiaceae	Conopodium majus	.	1	Open NL Ndist
Apiaceae	Daucus carota	.	151	Open NL Dist
Apiaceae	Heracleum sphondylium	.	23	Open Mesic Dist
Apiaceae	Pastinaca sativa	.	124	Open NL Dist
Apiaceae	Pimpinella saxifraga	.	7	Open NL Ndist
Apiaceae	Torilis japonica	.	37	Open Mesic Dist
Asteraceae	Achillea millefolium	.	954	Open NL Ndist
Asteraceae	Arctium minus	.	1	Open Mesic Dist
Asteraceae	Artemisia vulgaris	.	5	Open Mesic Dist
Asteraceae	Bellis perennis	.	16	Open NL Ndist
Asteraceae	Carduus nutans	.	12	Open NL Dist
Asteraceae	Carlina vulgaris	.	12	Open NL Dist
Asteraceae	Centaurea nigra	.	103	Open NL Ndist
Asteraceae	Centaurea scabiosa	.	112	Open NL Ndist
Asteraceae	Cirsium arvense	.	250	Open Mesic Dist
Asteraceae	Cirsium vulgare	.	79	Open Mesic Dist
Asteraceae	Conyza canadensis	.	95	Open NL Dist
Asteraceae	Crepis capillaris	.	639	Open NL Dist
Asteraceae	Crepis vesicaria	.	15	Open Mesic Dist
Asteraceae	Erigeron acer	.	1	Open NL Dist
Asteraceae	Filago minima	.	7	Open NL Dist
Asteraceae	Filago vulgaris	RDB-NT	3	Open NL Dist
Asteraceae	Gnaphalium sylvaticum	RDB-EN	3	Open NL Dist
Asteraceae	Gnaphalium uliginosum	.	1	Open Mesic Dist
Asteraceae	Hypochaeris glabra	RDB-VU	3	Open NL Dist
Asteraceae	Hypochaeris radicata	.	373	Open NL Ndist
Asteraceae	Lactuca virosa	.	1	Open Mesic Dist
Asteraceae	Leontodon autumnalis	.	82	Open NL Ndist
Asteraceae	Leontodon saxatilis	.	8	Open NL Ndist
Asteraceae	Leucanthemum vulgare	.	3	Open NL Ndist
Asteraceae	Picris echioides	.	18	Open Mesic Dist
Asteraceae	Pilosella officinarum	.	216	Open NL Ndist
Asteraceae	Senecio erucifolius	.	22	Open NL Dist
Asteraceae	Senecio jacobaea	.	159	Open NL Ndist
Asteraceae	Senecio sylvaticus	.	19	Open Mesic Dist
Asteraceae	Senecio viscosus	.	13	Open Mesic Dist
Asteraceae	Senecio vulgaris	.	71	Open Mesic Dist
Asteraceae	Sonchus arvensis	.	4	Open Mesic Ndist
Asteraceae	Sonchus asper	.	63	Open Mesic Dist
Asteraceae	Taraxacum officinale	.	77	Open Mesic Dist
Berberidaceae	Mahonia aquifolium	.	18	Shade Tolerant
Betulaceae	Betula pendula	.	4	Shade Tolerant

Boraginaceae	Anchusa arvensis	.	33	Open NL Dist
Boraginaceae	Echium vulgare	.	45	Open NL Dist
Boraginaceae	Myosotis arvensis	.	11	Open Mesic Dist
Boraginaceae	Myosotis discolor	.	1	Open NL Dist
Brassicaceae	Arabis hirsuta	.	41	Open NL Dist
Brassicaceae	Capsella bursa-pastoris	.	49	Open Mesic Dist
Brassicaceae	Cardamine hirsuta	.	6	Open Mesic Dist
Brassicaceae	Descurainia sophia	.	2	Open NL Dist
Brassicaceae	Sinapis arvensis	.	5	Open Mesic Dist
Brassicaceae	Sisymbrium officinale	.	11	Open Mesic Dist
Brassicaceae	Teesdalia nudicaulis	RDB-NT	1	Open NL Dist
Campanulaceae	Campanula rotundifolia	.	80	Open NL Ndist
Caprifoliaceae	Lonicera periclymenum	.	3	Shade Tolerant
Caryophyllaceae	Arenaria serpyllifolia	.	157	Open NL Dist
Caryophyllaceae	Cerastium arvense	.	15	Open NL Dist
Caryophyllaceae	Cerastium fontanum	.	193	Open NL Ndist
Caryophyllaceae	Cerastium glomeratum	.	33	Open NL Dist
Caryophyllaceae	Cerastium semidecandrum	.	8	Open NL Dist
Caryophyllaceae	Herniaria glabra	NR	1	Open NL Dist
Caryophyllaceae	Sagina apetala	.	2	Open NL Dist
Caryophyllaceae	Sagina procumbens	.	9	Open Mesic Dist
Caryophyllaceae	Scleranthus annuus	RDB-EN, BAP	3	Open NL Dist
Caryophyllaceae	Silene latifolia	.	54	Open NL Ndist
Caryophyllaceae	Silene vulgaris	.	24	Open NL Ndist
Caryophyllaceae	Spergula arvensis	RDB-VU	157	Open NL Dist
Caryophyllaceae	Spergularia rubra	.	28	Open NL Dist
Caryophyllaceae	Stellaria alsine	.	4	Open Mesic Ndist
Caryophyllaceae	Stellaria graminea	.	470	Open NL Ndist
Caryophyllaceae	Stellaria media	.	59	Open Mesic Dist
Celastraceae	Euonymus europaeus	.	1	Shade Tolerant
Chenopodiaceae	Chenopodium album	.	107	Open Mesic Dist
Clusiaceae	Hypericum humifusum	.	5	Open NL Ndist
Clusiaceae	Hypericum perforatum	.	194	Open NL Ndist
Convolvulaceae	Convolvulus arvensis	.	271	Open NL Dist
Crassulaceae	Sedum anglicum	.	20	Open NL Dist
Cyperaceae	Carex arenaria	.	314	Open NL Dist
Cyperaceae	Carex hirta	.	47	Open Mesic Ndist
Cyperaceae	Carex muricata	.	67	Open NL Dist
Cyperaceae	Carex pilulifera	.	8	Open NL Ndist
Dennstaedtiaceae	Pteridium aquilinum	.	659	Shade Tolerant
Dipsacaceae	Knautia arvensis	.	52	Open NL Ndist
Dipsacaceae	Scabiosa columbaria	.	80	Open NL Ndist
Dipsacaceae	Succisa pratensis	.	11	Open NL Ndist
Ericaceae	Calluna vulgaris	.	158	Open NL Ndist
Fabaceae	Anthyllis vulneraria	.	14	Open NL Ndist
Fabaceae	Cytisus scoparius	.	29	Open Mesic Ndist

Fabaceae	Hippocrepis comosa	.	24	Open NL Ndist
Fabaceae	Lathyrus pratensis	.	3	Open Mesic Ndist
Fabaceae	Lotus corniculatus	.	49	Open NL Ndist
Fabaceae	Lotus glaber	.	46	Open Mesic Ndist
Fabaceae	Medicago lupulina	.	407	Open NL Dist
Fabaceae	Medicago sativa subsp.falcata	.	7	Open NL Ndist
Fabaceae	Melilotus officinalis	.	6	Open NL Dist
Fabaceae	Ononis repens	.	90	Open NL Dist
Fabaceae	Ornithopus perpusillus	.	150	Open NL Dist
Fabaceae	Trifolium arvense	.	44	Open NL Dist
Fabaceae	Trifolium campestre	.	49	Open NL Dist
Fabaceae	Trifolium dubium	.	9	Open NL Dist
Fabaceae	Trifolium pratense	.	28	Open NL Dist
Fabaceae	Trifolium repens	.	211	Open Mesic Ndist
Fabaceae	Ulex europaeus	.	46	Open Mesic Ndist
Fabaceae	Vicia cracca	.	109	Open Mesic Dist
Fabaceae	Vicia hirsuta	.	88	Open Mesic Dist
Fabaceae	Vicia sativa	.	28	Open NL Dist
Fabaceae	Vicia sepium	.	8	Open Mesic Ndist
Fagaceae	Quercus robur	.	17	
Fumariaceae	Ceratocapnos claviculata	.	13	Shade Tolerant
Fumariaceae	Fumaria officinalis	.	22	Open Mesic Dist
Fumariaceae	Fumaria parviflora	RDB-VU, NS	1	Open NL Dist
Gentianaceae	Centaurium erythraea	.	12	Open NL Dist
Gentianaceae	Erodium cicutarium	.	32	Open NL Dist
Gentianaceae	Geranium dissectum	.	1	Open Mesic Dist
Gentianaceae	Geranium molle	.	166	Open NL Dist
Gentianaceae	Geranium robertianum	.	5	Shade Tolerant
Juncaceae	Juncus bufonius	.	11	Open Mesic Dist
Juncaceae	Juncus effusus	.	30	Open Mesic Ndist
Juncaceae	Luzula campestris	.	7	Open NL Ndist
Juncaceae	Luzula multiflora	.	85	Open NL Ndist
Lamiaceae	Clinopodium acinos	RDB-VU, BAP	105	Open NL Dist
Lamiaceae	Clinopodium ascendens	.	3	Open Mesic Dist
Lamiaceae	Clinopodium vulgare	.	3	Open NL Ndist
Lamiaceae	Galeopsis tetrahit	.	1	Open Mesic Dist
Lamiaceae	Glechoma hederacea	.	279	Shade Tolerant
Lamiaceae	Mentha arvensis	.	1	Open Mesic Ndist
Lamiaceae	Prunella vulgaris	.	94	Open NL Ndist
Lamiaceae	Stachys sylvatica	.	3	Open Mesic Ndist
Lamiaceae	Teucrium scordium	RDB-EN,BAP,NR	199	Open Mesic Ndist
Lamiaceae	Teucrium scorodonia	.	253	Open NL Dist
Lamiaceae	Thymus polytrichus	.	11	Open NL Dist
Linaceae	Linum catharticum	.	5	Open NL Dist
Malvaceae	Malva moschata	.	2	Open NL Dist

Oleaceae	Ligustrum vulgare	.	2	Shade Tolerant
Onagraceae	Chamerion angustifolium	.	3	Open Mesic Dist
Papaveraceae	Papaver dubium	.	11	Open NL Dist
Papaveraceae	Papaver rhoeas	.	4	Open Mesic Dist
Pinaceae	Pinus nigra	.	2	Shade Tolerant
Pinaceae	Pinus sylvestris	.	8	Shade Tolerant
Plantaginaceae	Plantago coronopus	.	5	Open NL Dist
Plantaginaceae	Plantago lanceolata	.	953	Open NL Ndist
Plantaginaceae	Plantago major	.	27	Open Mesic Ndist
Poaceae	Agrostis canina	.	1	Open Mesic Ndist
Poaceae	Agrostis capillaris	.	552	Open NL Ndist
Poaceae	Agrostis stolonifera	.	1005	Open Mesic Ndist
Poaceae	Aira praecox	.	18	Open NL Dist
Poaceae	Alopecurus pratensis	.	1	Open Mesic Ndist
Poaceae	Anthoxanthum odoratum	.	352	Open NL Ndist
Poaceae	Arrhenatherum elatius	.	675	Open Mesic Ndist
Poaceae	Brachypodium sylvaticum	.	1	Shade Tolerant
Poaceae	Bromus hordeaceus	.	47	Open NL Dist
Poaceae	Bromus sterilis	.	2	Open Mesic Dist
Poaceae	Calamagrostis epigejos	.	85	Open Mesic Ndist
Poaceae	Dactylis glomerata	.	515	Open Mesic Ndist
Poaceae	Deschampsia flexuosa	.	443	Open NL Ndist
Poaceae	Elytrigia repens	.	78	Open Mesic Dist
Poaceae	Festuca longifolia	NR	48	Open NL Ndist
Poaceae	Festuca ovina	.	306	Open NL Ndist
Poaceae	Festuca rubra	.	1053	Open NL Dist
Poaceae	Helictotrichon pratense	.	18	Open NL Ndist
Poaceae	Holcus lanatus	.	889	Open Mesic Ndist
Poaceae	Holcus mollis	.	585	Shade Tolerant
Poaceae	Koeleria macrantha	.	110	Open NL Ndist
Poaceae	Lolium perenne	.	80	Open Mesic Ndist
Poaceae	Phleum bertolonii	.	258	Open NL Ndist
Poaceae	Poa angustifolia	.	102	Open NL Dist
Poaceae	Poa annua	.	39	Open Mesic Dist
Poaceae	Poa humilis	.	16	Open NL Dist
Poaceae	Poa pratensis sens.str.	.	151	Open NL Ndist
Poaceae	Poa trivialis	.	1	Shade Tolerant
Poaceae	Trisetum flavescens	.	29	Open NL Ndist
Poaceae	Vulpia bromoides	.	9	Open NL Dist
Polygonaceae	Fallopia convolvulus	.	34	Open NL Dist
Polygonaceae	Persicaria maculosa	.	13	Open Mesic Dist
Polygonaceae	Polygonum aviculare	.	63	Open Mesic Dist
Polygonaceae	Rumex acetosa	.	108	Open NL Ndist
Polygonaceae	Rumex acetosella	.	706	Open NL Dist
Polygonaceae	Rumex conglomeratus	.	1	Open Mesic Ndist
Polygonaceae	Rumex crispus	.	6	Open Mesic Dist

Polygonaceae	Rumex obtusifolius	.	6	Open Mesic Dist
Primulaceae	Anagallis arvensis	.	9	Open NL Dist
Ranunculaceae	Ranunculus repens	.	66	Open Mesic Ndist
Ranunculaceae	Thalictrum minus	.	1	Open NL Dist
Resedaceae	Reseda lutea	.	532	Open NL Dist
Resedaceae	Reseda luteola	.	59	Open NL Dist
Rosaceae	Agrimonia eupatoria	.	22	Open Mesic Dist
Rosaceae	Aphanes arvensis	.	32	Open NL Dist
Rosaceae	Crataegus monogyna	.	7	Shade Tolerant
Rosaceae	Fragaria vesca	.	1	Open NL Ndist
Rosaceae	Potentilla argentea	RDB-NT	21	Open NL Ndist
Rosaceae	Potentilla erecta	.	5	Open NL Ndist
Rosaceae	Potentilla reptans	.	42	Open NL Ndist
Rosaceae	Potentilla sterilis	.	1	Open NL Ndist
Rosaceae	Rubus fruticosus agg.	.	147	Shade Tolerant
Rosaceae	Rubus idaeus	.	1	Shade Tolerant
Rosaceae	Sanguisorba minor	.	2	Open NL Ndist
Rubiaceae	Galium aparine	.	5	Open Mesic Dist
Rubiaceae	Galium saxatile	.	312	Open NL Ndist
Rubiaceae	Galium verum	.	898	Open NL Ndist
Scrophulariaceae	Chaenorhinum minus	.	18	Open NL Dist
Scrophulariaceae	Digitalis purpurea	.	15	Shade Tolerant
Scrophulariaceae	Euphrasia nemorosa	.	5	Open NL Dist
Scrophulariaceae	Euphrasia officinalis agg.	.	19	Open NL Dist
Scrophulariaceae	Linaria vulgaris	.	173	Open NL Dist
Scrophulariaceae	Odontites vernus	.	25	Open NL Dist
Scrophulariaceae	Verbascum nigrum	.	12	Open NL Dist
Scrophulariaceae	Verbascum thapsus	.	2	Open NL Dist
Scrophulariaceae	Veronica arvensis	.	20	Open NL Dist
Scrophulariaceae	Veronica chamaedrys	.	798	Open NL Ndist
Scrophulariaceae	Veronica officinalis	.	20	Open NL Ndist
Scrophulariaceae	Veronica persica	.	4	Open Mesic Dist
Scrophulariaceae	Veronica polita	.	1	Open NL Dist
Scrophulariaceae	Veronica serpyllifolia	.	14	Open NL Ndist
Solanaceae	Solanum nigrum	.	12	Open Mesic Dist
Urticaceae	Urtica dioica	.	205	Open Mesic Ndist
Urticaceae	Urtica urens	.	1	Open Mesic Dist
Violaceae	Viola arvensis	.	10	Open NL Dist
Violaceae	Viola riviniana	.	1	Open NL Dist
Violaceae	Viola tricolor	RDB-NT	1	Open NL Dist

Adult spiders were identified to species following Roberts (1987, 1996); juveniles and sub-adults were not identified due to the lack of developed reproductive structures. Identification of carabids followed Luff (2007) and ants followed Bolton and Collingwood (1975), Skinner and Allen (1996) and Blacker and Collingwood (2002).

Species were classified according to habitat descriptions for spiders in Harvey *et al.*, (2002) and Roberts (1996), and for carabids Luff (1998, 2007). For ants we consulted an expert entomologist to ascertain habitat descriptions. Information from Hill *et al.*, (2004) and Grime (2007) where used to categorise vascular plants. Species designations for vascular plants and ants were obtained from the UK Joint Nature Conservation

Sources

Council (JNCC 2011), lists of Nationally Notable species for spider were obtained from Harvey *et al.* (2002) and for designated carabid species Luff (1998) was consulted. UK Biodiversity Action Plan species were sourced from UK Biodiversity Group (1999).

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Appendix A3.3. Heathland and ruderal reference sites sampled for ground-active invertebrates, showing site designations (SSSI=Site of Special Scientific Interest, SAC=Special Area of Conservation, NNR=National Nature Reserve) and grid references (UK Ordnance Survey) of transect locations.

Site	Notes
Deadman's Graves SSSI, SAC TL 775744, TL 776743, TL 776742	All three transects were located in short sparse vegetation with large areas of exposed acidic sand on a heavily disturbed rabbit warren.
Eriswell Low Warren SSSI TL 739793, TL 740793, TL 739793	A sheep grazed site with a series of old plough cleaning lines, that are re-ploughed as needed to create disturbance for rare plants, most recently in 2003. Rabbit grazing and burrows along the lines have maintained exposed substrate. All three transects were placed along ridges of plough lines in broken short vegetation.
Icklingham Plains SSSI TL 759734, TL 759735, TL 758735	All three transects were positioned in lichen-dominated acidic grass heath affected by heavy rabbit activity, with short vegetation and exposed sand.
Maidscross Hill SSSI, SAC TL 729825, TL 730825, TL 726823	One transect was placed along the south facing slope of a former gravel-pit with sparse vegetation and exposed substrate, the remaining two were on short rabbit-grazed turf.
Wangford Warren SSSI, SAC TL 757840, TL 758841, TL 757842	Mechanically disturbed areas at the site are ploughed approximately annually to maintain open sand at the foot of a stabilised dune. One transect was positioned in ploughed unvegetated open sand, the remaining two in lichen-dominated grass heath.
Runway Field (adjacent to Wangford Warren) TL 757840, TL 757839, TL 756837	Reverted from arable after inundation by windblown sand, the site includes areas of heavy rabbit activity and one annually ploughed strip bordering Wangford Warren. One transect was positioned along the ploughed strip and the other two within areas of short rabbit-grazed turf.
Thetford Heath SSSI, SAC TL 854795, TL 849795, TL 846795	All three transects were placed in closely sheep and rabbit grazed calcareous grass-heath, with short and in places broken sward.
Weeting Heath NNR, SAC TL 757883, TL 758882, TL 757880	All transects were placed in short rabbit-grazed swards with patches of exposed substrate; two in an area of deep acidic sand disturbed by rabbit warrens and the third along the fence line of an enclosed rabbit grazed area of lichen-dominated calcareous grass heath.

Appendix A3.4. Results of Generalised Linear Models (χ^2, F and p-value) comparing abundance and species richness of specialist (Spec) and generalist shade-tolerant (Gen) species among the treatment plots and heathland reference sites. Tukey pairwise comparisons were used to define homogenous sub-sets (a-c ranked highest to lowest); means that share a superscript do not differ significantly (P > 0.05).

Abundance	**Variable**	**Year**	**Covariate**	**C**	**S**	**H**	**D**	**FP**	**AP**	**TS**	**Test**	**Statistic**	**P-value**
Carabids	Spec ^{3}	1	soil	b	ab	ab	a	a	a	ab	χ^2	20.93	0.002
	Spec ^{3}	2	soil	c	bc	bc	ab	ab	a	a	χ^2	50.11	<0.001
	Gen ^{2}	1	block	a	a	a	a	a	a	a	F	4.12	0.002
	Gen ^{2}	2		a	a	a	a	a	a	a	F	1.66	0.150
Spiders	Spec ^{2}	1	block	b	b	a	b	b	b	b	F	8.01	<0.001
	Spec ^{2}	2	block	a	a	a	a	a	a	a	F	1.85	0.109
	Gen ^{2}	1	soil	a	a	a	b	bc	bc	c	F	23.91	<0.001
	Gen ^{2}	2		a	a	ab	a	ab	a	b	F	4.27	0.001
Ants	Spec ^{2}	1		a	a	a	a	a	a	a	F	0.49	0.816
	Spec ^{2}	2		a	a	a	a	a	a	a	F	0.79	0.578
	Gen ^{3}	1	block	b	b	ab	ab	a	b	a	χ^2	42.30	<0.001
	Gen ^{3}	2		a	a	a	a	a	a	a	χ^2	7.71	0.260
Plants	Spec ^{2}	1	soil	b	ab	ab	a	a	a	a	F	8.48	<0.001
	Spec ^{3}	2	soil, block	b	b	ab	ab	ab	a	a	χ^2	43.28	<0.001
	Gen ^{2}	1	soil, block	b	a	ab	a	a	a	ab	F	6.90	<0.001
	Gen ^{3}	2	soil, block	b	a	ab	a	a	ab	ab	χ^2	23.18	0.001
Richness	**Variable**	**Year**	**Covariate**	**C**	**S**	**H**	**D**	**FP**	**AP**	**TS**	**Test**	**Statistic**	**P-value**
Carabids	Spec ^{2}	1		a	a	a	a	a	a	a	F	1.02	0.423
	Spec ^{2}	2		bc	c	bc	abc	abc	ab	a	F	4.84	<0.001
	Gen ^{2}	1		a	a	a	ab	a	b	ab	F	4.11	0.002
	Gen ^{2}	2		ab	ab	ab	ab	a	ab	b	F	2.57	0.029
Spiders	Spec ^{2}	1		ab	ab	a	ab	b	ab	b	F	4.08	0.002
	Spec ^{2}	2	block	a	a	a	a	a	a	a	F	0.94	0.473
	Gen ^{2}	1		c	c	bc	abc	abc	ab	a	F	6.48	<0.001
	Gen ^{2}	2		a	a	a	a	a	a	a	F	1.12	0.361
Ants	Spec ^{1}	1	block	a	a	a	a	a	a	a	F	1.24	0.302
	Spec ^{1}	2	block	a	a	a	a	a	a	a	F	1.16	0.340
	Gen ^{1}	1		a	a	a	a	a	a	a	F	1.59	0.167
	Gen ^{1}	2	block	a	a	a	a	a	a	a	F	0.92	0.490
Plants	Spec ^{2}	1	soil	b	ab	ab	a	ab	ab	ab	F	4.78	0.001
	Spec ^{2}	2	soil, block	c	c	bc	abc	bc	b	ab	F	6.32	<0.001
	Gen ^{2}	1	soil	b	ab	ab	a	ab	ab	b	F	4.71	0.001
	Gen ^{2}	2	soil, block	a	a	a	a	a	a	a	F	4.66	0.001

Variable superscript indicates which model type used; 1 = linear normal, 2 = square root linear, 3 = negative binomial. Categorical soil or forest block covariates included if significant (P < 0.05)

Chapter 4

Multi-taxa trait responses to physical disturbance

Abstract

We examined whether trait responses to physical disturbance were consistent among two arthropod groups (carabids, spiders) and vascular plants, considering physiological attributes, life history and morphological or behavioural correlates of dispersal ability. Understanding biodiversity responses to environmental stressors has been enhanced by improved trait analysis techniques. But functional understanding of terrestrial arthropod assemblages has been limited compared to that of plants and freshwater invertebrates. We predicted greater intensity of disturbance would favour arthropods with small body size and greater dispersal ability and plants with short stature, therophyte life history and wind-dispersed seed. We sampled 14 738 arthropods and 10 624 plants, comprising 361 species, across a well-replicated experimental gradient of disturbance intensity. Associations among physiological traits, habitat association and rarity were examined by Principal Coordinates Analysis and traits were related to disturbance intensity by the fourth-corner statistic.

Ecological interpretations of responses were consistent, but how these related to individual physiological traits varied among taxa. Assemblages forming after disturbance comprised smaller carabids and plants, but larger spiders. Responses of traits relating to dispersal were complex. Frequency of winged carabids increased. Frequency of animal-dispersed plants decreased, but there was greater representation of small-seeded plant species in assemblages after disturbance. For spiders, individuals with the ability to disperse aerially were not more frequent; however, large body size (also associated with an active hunting strategy) may allow terrestrial dispersal. Individuals associated with dry-open habitats increased in arthropod and plant assemblages after disturbance; in this landscape resulting in greater abundance of threatened carabids and plants. For carabids, abundance of herbivorous species increased with disturbance intensity, reflecting greater representation of plants with a therophyte life history.

Trait shifts for carabid and plant assemblages were broadly as predicted and consistent with those observed previously in other disturbance regimes, building generality for these taxa. However, spiders did not follow expected responses in terms of traits, although functional responses were consistent. When using trait-based approaches to characterise functional responses, we advise against extrapolating responses across taxonomic groups with differing life forms and histories.

4.1 Introduction

There is an urgent need to increase our understanding of how biodiversity will respond to environmental change and perturbation (Millennium Ecosystem Assessment 2005). Describing responses in terms of richness or diversity does not improve understanding of ecological function. Understanding responses of species composition to perturbation is valuable but context-specific, so that generality is not achieved; rather we require greater understanding of how functional attributes and traits of species assemblages respond to environmental stressors (Gray et al. 2007; McGill et al. 2006).

Classifying species according to their functional traits and assessing how traits respond to environmental stressors allows such predictive generality (Moretti and Legg 2009). This approach has already been used in studies examining plant functional trait responses to environmental disturbances such as inundation (Kyle and Leishman 2009), fire (Keith et al. 2007; Pausas et al. 2004), grazing (Adler et al. 2004; McIntyre and Lavorel 2001) and potential response to climate change (Diaz and Cabido 1997). However, fewer studies have examined animal traits and of these most have considered freshwater invertebrates for which well-characterised life history traits have been related to water quality and river dynamics (Doledec and Statzner 2010; Feio and Doledec 2012; Ilg and Castella 2006; Poff 1997). Functional trait responses of terrestrial invertebrates are less understood; furthermore, most trait-based analyses conducted to date have focused on single taxa and often single trophic levels (Langlands et al. 2011; Ribera et al. 2001). What is lacking is an understanding of trait response to environmental stressors integrated across diverse taxonomic groups and trophic levels, supporting assessments of changing ecosystem functions and species disappearances (Gray et al. 2007).

To have predictive generality, life history traits used for analysis need to represent meaningful ecological or demographic functions or properties, for example, size, dispersal ability, trophic guild, and geographical distribution (Henle et al. 2004). For example, large body size is one of the most commonly cited traits promoting extinction (McKinney 1997), at least in part related to larger area-requirements and associated lower density, and slower reproductive rate. The representation of species with small body size has been shown to increase in disturbed environments (Ribera et al. 2001). Although larger species of invertebrates may be more susceptible to direct mortality by disturbance, body size is also correlated with other functional traits such as fecundity and mobility (Kotze and O'Hara 2003; Williams et al. 2010). Species' size is often related to disturbance in relation to the r-*K* continuum, postulating that r-selected species (small sized, short generation time) are better able to contend with highly disturbed habitats, whereas K-selected species (larger size, slow growing) are better suited to more stable habitats (Chiu and Kuo 2012; Statzner and Beche 2010). In ephemeral or deteriorating landscapes, greater dispersal ability should be favoured to increase colonisation of new resources (Heino and Hanski 2001). Dispersal is seen as one of the most important traits for assemblage recovery after disturbance in both arthropods (Malmstrom 2012; Mullen et al. 2008) and plants (Kyle and Leishman 2009; Moretti and Legg 2009). The ability to disperse aerially has been used frequently to differentiate between good and bad dispersal ability for arthropods and plants. Roff (1990) suggested that flight ability in insects is largely determined by habitat stability, with unstable and early successional habitats favouring the presence of aerial dispersing species.

We created an experimental gradient of physical disturbance intensity in an open-habitat network and contrasted the trait responses of two arthropod groups and vascular plants. Disturbance causes the removal of biomass and organisms, profoundly influencing the ecological functions and species composition of non-equilibrium ecosystems (Shea et al. 2004; Sousa 1984). By altering vegetation structure, disturbance influences both microclimate and moisture which are key characteristics affecting the composition of invertebrate assemblages (Entling et al.

2007; Perner and Malt 2003; Schirmel and Buchholz 2011). We examined trait responses of carabids, spiders and vascular plants using the fourth-corner statistic (Dray and Legendre 2008).

Both carabids (ground beetles) and spiders are species-rich groups, many have specific habitat requirements and assemblages respond quickly to changes in the environment. The carabid family is well studied; life histories are well known for northern hemisphere species and have been used to examine disturbance and landscape change (Desender et al. 2010; Ribera et al. 2001). Spiders are often used in community analyses due to their abundance, species diversity and ability to colonise most habitats (Buchholz 2010; Perner and Malt 2003; Wise 1993). However, their previous use in trait based analysis has been limited compared to carabids (though see Langlands et al. 2011 and Lambeets et al. 2008). Reasons for the deficiency of spider research in the trait literature may be due to the lack of species-specific information. However, in contrast to many other regions in the world, considerable biological and autoecological information exists for the European spider fauna. Vascular plants provide an excellent comparative group as species-specific traits are well known (Cornelissen et al. 2003) and trait-disturbance responses have been generalised.

Habitat manipulations covered a range of disturbance intensities to enable us to address the following questions: 1) does disturbance cause trait shifts? 2) Are general trait responses similar across contrasting taxonomic groups, such as effects on size, mobility, phenology, rarity and range extent? 3) Do trait shifts in response to physical disturbance concur with responses to other disturbance types such as fire, flooding and management intensification? We predict that arthropod species responding poorly to high intensities of disturbance are those with large bodies, late breeding seasons and poorer powers of dispersal, while plant species with slow maturation, tall growth types, short-lived seed banks and lacking mechanisms of seed dispersal would also respond poorly to disturbance.

4.2 Methodology

4.2.1 Study design

Our study was conducted within Thetford Forest, a conifer-dominated plantation established in the early 20th century, occupying 185 km^2 of Breckland, eastern England (0°40'E, 52°27'N). This region is characterised by a semi-continental climate, sandy, soils and historically supported characteristic species associated with heathland and ruderal land-uses (Dolman and Sutherland 1992). Forest management consists of clear-felling (typically at 60-80 years) and replanting of even-aged coupes (mean 9.0 ha ± 8.6 SD) subdivided by a network of forestry trackways; these support diverse carabid and spider assemblages comprising both open-habitat and forest species (Bertoncelj and Dolman in press; Pedley et al. 2013a; Pedley et al. 2013b).

Six mechanical disturbance treatments, representing a gradient of intensity, plus a set of non-intervention controls, were each replicated nine times within the trackway system in February 2009. Each treatment replicate comprised a single plot 150 m long and with a mean width of 4 m, allocated randomly to one of 63 trackways that were: at least 9 m wide (mean 13.5 m ± 3.7 SD, range 9-24 m) and located within coupes aged 10-25 years to avoid confounding effects of shade and insolation (Fig. 4.1). Treatments were located at least 100 m from plantation edges, recently felled coupes or other open habitats. Treatments, ranked by severity, comprised: 1) sward cutting; 2) cutting with removal (clippings removed from plots); vegetation and soil disruption by 3) disc harrowing, or 4) forest ploughing; 5) vegetation destruction and soil disturbance by agricultural ploughing; and 6) removal of both above- and below-ground plant material, litter and organic soil horizons by turf stripping. For further treatment details see Pedley et al. (2013b).

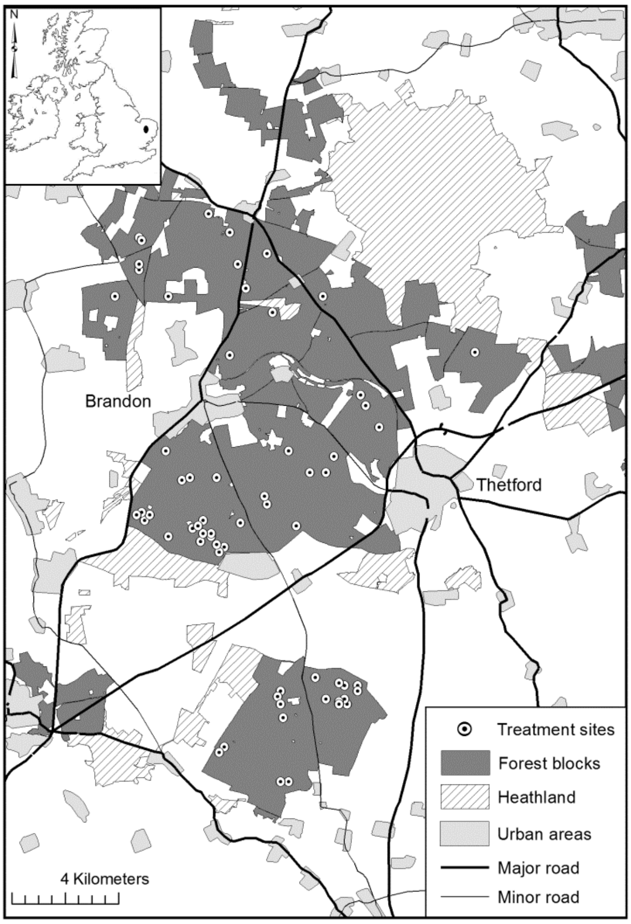

Fig. 4.1. The distribution of treatment plots within Thetford Forest.

4.2.2 Sampling protocol

In each plot, frequency of each vascular plant species was recorded from 20 1 m x 1 m quadrats placed regularly along the main axis of the plot during May to August 2010. Spiders and carabids were sampled in each treatment plot with pitfall traps set in May, June and late July/early August 2010, 15 to 17 months after the application of disturbance treatments. Traps were set in a single transect along the centre of each treatment plot, 37.5 m in from each end, with six individual traps (each 7.5 cm deep, 6.5 cm in diameter, filled with 50 ml of 70% ethylene glycol) set 15 m apart and opened for seven consecutive days in each period. Traps in each transect were combined to give one composite sample per treatment plot. Pitfall trap catches, as with any tapping method, have inherent biases and can be influenced by factors including habitat structure, weather conditions, preserving fluid and animal activity (Topping and Sunderland 1992). However, Luff and Eyre (1988) suggests that pitfall trapping is successful for creating pitfall catch indexes to interpret ecological differences between areas as long as it is remembered that the classification is not based on population density but on the actual catch. In our study, standardized pitfall trapping is an appropriate collection method as we aimed to compare biological patterns of the trappable invertebrate community as affected by disturbance and not complete inventories.

Adult spiders were identified to species following Roberts (1987, 1996); juvenile and sub-adult specimens were not identified due to the lack of developed reproductive structures. Carabid identification followed Luff (2007), plant taxonomy followed Stace (2005).

4.2.3 Species traits

For carabids, spiders and vascular plants, we selected life history traits that were considered likely to respond to disturbance, and for which species-specific information was available from published literature. It was not possible to quantify identical sets of traits for each of the contrasting taxonomic groups; rather we aimed to quantify consistent traits for physiological (e.g. body size, life form, diet) and ecological (habitat association, UK range extent and rarity) attributes (Table 4.1).

Table 4.1. Traits considered for carabids, spiders and vascular plants. Further details of each trait and source references are provided in Appendix A4.1. Data type given in brackets (Cont = continuous; Ord = ordinal, number of classes; Nom = nominal, number of classes)

Trait Type	**Carabid trait**	**Code**	**Spider trait**	**Code**	**Plant trait**	**Code**
Physiological	Body size	Size [Cont]	Body size	Size [Cont]	Height	Hght [Cont]
	Activity length	Act.Lgth [Ord, 3]	Activity length	Act.Lgth [Ord, 3]	Primary life form	LifeForm [Ord, 5]
	Activity period	Act.Peri [Ord, 3]	Moisture preference	Aridity [Cont]	Life history	LifeType [Ord, 3]
	Breeding season	Spring [Nom, 2]	Shade preference	Shade [Cont]	Woodiness	Woody [Non, 2]
	Carnivorous	Carn [Nom, 2]	Ballooning	Balloon [Nom, 2]	Light	Light [Ord, 6]
	Herbivorous	Herbi [Nom, 2]	Active hunter	Active [Nom, 2]	Moisture	Moist [Ord, 7]
	Omnivores	Omni [Nom, 2]	Running hunter	Run [Nom, 2]	Animal dispersed	Dsp.Animal [Non, 2]
	Brachypterous	Brachy [Nom, 2]	Ambush hunter	Ambush [Nom, 2]	Wind dispersed	Dsp.Wind [Non, 2]
	Wing-dimorphic	Dimorp [Nom, 2]	Stallking hunter	Stalk [Nom, 2]	Dispersule weight	Dsp.Wght [Ord, 7]
	Macropterous	Macro [Nom, 2]			Lateral spread	Lat.Spread [Ord, 4]
					Seed bank	Seed.Bank [Ord, 4]
Ecological	Habitat requirement	Hab.Req [Ord, 3]	Niche Breadth	Niche [Ord, 3]	Distribution	UK10km [Cont]
	Species distribution	Distrib [Ord, 3]	Habitat requirement	Hab.Req [Ord, 3]	Designation	Threat [Non, 2]
	Designated species	Threat [Nom, 2]	Distribution	UK10km [Cont]		
			Designation	Threat [Nom, 2]		

4.2.4 Environmental parameters

Disturbance intensity was quantified in terms of two vegetation structure variables, hereafter referred to as ‘disturbance parameters’: vegetation height, measured using a sward stick (diameter 90 mm, weight 250 g, following Dolman and Sutherland (1992)), and percentage of bare substrate, visually estimated within 20 cm x 20 cm, both measured at 40 points distributed along the centre of each treatment plot.

4.2.5 Analysis

The effect of disturbance on life history traits was examined separately for each taxonomic group, using fourth-corner analysis (Dray and Legendre 2008), that tests the link between species traits (matrix Q) and environmental parameters (matrix R) via species occurrence across sites (matrix L). The procedure tests whether the observed degree of linkage among traits and environmental attributes differs significantly from that expected by chance, given the observed structure of species abundances and environment measures across sites, using randomisation and permutation. The fourth-corner approach has recently been used in conjunction with emergent group techniques (Aubin et al. 2009) and RLQ analysis (Brind'Amour et al. 2011). By directly testing individual traits with environmental factors, fourth-corner analysis provided a mechanistic understanding of traits along an environmental gradient in contrast to emergent group analysis that purely described species clustering based on shared traits (Aubin et al. 2009). Likewise, RLQ provided descriptive grouping of species, traits and environmental variables after significant trait-environment relationships where first identified using fourth corner procedures (Brind'Amour et al. 2011). In both studies fourth-corner provided a robust tool for direct examination of traits and environmental factors.

To assess the strength of observed trait-environment linkage against a null model, we randomised the presence-absence of individual species relative to disturbance parameters (sward height and extent of bare ground), permuting within columns of matrix L (model 1). It was not necessary to also re-sample the species-trait relationship (matrix Q) or the environment-site relationship (matrix R), due to *a priori* environmental treatments and classification of traits from literature rather than empirical sampling (Dray and Legendre 2008). Analyses were conducted with 9999 permutations in the statistical software R (R Development Core Team 2012) using the ade4 package (Dray and Dufour 2007). Prior to analysis of spider abundance data a Hellinger transformation was applied to compensate for reduced total abundance along the disturbance gradient, following Aubin et al. (2009). Fourth-corner probability values were subjected to Holm’s correction to compensate for multiple testing (Holm 1979) following Aubin et al. (2009) and Pekin et al. (2011); results remaining significant were plotted against ranked severity of disturbance treatment.

Assemblage composition of each of the three taxa was geographically structured across the study region. For all taxa, the first axis of a non-metric multidimensional scaling (NMDS) ordination (performed on the species abundance-site matrix) was significantly related to latitude and longitude (Mantel tests (Legendre and Legendre 1998): $P < 0.001$ for invertebrates and $P < 0.01$ for plants); for carabids the second NMDS axis was also spatially auto-correlated ($P = 0.024$). This is unsurprising and may relate to geographic gradients of soil (with greater representation of rendzinas in the south and west, and of podzols in the central part of the study area), climate (Dolman et al. 2010) or land-use history (Eycott et al. 2006). Importantly, treatments were randomly imposed onto this geographic pattern (Analysis of variance: latitude $F_{6, 56}=1.014$, $P=0.426$; longitude $F_{6, 56}=1.396$, $P=0.232$) allowing trait responses to disturbance to be examined without confounding geographic effects.

Covariance among traits was examined for each taxonomic group using Principal Coordinates Analysis (PCoA) of the trait dissimilarity matrix (treating traits as variables and species as samples), calculated using the Gower coefficient (Gower 1971) with continuous traits standardised to zero mean and unit variance. Associations were visualised by plotting trait vectors, based on the Spearman rank correlation relative to the first two PCoA axes, following Langlands et al. (2011). For each taxa, to examine the influence of phylogeny in trait space species were grouped according to the six most dominant families (plants and spiders) or tribes (carabids). PCoA was conducted in the vegan package (Oksanen et al. 2010) in R.

4.3 Results

Traits were collated for 72 carabid, 125 spider and 164 vascular plant species, from a recorded pool of 73 carabid, 138 spider and 181 plant species. The 361 species for which we obtained trait data were represented by 3356 carabids, 11 382 spiders and 10 624 plant observations.

4.3.1 Carabids

Eight of the 13 carabid traits had significant links to at least one disturbance parameter when examined by fourth-corner analysis (Table 4.2). Mean body size decreased and the abundance of herbivores was greater, with greater disturbance intensity (Fig. 4.2a, b). Macropterous (winged) species were more abundant with greater disturbance intensity while the abundance of brachypterous (with vestigial wings) species in the most intense treatment was reduced compared to controls (Fig. 4.2c). The abundance of carabids associated with dry-open habitat increased with disturbance and generalist-shade tolerant individuals decreased (Fig. 4.2d). Threatened carabids were more abundant with disturbance, particularly at the most intense disturbance treatment (Fig. 4.2e).

The first two axes of the PCoA for carabids represented 52.3% of the variation in traits among species (Fig. 4.3a). Highest scores along axis one related to dry-open habitat association and macroptery, whereas lower scores were associated with larger body size, carnivory, brachyptery and generalist-shade tolerance (Fig. 4.3a, Appendix A4.2). For axis two, high values were associated with traits representing temporal aspects of life history such as the period of adult activity and spring breeding, and with large UK range extent. Low values for axis two relate to later activity period, autumn breeding and larger body size.

Although most traits were well separated, correlation between several traits is evident. Most species associated with dry-open habitat were also macropterous. In contrast, species associated with open-mesic habitat were likely to be carnivorous, widely distributed and wing-dimorphic, while generalist-shade tolerant species tended to be brachypterous omnivores.

Clustering of the main tribes in the PCoA showed phylogenetic influences on traits (Fig. 4.3a). The Zabrini and Harpalini were clustered to the right of the ordination and associated with herbivory, macroptery and narrow- and medium-niche breadth. Carabini and Pterostichini were to the left of the ordination and associated with carnivory, brachyptery, wide distribution and large body size. Bembidiini and Lebiini were higher on axis two and associated with wide niche breadth, wing dimorphism, spring breeding and small body size.

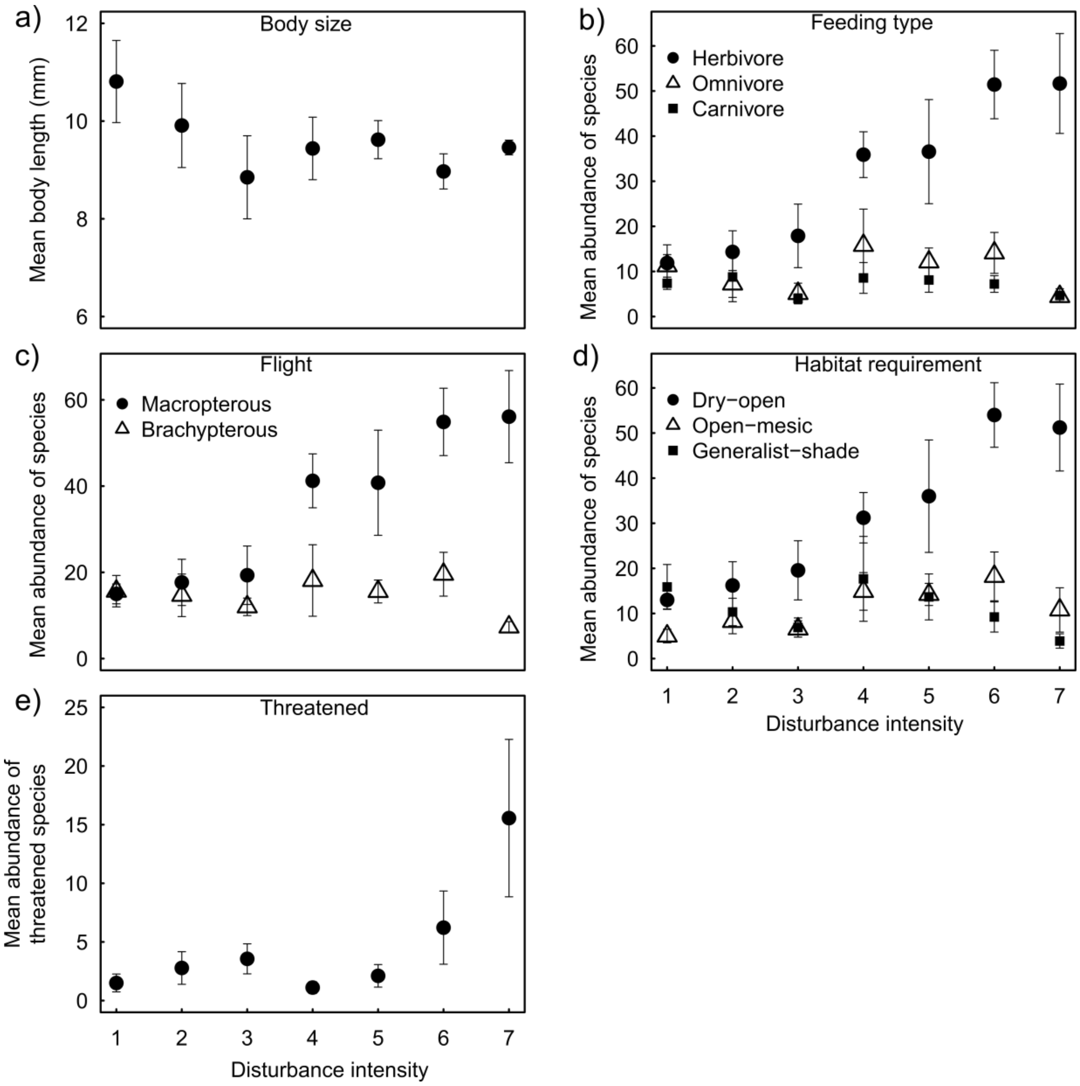

Fig. 4.2. Mean abundance ± SE of significant fourth-corner carabid traits against disturbance intensity: 1 = control, 2 = cutting, 3 = cutting and removal, 4 = disc harrow, 5 = forest plough, 6 = agricultural plough, 7= turf strip.

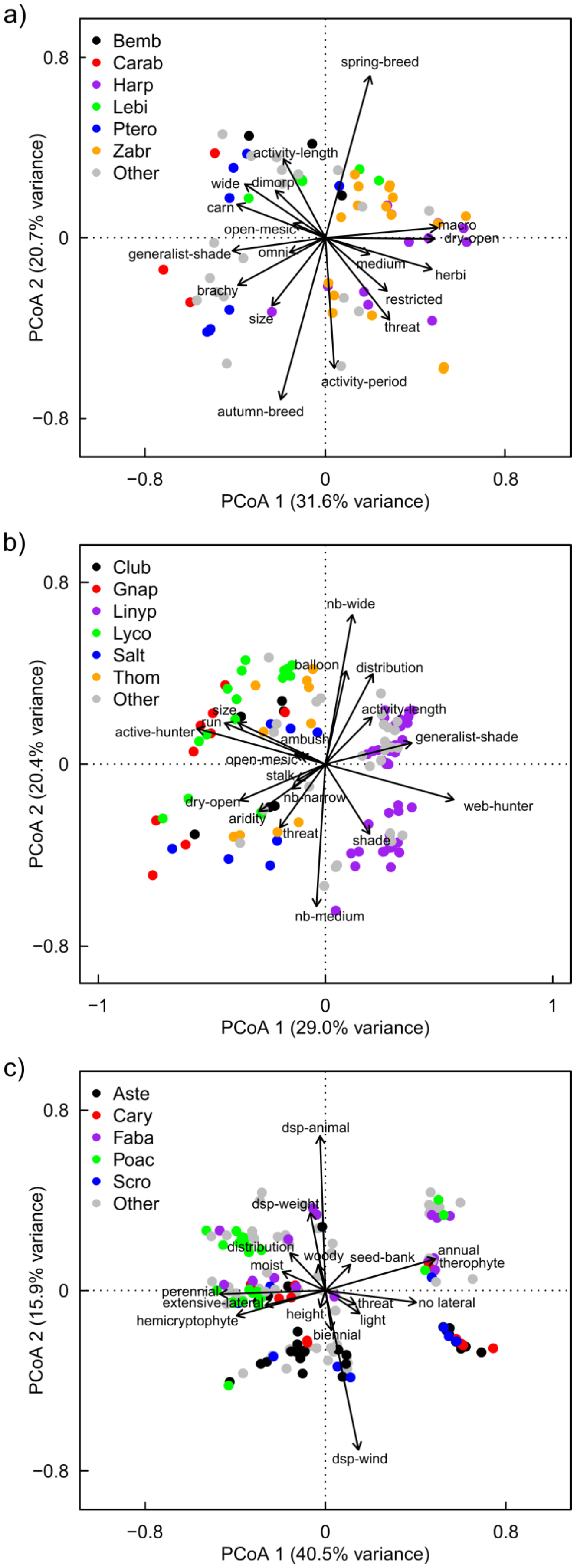

Fig. 4.3. Principal coordinate analysis (PCoA) of the similarity based on a) 18 traits of 72 carabids species, b) 18 traits of 125 spider species, c) 17 traits of 164 vascular plants species. For trait descriptions see Table 4.1. For clarity the vascular plant ordination only uses dominant ordinal groups for life-history (‘hemicryptophyte’ and ‘therophyte’), and lateral spread (‘no vegetative spread’ and ‘extensive lateral spread’). Trait vectors represent the Spearman correlation, with the length and direction indicating the relationship with PCoA axes. For each taxon, dominant families (tribes for Carabidae) are display by colour with the remaining species pooled and display in grey. Carabid tribes, Bemb = Bembidiini, Carab = Carabini, Harp = Harpalini, Lebi = Lebiini, Ptero = Pterostichini, Zabr = Zabrini. Spider families, Club = Clubionidae, Gnap = Gnaphosidae, Liny = Linyphiidae, Lyco = Lycosidae, Salt = Salticidae, Thom = Thomisidae. Vascular plant families, Aste = Asteraceae, Cary = Caryophyllaceae, Faba = Fabaceae, Poac = Poaceae, Scro = Scrophulariaceae.

Table 4.2. Results of fourth-corner analyses performed on plant, carabid and spider assemblages, with disturbance parameters (sward height and extent of bare ground) related to species traits (see Table 4.1 for trait descriptions) with permutation model 1 using 9999 permutations. Significant relationships ($p<0.05$, after Holm's correction) are indicated with a plus (+) for positive or minus (-) for negative relationship. Unfilled cells indicate a non-significant relationship.

Trait Type	**Carabids**	**Sward height**	**Bare ground**	**Spiders**	**Sward height**	**Bare ground**	**Plants**	**Sward height**	**Bare ground**
Physiological	Size	+		Size	-	+	Height	+	-
	Act.Lgth			Act.Lgth			LifeForm	-	+
	Act.Peri			Aridity	-		LifeType	-	+
	Spring			Shade	+		Woody		
	Carn	+	-	Balloon			Light	-	+
	Herbi	-	+	Active	-	+	Moist	+	-
	Omni	+	-	Run	-		Disp.Animal	+	
	Brachy	+	-	Ambush			Disp.Wind		
	Dimorp			Stalk			Disp.Wght	+	
	Macro	-	+				Lat.Spread		-
							Seed.Bank		
Ecological	Hab. Req	+	-	Niche			UK10km	+	-
	Distrib			Hab.Req	+		Threat	-	+
	Threat	-	+	UK10km	+				
				Threat					

4.3.2 Spiders

Seven spider traits from the thirteen tested were significantly related to at least one disturbance parameter (Table 4.2), although correlations were weaker than for carabids. In contrast to trait responses of carabids, mean body size increased with greater disturbance intensity (Fig. 4.4a). The mean aridity value increased with disturbance (Fig. 4.4b), and shade values decreased, although the response was variable (Fig. 4.4c). The abundance of active-hunting spiders increased and web-hunting species decreased with greater disturbance (Fig. 4.4d). Of the active-hunting spiders, running hunters increased in abundance more than ambush and stalking species (Fig. 4.4e). Generalist-shade and open-mesic species decreased in abundance with greater disturbance and dry-open habitat species increased (Fig. 4.4f). Although variable, the mean UK range extent for spiders was smaller with greater disturbance (Fig. 4.4g).

For spiders, the first two PCoA axes represented 49.4% of the variation in species' life history traits (Fig. 4.3b). Greater scores on axis one were associated with a web-hunting strategy, larger UK range and generalist-shade tolerance, while large body size, active-hunting strategy and running hunters were negatively associated with this axis and strongly intercorrelated (Fig. 4.3b, Appendix A4.2). On the second axis positive values represented a larger UK range, wider habitat niche and ballooning habit and were also intercorrelated, while negative scores were associated with medium habitat niche, web-hunting strategy and species with a UK rarity designation. Dry-open habitat associated species tended to also have the highest aridity scores, narrowest habitat niche and were more likely to be rare in the UK.

Traits were again related to phylogeny, with strong clustering of families in the PCoA ordination (Fig. 4.3b). The Linyphiidae were associated with a generalist-shade tolerance, web hunting strategy and small body size, while the Lycosidae, Gnaphosidae, Thomisidae and Clubioidae were loosely clustered to the left of the ordination and associated with active hunting strategies and large body size. These groups were separated along the second PCoA axis, with those lower on this axis being narrow niche species of dry-open habitats and more likely to be rare in the UK, in contrast to species associated with wider niche breadth and open-mesic habitat that were located higher on this axis.

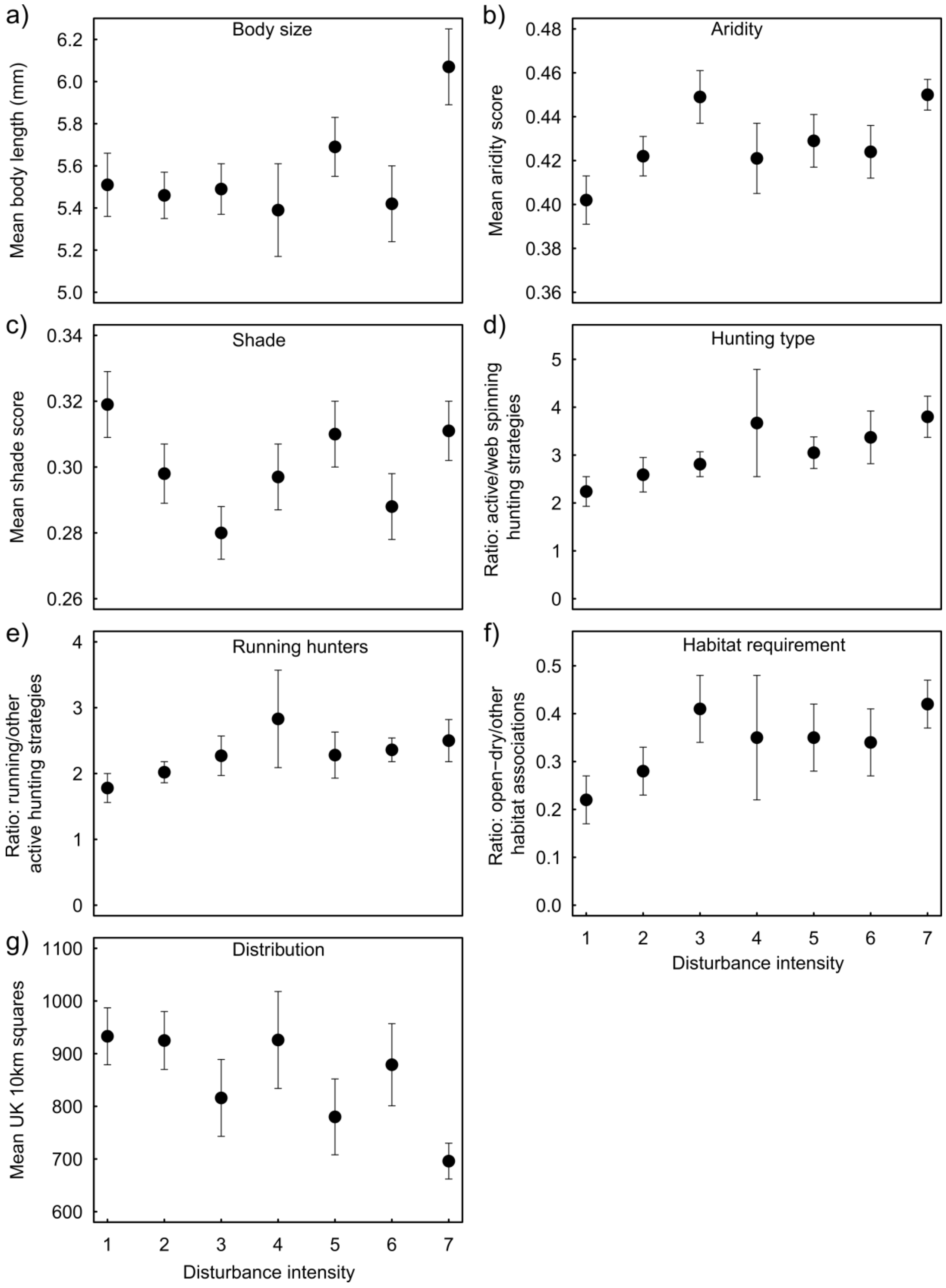

Fig. 4.4. Mean abundance ± SE of significant fourth-corner spider traits against disturbance intensity. See Fig. 4.2 for disturbance intensity order.

4.3.3 Vascular plants

Ten of the thirteen vascular plant traits were significantly related to the gradient of disturbance (Table 4.2). With greater disturbance, mean maximum plant height was less (Fig. 4.5a) and the ratio of therophytes to non-therophytes increased (Fig. 4.5b). The mean Ellenberg light score was higher (Fig. 4.5c), while mean Ellenberg moisture score decreased with increased disturbance (Fig. 4.5d). The ratio of plants with animal-dispersed seed decreased with increasing disturbance intensity over those with non-animal dispersed seeds (wind dispersed or no apparent adaptation for seed dispersal) (Fig. 4.5e). The abundance of plants with small seed (<0.5mg) was greater with more disturbance (Fig. 4.5f). In the most intensive disturbance treatments, plants with no or little vegetative spread increased in abundance (Fig. 4.5g). Mean UK range extent was less in two of the disturbed treatments, including the most intense (Fig. 4.5h), and the mean abundance of designated species increased with disturbance (Fig. 4.5i).

PCoA axes one and two represented 56.4% of the variation in plant traits (Fig. 4.3c). Species located higher along axis one were associated with therophyte life form and no lateral spread, whereas negative values on this axis were associated with perennial life history, hemicryptophyte life forms, high moisture scores and larger UK range extent. High values on axis two were associated with large seed weight and animal dispersed seeds, and to a lesser extent, larger UK range, while negative values on axis two were associated with wind dispersed seeds.

Strong intercorrelation of traits indicates that hemicryptophytes were mostly species with extensive lateral spread. Plants with therophyte growth form (that do not survive the adverse season vegetatively) by definition have an annual (not paucennial or perennial) life history; thus these attributes had identical PCoA scores. Species with high light scores were likely also to have UK designation.

Although some clustering was apparent in the ordination (Fig. 4.3c) families were less tightly grouped compared to invertebrate groups. The majority of the Poaceae (grasses) clustered to the left of the plot and were associated with a perennial life history, increased lateral spread and moist habitats. Interspersed with Poaceae but confined to the top of the plot were the Fabaceae (both hemicryptophyte and woody species).

Loosely clustered at the bottom of the plot and thus associated with smaller seed size, greater probability of wind dispersal and a biennial life history, were Asteraceae (hemicryptophytes), Caryophyllaceae (herbs and small shrubs) and Scrophulariaceae (herbs and woody species).

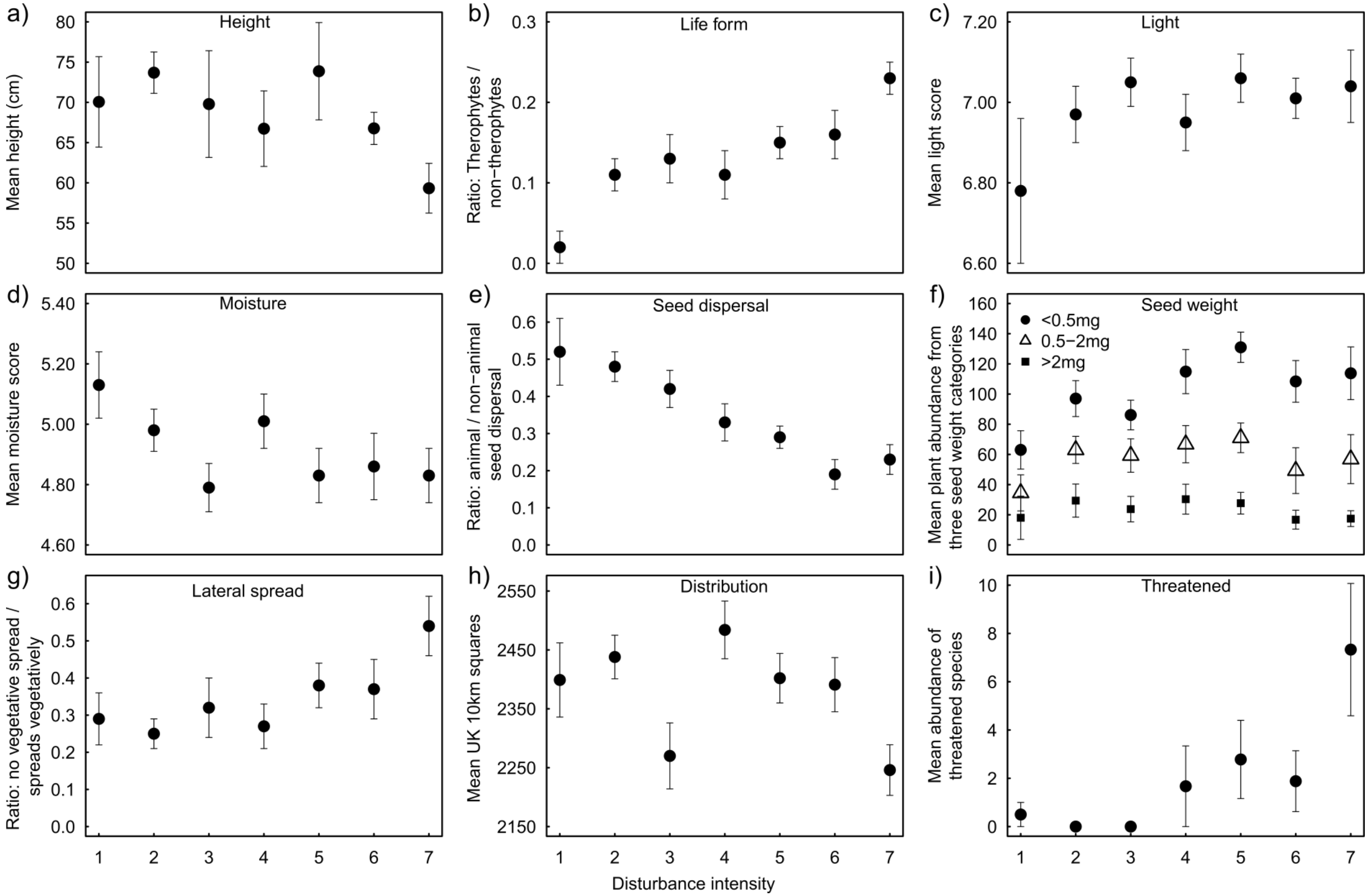

Fig. 4.5 Mean abundance ± SE of significant fourth-corner vascular plant traits against disturbance intensity. See Fig. 4.2 for disturbance intensity order.

4.4 Discussion

This is the first study to contrast trait responses from two diverse terrestrial arthropod groups to those of vascular plants, along a single environmental gradient. We amassed individual species traits for 361 species and analysed the abundance of 14 738 arthropods and 10 624 plant observations. Although ecological interpretations of trait response were broadly consistent, how this translated into physiological traits differed markedly among taxa. This was further complicated by the fact that individual physiological traits influence contrasting ecological and functional responses. For carabids and plants, trait shifts were broadly as predicted and followed those of other disturbance regimes reported in the literature (De Bello et al. 2005; Ribera et al. 2001). However, spiders did not follow expected response patterns and, in general, trait shifts were weaker than other groups.

4.4.1 Mobility

Abundance of macropterous carabids increased with disturbance intensity, corresponding with other research investigating both management intensity (Mullen et al. 2008; Ribera et al. 2001) and post-fire response (Moretti and Legg 2009). At high levels of disturbance, small seeded plants and species with no lateral spread increased. Lateral spread may be an effective strategy for exploiting vacant space created by localised small-scale disturbance, such as disruption of vegetation that damages but does not kill many plants. However, colonisation following large scale or intensive disturbance requires greater mobility, such as wind generated dispersal (Kleyer 1999). These results concur with the general pattern that greater dispersal ability allows quicker response following disturbance, as has also been found for terrestrial arthropods (Lambeets et al. 2008; Malmstrom 2012), plants (McIntyre et al. 1995) and aquatic invertebrates (Matthaei and Townsend 2000; Smale 2008).

Carabid body size is often negatively linked with dispersal ability (Kotze and O'Hara 2003; Ribera et al. 2001); in this study larger body size was associated with brachypterous species. Ribera (2001) found that with increased management intensity in the Scottish landscape, smaller, more mobile species were able to respond quicker. Kotze and O’Hara (2003) have shown that small-bodied species with greater dispersal ability have declined less as a result of habitat change and destruction than large-bodied species in the last 50-100 years in Western Europe.

Interestingly, wing dimorphism in carabids, a trait expected to benefit species colonising new habitat (Niemela and Spence 1991) or heterogeneous and disturbed landscapes (Kotze and O'Hara 2003), was not significant in the analysis. It is thought that within wing-dimorphic species, winged individuals have a dispersal advantage when landscapes are fragmented or heavily disturbed, but when suitable habitat is found, non-winged individuals, or individuals of species able to reabsorb wing muscles, will have a colonisation and breeding advantage (Desender 2000; Roff 1990). The scale of our study area, and hence isolation of sites, may not have exceeded a threshold where wing dimorphic carabid species have an advantage over macropterous species.

For spiders, there was no evidence that disturbed treatments favoured species that are able to disperse aerially, differing from our original predictions and findings from inundation disturbance (Lambeets et al. 2008), but consistent with post-fire response of grassland assemblages (Langlands et al. 2011). Like these previous studies, the method of assigning aerial dispersal ability using literature-based designations only includes those species that have published evidence of ballooning activity and is unable to distinguish between ballooning effectiveness. Although a challenging problem, greater understanding of spider ballooning behaviour for a wider range of species would significantly improve trait-based analyses for this group. Landscape structure may be a significant factor in ballooners' ability to colonise and ballooning has been found to be a significant source of colonists in large areas of barren habitat, such as after volcanic eruption (Crawford et al. 1995). However, in smaller grained mosaic habitats the ability of passive flight to find suitable habitat fragments may not be as effective.

Active-hunting spiders, in particular those that run (rather than stalking or ambush hunters), increased in abundance with greater disturbance intensity. This may be related to two processes, suitability of the vegetation structure for that foraging mode, and dispersal ability. Sparse and/or shorter vegetation structure may facilitate the movement of running predatory invertebrates (Bonte et al. 2003; Harvey et al. 2008). For one of the dominant ground-running species in this study (*Pardosa monticola*), terrestrial movements over a lifetime are estimated at 280 m (Bonte et al. 2003), with daily rates of 30-40 m estimated for female natal dispersal (Bonte et al. 2007). Within the trackway network of the current study landscape, maximum daily dispersal distance for *P. monticola* of 50 m and average daily dispersal of 11.8 m have been recorded (Waiboonya 2010). Terrestrial movements of this length may be sufficient to colonise after local disturbances at small to medium spatial scales. Langlands et al. (2011) suggested that due to the scale of their study patches (300 m x 300 m) terrestrial movements may have been sufficient to colonise after fire. In addition, both running and body size traits were linked in our study, and it is likely that for terrestrial dispersing spiders, larger running species may be able to colonise quicker after disturbance than smaller species. Larger spiders are able to travel relatively great distances by terrestrial movements; for example in north America, terrestrial movements of the large brown tarantula (*Aphonopelma hentzi*) have been recorded up to 1300 m over less than 20 days (Janowski-Bell and Horner 1999). The unpredicted and contrasting dispersal response of spiders compared to carabids highlights the need for trait-based studies to examine a range of arthropod groups.

4.4.2 Size and phenology

Larger body size in carabids is often associated with more stable habitats (Blake et al. 2003; Cole et al. 2002; Kotze and O'Hara 2003). Vascular plant maximum height shows a similar response, disturbance favouring species with shorter stature or compact rosettes (Kyle and Leishman 2009; McIntyre et al. 1995). In this study, carabid body size and vascular plant maximum height were both smaller at higher intensities of disturbance. Although larger species may be more susceptible to direct mortality from disturbance, it is commonly suggested that size is linked with other functional traits which are either favoured, or filtered, by the disturbance regime (Gaston and Blackburn 2000; Langlands et al. 2011; Ribera et al. 2001). In particular, carabid body size is often negatively related to winged dispersal, as discussed above.

In contrast for spiders the predicted body size response was not found, as body size was greater with greater disturbance intensity. Lambeets et al. (2008), having first separated Linyphiidae and Lycosidae groups in their analysis of flooding disturbance, found opposing body size responses for the two spider groups, with Linyphiidae increasing in size and Lycosidae decreasing in size with disturbance. Langlands et al. (2011) found larger spider body length immediately after fire and reported that body size was correlated with burrowing, and could therefore not tell which functional attribute explained the response. As mentioned above, we found spider body size correlated to terrestrial dispersal ability, which may be the functional attribute responsible for our findings of increased body size.

Vascular plant maximum height was correlated with primary growth form and life history. High intensity disturbance increased the abundance of therophytes over other growth forms. Therophytes are associated with a ruderal strategy and correspond with reported responses to soil, inundation and grazing disturbance (Kyle and Leishman 2009; Lavorel et al. 1998; McIntyre et al. 1995). McIntyre et al. (1995) found that soil disturbance opens space and favours species with effective dispersal and quick resource exploitation, e.g. rosette therophytes. Grazing gave higher proportions of therophytes and also hemicryptophytes (McIntyre et al. 1995). Therophytes, with an annual life cycle and herbaceous growth, are able to exploit disturbed areas quickly and reproduce despite frequent disturbance (Cornelissen et al. 2003). For the hemicryptophytes, having perennating buds at ground level is a more effective strategy at low levels of disturbance, such as grazing (McIntyre and Lavorel 2001) or the cutting treatments used in the current study.

As with annual plants, invertebrates with short generation times may be favoured by greater levels of disturbance. The r-*K* continuum theory predicts that smaller species with faster reproductive capacities are better adapted than larger species with slower reproductive capacities in unstable habitats (Reznick et al. 2002). For carabids, we found that smaller body size correlated with spring breeding in our analysis of linked traits. Larger carabids species are usually autumn breeders with overwintering larvae, whereas, smaller species are often spring breeders with faster growing larvae (Mullen et al. 2008) and over-winter as adults (Ribera et al. 2001). Generally, larger species and species with winter larvae are longer-lived than species with summer larvae (Lovei and Sunderland 1996), and longer life cycles require more stable habitats (Blake et al. 1994; Cole et al. 2002). Cole et al. (2002) found that large *Carabus* beetles were only found in low-intensity management sites in their study of agricultural land use in Scotland. They suggested that the large size and long life cycle make *Carabus* species relatively K-selected and more suited to stable habitats. In addition, the larval stage for carabids is especially vulnerable to disturbance because during this stage mobility is reduced, the larvae has weak chitinization and it must also find sufficient food to develop (Lovei and Sunderland 1996). Therefore, species with long larval stages and/or whose larval stage corresponds with the timing of disturbance regimes are likely to suffer greater mortality. Our results for carabids tend to match those of other studies which find small size and spring breeding related to greater disturbance.

4.4.3 Trophic guild

Davies et al. (2000) found that predatory beetles were no more vulnerable to habitat fragmentation than phytophagous species, whereas Vanbergen et al. (2010) found phytophage carabids more sensitive than zoophage to landscape structure. In our study, the abundance of herbivorous carabids increased with disturbance. Resource supply is likely to influence the presence of certain trophic guilds. Many of the herbivorous carabids are seed eaters, such as some Harpalini and Zabrini, and it is likely that these species were able to take advantage of the large seed resource produced by annual plants that also responded positively to disturbance. Harvey et al. (2008) found that increased plant diversity had a positive effect on herbivorous carabid richness, whereas, carnivorous species increased in plots with greater vegetation structural diversity, preferring habitat with greater above ground biomass but openness at ground level. Control plots in this study are dominated by grasses and are therefore less species rich than disturbed plots (Pedley et al. 2013b). However, control plots may provide greater diversity of microhabitat structures and hence niche availability than intensely disturbed plots. For predatory carabids, such as certain species of *Carabus* that feed on a range of soft bodied prey, increased disturbance may lead to reduced prey availability due to desiccation in exposed habitat.

4.4.4 Rarity and distribution

Intense disturbance can create extreme environments that may be more suited to specialist species. With increasing disturbance intensity, we found greater abundance of threatened carabid and designated plant species, and an increased representation of species with either smaller geographical distribution (spiders and plants) and/or narrower habitat requirements (spiders and carabids). At low levels of disturbance, assemblages contained more generalists. In groups where we could obtain traits relating to abiotic tolerances, both the spider and plant assemblages had greater representation of species associated with arid and open habitats at greater disturbance intensity. Lambeets et al. (2008) found the opposite response for specialist riparian arthropods; species were displaced by eurytopic species at very high and very low levels of disturbance. It is likely that the response of rare or narrowly distributed species will depend on the regional species pool and spatial scale of disturbance. The regional assemblage in our study habitat contains many arenicolous and xerophilic species associated with early successional habitat (Dolman et al. 2012). Disturbance that creates open vegetation and bare substrate would be expected to benefit many of these species; however, in other regions where early successional habitats are rare, more generalist species may dominante the colonists. Also, at national or international scales, overall effects of habitat change may result in generalist strategies becoming dominant (Kotze and O'Hara 2003).

4.4.5 Conclusions

Fourth-corner analysis enabled the direct testing of traits along a single environmental gradient with high statistical power for multiple taxonomic groups; previous research has also found the fourth-corner procedure to be a powerful tool to test functional traits (Aubin et al. 2009; Brind'Amour et al. 2011). However, some limitations exist, for example, the fourth-corner procedure does not incorporate linked traits, phylogeny or spatial autocorrelation (Langlands et al. 2011).

Changes in environmental conditions due to disturbance filtered traits in mostly predictable ways. Although there were general consistencies in the functional response, e.g. dispersal, responses do not always depend on the same physiological trait. For vascular plants, our results were consistent with previous findings along disturbance gradients and were typical of a ruderal strategy: perennials, shrubs and woody species were replaced with annuals and short statured herbaceous species after disturbance (De Bello et al. 2005; Kyle and Leishman 2009). Likewise for carabids, disturbance promoted similar shifts in functional traits reported for other disturbance regimes (Ribera et al. 2001; Samu et al. 2010), promoting species with small size and greater dispersal ability, which are better adapted to unstable habitats. However, the spider assemblage did not correspond with our original predictions; spiders were the only group where aerial dispersal was not significant and the abundance of large species increased with disturbance.

Disturbance shapes biological communities over varying intensities, frequencies and spatial scales, including small-scale recurring disturbance (Lambeets et al. 2008; Prinzing et al. 2007) and more singular larger scale disturbance (Malmstrom 2012; Moretti et al. 2004). By altering the intensity of the disturbance at a single spatial scale, we have shown that patterns of functional response differ according to the taxonomic group. Others have demonstrated biological patterns vary with the spatial scale of study (Dumbrell et al. 2008; Sanders et al. 2007) but as yet, terrestrial invertebrate trait responses to spatial scale have rarely been tested. Our results concur with those of studies conducted at different spatial scales, indicating that general predictability may be afforded for both carabids and vascular plants. However, within the two arthropod groups, very different trait responses were recorded. Predictive generalisation needs to be cautious when comparing across taxa as different traits may response in functionally similar ways and the response patterns may be scale dependant.

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Appendix A4.1. Traits considered for carabids, spiders and vascular plants including details of each trait and source references. Data type given in brackets (Cont = continuous; Ord = ordinal, number of classes; Nom = nominal, number of classes). To ensure ordinal variables had a useable number of species per category, levels were partly determined by the numbers of shared species so that uncommon sub-categories were merged into broader classes.

Trait Type	**Carabid**	**Code**	**Attribute and source**
Physiological	Body size	Size [Cont]	Average body size in mm. (Luff 2007)
	Activity length	Act.Lgth [Ord, 3]	1=short (1-3 months); 2=medium (4 months); 3=long (>5 months). (Luff 2007)
	Activity period	Act.Peri [Ord, 3]	Main period when species is active, either foraging or breeding. 1=spring (early); 2=summer (mid); 3=autumn (late). (Luff 2007)
	Breeding season	Spring [Nom, 2]	Either spring breeding or autumn breeding. (Desender et al. 2010; Ribera et al. 2001)
	Carnivorous	Carn [Nom, 2]	1=carnivores (Harvey et al. 2008; Ribera et al. 2001)
	Herbivorous	Herbi [Nom, 2]	1=herbivores (Harvey et al. 2008; Ribera et al. 2001)
	Omnivores	Omni [Nom, 2]	1=omnivores (Harvey et al. 2008; Ribera et al. 2001)
	Brachypterous	Brachy [Nom, 2]	1=brachypterous species (Luff 2007; Lin et al. 2007)
	Wing-dimorphic	Dimorp [Nom, 2]	1=wing dimorphic speices (Luff 2007; Lin et al. 2007)
	Macropterous	Macro [Nom, 2]	1=macropterous species (Luff 2007; Lin et al. 2007)
Ecological	Habitat requirement	Hab.Req [Ord, 3]	1=open-dry ('dry); 2=open-mesic ('mesic'); 3=generalist-shade tolerant ('shade'). (Luff 2007)
	Species distribution	Distrib [Ord, 3]	1=restricted; 2=medium; 3=wide. (Luff 2007)
	Designated species	Threat [Nom, 2]	1=has designation in the UK (RDB, BAP, Na, Nb)(JNCC 2011)
Type	**Spider**	**Code**	**Attribute and source**
Physiological	Body size	Size [Cont]	Female body size in mm (Roberts 1996)
	Activity length	Act.Lgth [Ord, 3]	Number of months adult females active 1=short (3-5 months); 2=medium (6-7 months); 3=long (>7 months). (Harvey et al. 2002)
	Moisture preference	Aridity [Cont]	Standardised niche parameters between 0 and 1. Niche position is 0 for the species which prefer the moistest habitats and 1 for the species which prefer the driest habitats. (Entling et al. 2007)
	Shade preference	Shade [Cont]	Standardised niche parameters between 0 and 1. Niche position is 0 for the species which prefer the most open habitats and 1 for the species which prefer the most shaded habitats. (Entling et al. 2007)
	Ballooning	Balloon [Nom, 2]	1= species listed as ballooning in Bell et al. (2005)
	Active hunter	Active [Nom, 2]	1=active hunting strategy (Uetz et al. 1999)
	Running hunter	Run [Nom, 2]	1=running hunters (Uetz et al. 1999)

	Ambush hunter	Ambush [Nom, 2]	1=ambush hunters (Uetz et al. 1999)
	Stallking hunter	Stalk [Nom, 2]	1=stalking hunters (Uetz et al. 1999)
Ecological	Niche Breadth	Niche [Ord, 3]	Habitat specifity 1='narrow' 2='medium' 3='wide'. Calculated from Harvey (personal data)
	Habitat requirement	Hab.Req [Ord, 3]	1=open-dry ('Dry'), 2=open-mesic ('mesic'), 3=generalist-shade tolerant ('generalist-shade'). (Harvey et al. 2002; Roberts 1996)
	Distribution	UK10km [Cont]	Number of 10 km squares in which the species has been recorded in the UK. (Harvey, personal data)
	Designation	Threat [Nom, 2]	1=has designation in the UK (RDB, BAP, Na, Nb). (Harvey et al. 2002)

Type	**Plant**	**Code**	**Attribute and source**
Physiological	Height	Hght [Cont]	Maximum plant height in cm. (Hill et al. 2004)
	Primary life form	LifeForm [Ord, 5]	1=Mega/meso/microphanerophyte; 2=Chamaephyte; 3=Hemicryptophyte; 4=Non-bulbous geophyte; 5=Therophyte. (Hill et al. 2004)
	Life history	LifeType [Ord, 3]	1=perennial; 2=biennial; 3=annual (Hill et al. 2004)
	Woodiness	Woody [Non, 2]	1=woody species (Hill et al. 2004)
	Light	Light [Ord, 6]	Ellenberg indicator (1-9). 1=most shade, 9=most open (Hill et al. 2004)
	Moisture	Moist [Ord, 7]	Ellenberg indicator (1-9). 1=most dry, 9= most wet. (Hill et al. 2004)
	Animal dispersed	Dsp.Animal [Non, 2]	1=seeds dispersed by animals (Grime et al. 2007)
	Wind dispersed	Dsp.Wind [Non, 2]	1=seeds dispersed by wind (Grime et al. 2007)
	Dispersule weight	Dsp.Wght [Ord, 7]	1=too small to be measured easily; 2=≤ 0.20 mg; 3=0.21-0.50 mg; 4=0.51-1.00 mg; 5=1.01-2.00 mg; 6=2.01-10.00 mg; 7=≥ 10 mg. (Grime et al. 2007)
	Lateral spread	Lat.Spread [Ord, 4]	1=little or no vegetative spread; 2=Tussock-forming graminoid, may slowly spread; 3=Rhizome shortly creeping; 4=Rhizome far-creeping. (Hill et al. 2004)
	Seed bank	Seed.Bank [Ord, 4]	1=transient seed banks present during the summer and germinated synchronously in autumn; 2=transient seed banks present during winter and germinated synchronously in late winter or spring; 3=a small amount of seed persists in the soil, often for >5 years but concentrations of seed in the soil are only high after seed has just been shed; 4=there is a large bank of long persistent seeds in the soil throughout the year. (Grime et al. 2007)
Ecological	Distribution	UK10km [Cont]	Number of 10 km squares in which the species has been recorded in the UK. (Hill et al. 2004)
	Designation	Threat [Non, 2]	1=has designation in the UK (JNCC 2011)

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Appendix A4.2. Trait loadings for PCoA axis 1 and 2. Scores greater than 0.5 are shown in bold.

	PCoA-1	**PCOA-2**		**PCoA-1**	**PCOA-2**		**PCoA-1**	**PCOA-2**
Carabid			**Spider**			**Plant**		
Body size	**-0.694**	**-0.715**	Body size	**-1.235**	0.490	Height	-0.089	-0.184
Act.Lgth	-0.383	**0.583**	Act.Lgth	0.408	0.345	Therophyte	**0.867**	0.155
Act.Peri	0.078	**-0.920**	Aridity	-0.127	-0.076	Hemicryptophyte	**-0.762**	-0.136
Autumn-breed	-0.284	**-0.834**	Shade	0.087	-0.116	Annual	**0.867**	0.155
Spring-breed	0.284	**0.834**	Balloon	0.144	**0.544**	Biennial	0.033	-0.136
Carnivore	**-0.545**	0.166	Active-hunt	**-0.909**	0.211	Perenial	**-0.900**	-0.020
Herbivore	**0.693**	-0.166	Web-hunt	**0.909**	-0.211	Woodiness	-0.027	0.061
Omnivore	-0.138	-0.046	Run	**-0.654**	0.223	Light score	0.435	-0.183
Brachy	-0.494	-0.217	Ambush	-0.132	0.037	Moisture score	**-0.761**	0.207
Dimorp	-0.215	0.165	Stalk	-0.099	-0.048	Dsp.animal	-0.042	**0.767**
Macro	**0.709**	0.052	Nb-narrow	-0.128	-0.081	Dsp.wind	0.272	**-0.821**
Dry-open	**0.715**	-0.006	Nb-medium	-0.059	**-0.792**	Dsp.weight	-0.430	**1.387**
Open-mesic	-0.180	0.066	Nb-wide	0.188	**0.872**	No.lateral	**0.776**	-0.064
Generalist-shade	**-0.535**	-0.060	Dry-open	-0.444	-0.159	Ex.Lateral	-0.411	-0.064
Restrict.dist	0.266	-0.186	Open-mesic	-0.140	0.039	Seed.bank	0.388	0.252
Medium.dist	0.181	-0.055	Generalist-shade	**0.584**	0.120	Distribution	**-0.614**	0.405
Wide.dist	-0.447	0.241	Distribution	**0.671**	**1.072**	Threatened	0.091	-0.026
Threatened	0.332	-0.344	Threatened	-0.158	-0.185			

Chapter 5

Comparing remnant habitat, linear strips and ephemeral stepping stones: functional trait responses of ground-active spiders

Abstract

Habitat loss and fragmentation has reduced connectivity in many modern landscapes. The value of connectivity elements in the landscape requires evidence from multiple species and the use of functional traits allows predictions that can guide network restoration. Functional trait and species composition of spider assemblages in open habitats were compared among contrasting landscape elements each comprising a different configuration of open habitat: 1) relict habitat patches (of heathland), 2) permanent linear elements (trackways) potentially allowing dispersal by percolation of resident populations, and 3) ephemeral stepping stone patches (clear felled and replanted forestry coupes) potentially allowing dispersal by meta-population dynamics.

Linear elements and ephemeral patches were set in a matrix of closed-canopy forest within a plantation-heathland landscape mosaic. Assemblages were sampled by pitfall trapping of 14 338 adult individuals from 143 species, and morphological, functional and life history traits were analysed by principal coordinate and fourth corner analyses. Sampling along a chronosequence confirmed that ephemeral patches supported assemblages distinct from closed-canopy plantation for approximately five to seven years after planting. However, contrary to expectation, ephemeral patches were not primarily colonised by small-bodied species capable of dispersal by ballooning, but by large-bodied active ground-hunting species tolerant of arid conditions. The spider assemblage of linear elements differed more from heath reference sites than did that of ephemeral patches, with greater representation of generalist and shade tolerant species, reflecting greater edge influence of the adjacent matrix. In contrast, species restricted to remnant patches included small-bodied and nationally scarce habitat specialists that were not recorded from either the linear elements or ephemeral patches, despite potential for dispersal by ballooning. Ephemeral stepping stones provide suitable connectivity for the majority of the heathland assemblage, whereas increased habitat quality is needed to combat detrimental edge effects in linear elements.

5.1 Introduction

Land-use change has caused habitat removal and fragmentation, a major cause of biodiversity loss (Millennium Ecosystem Assessment 2005). In human modified landscapes with low connectivity, many organisms survive in patchy isolated populations (Saunders et al. 1991). Some generalist species can use surrounding matrix habitats for dispersal, whereas specialist species often require connecting elements of suitable quality. Enhanced network connectivity is promoted to mitigate the negative effects of fragmentation and facilitate population survival (Bennett and Mulongoy 2006; Chetkiewicz et al. 2006), but may comprise different configurations of landscape elements including corridors, stepping stones or a less hostile matrix (Bennett 2003). The restoration of ecological connectivity at landscape scales requires evidence for the relative performance of such alternative configurations for multiple species. Examining responses in terms of functional, ecological and life history traits supports generalisation that could be applied to other ecological systems (McGill et al. 2006).

Connectivity is often thought of as corridors enabling species to pass between primary habitat patches (Simberloff et al. 1992) to recolonise vacant habitat or enhance population rescue and facilitate regional population persistence via metapopulation dynamics (Hanski 1999), or assist range responses to climate change (Krosby et al. 2010). The use of corridors has been reported for many species over the last two decades (Gilbert-Norton et al. 2010; Haddad et al. 2003; Tewksbury et al. 2002). For slow-dispersing species, corridors of suitable quality may allow percolation of populations over generations (Bennett 2003). However, corridors are controversial and have been criticised for negative effects such as the spread of invasive taxa, poor cost effectiveness and increased edge effects (Gilbert-Norton et al. 2010; Hobbs 1992). Stepping stones (separate patches connecting otherwise isolated habitat) may provide more effective connectivity than corridors for some mobile species (Schultz 1998). For species that are associated with early successional or disturbed habitat, stepping stones are likely to be ephemeral in the landscape and metapopulation persistence may require greater dispersal ability (Amarasekare and Possingham 2001; Johst et al. 2002; Loehle 2007). In addition, the habitat provided by the wider landscape matrix is an important determinant of movement between isolated habitats for many species

(Haynes and Cronin 2006; Ricketts 2001) and can influence dispersal success through corridors and stepping stones (Baum et al. 2004). Despite the abundance of literature regarding corridors, the relative benefits of corridor linkages over stepping stones remain poorly understood. Furthermore, the use and efficacy of connective elements has often been verified through their use by a single species rather than understanding trait and assemblage responses.

Our study area is a heathland region in which extensive plantation forest has been established over open habitats, including grass heath and farmland, with the remaining heathland fragmented into isolated relict patches. Plantation landscapes provide a study system that contains open habitat elements, configured in the form of ephemeral stepping stone patches and linear corridors, both embedded in a forest matrix. Plantation forests in temperate regions have high species richness compared to surrounding open habitat and natural woodland, largely due to open-habitat species colonising clear-felled ephemeral sites (Fahy and Gormally 1998, Butterfield et al 1995, Oxbourgh et al 2005, Niemela et al 1993, Mullen et al 2008). Open habitat species infiltrating open areas within plantations managed by clear-fell rotation provide an excellent opportunity to examine colonisation after regular, systematic disturbance events.

Within this landscape we examine species trait and assemblage responses of epigeic (ground-active) spider assemblages to open habitat elements of contrasting configuration: 1) ephemeral stepping stones, in the form of a chronosequence of clear-felled pine coupes, 2) permanent linear connecting elements, in the form of forestry trackways, and 3) remnant patches of open habitat. We use this system to answer the following questions: Do open habitat assemblages form and for how long do these persist in ephemeral patches? Do spider assemblages in open linear and ephemeral habitat within the plantation resemble those of pre-plantation semi-natural habitat typical of the region, or have they been filtered in ways that can be predicted by species traits? Three alternative colonisation hypotheses are possible for the forestry elements, 1) assemblages in ephemeral and linear habitat will resemble those of semi-natural open habitat until canopy closure, 2) assemblages in ephemeral and linear elements will comprise a reduced sub-set of species lacking the rarest and most specialised due to reduced habitat quality, 3) compared to assemblages within linear elements, ephemeral habitat will lack less mobile species due to poorer dispersal ability. We predicted that assemblages developing in ephemeral patches of open habitat will be represented by small-bodied, aerial-dispersing, habitat generalists, whereas linear connecting trackways will have assemblages dominated by large-bodied, active-hunting generalists.

5.2 Methodology

5.2.1 Study site and design

Our study area is in Breckland in eastern England, a heath region characterised by semi-continental climate, sandy, nutrient-poor soil and a long history of grazing and episodic cultivation (Dolman and Sutherland 1992). Breckland supports 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).

Thetford Forest, occupying 185 km^2 of Breckland (0°40'E, 52°27'N) was planted in the early 20th century and is the largest lowland conifer forest in the UK. It is dominated by conifer plantations, with 80% comprising Corsican (*Pinus nigra*) and Scots (*P. sylvestris*) pine, and is managed by clear-felling (typically at 60-80 years) and replanting of even-aged coupes (mean area 9.0 ha ± 8.6 SD). After felling, coupes are cleared of coarse woody debris before ploughing of planting lines that exposes areas of bare mineral substrate. Replanting takes place the following winter. Open conditions in coupes are available for up to 10 years, after which dense canopy cover increases with tree height and age, peaking to full canopy closure after 20 years (Hemami et al. 2005). Young coupes therefore provide ephemeral open habitat before succeeding to closed canopy forest. Open habitat carabid species persist for approximately five years following planting (Lin 2005), but for ground-active spiders associated with open habitats, the suitability of clear-felled and newly planted coupes and the duration of appropriate conditions are unknown. We define plantation growth stages following Hemami et al. (2005); restocked (0-4 years after planting), pre-thicket (5-10 years), thicket (11-20 years), pole (21-30 years) and pre-felling (>30 years).

Coupes are subdivided by a network of forestry trackways that provide management access. Within the forest there are approximately 1290 km of trackways (average width 14 m), providing a potential open habitat resource of 18 km^2, equivalent to a fifth (21 %) of the designated extent of grass-heath remaining in the region (83 km^2). Trackways comprise two elements: a central wheeling with sparse vegetation and exposed substrate, flanked by vegetated verges that are cut annually to facilitate access, but that lack bare substrate. Trackways vary in width (mean 13.7 m ± 5.8 SD, range 5-50 m, from a sample of n=93), substrate (sand, 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, trackways within or bordering pole and pre-fell coupes are too shaded by mature trees to provide suitable linear habitat for heathland species (Pedley et al. 2013).

Eight reference sites comprising remnant patches of heathland and ruderal habitat were also sampled. These were all considered important for regionally vulnerable invertebrate and plant communities and, along with marginal agricultural sites, represent the dominant pre-plantation habitat. Sites were distributed around the northern, western and south-eastern margins of the forest. Sites included one National Nature Reserve (NNR) and six Sites of Special Scientific Interest (SSSI), of which five were also Special Areas of Conservation (SAC). Reference sites (mean area 106 ha ± 130 SD) were less than 8 km from sampled forest sites with the majority bordered by a mixture of plantation forest and intensive agricultural fields. Within reference sites, sampled areas comprised physically disturbed habitat, including grass heath heavily grazed by both sheep and rabbits, and recently ploughed areas associated with heathland management.

5.2.2 Sampling

Ground active spiders were sampled by pitfall transects that formed the unit of replication for analysis. Individual trackway elements were sampled, each by one transect. However, insufficient coupes and heathland sites were available to provide a similar number of replicates and therefore, two transects were placed within coupes and heathland patches; we recognise this represents a degree of pseudoreplication.

Two sampling transects, separated by 50 m to ensure independence, were established in each of the eight heathland reference sites (hereafter ‘remnant patches’) and in each of 36 second rotation forest coupes (hereafter ‘ephemeral patches’) representing a chronosequence of eight planting ages (Fig. 5.1). In order to represent the initial open stages of the plantation cycle and identify the length of time that open habitat is available to non-forest species, the chronosequence sampled comprised: clear-felled but unplanted patches (year 0, five replicates, mean 5.7 ha ± 1.5 SD), one year old (year 1; five replicates, mean 11.1 ha ± 2.7 SD), three year old (year 3; five replicates, mean 6.9 ha ± 3.5), five year old (year 5; five replicates, mean 11.4 ha ± 5.4 SD), seven year old (year 7; four replicates, mean 7.2 ha ± 3.4 SD), nine year old (year 9; four replicates, mean 12.4 ha ± 4.2 SD), 13 year old (year 13; four replicates, mean 8.4 ha ± 2.4 SD) and 21 year old sites (year 21; four replicates, mean 9.8 ha ± 3.4 SD). Closed canopy habitat was represented by 21 year old coupes; this age class was chosen as it was assumed that this would go beyond the suitable open period and therefore allow a distinction between the ephemeral open stage and the background forest assemblage.

Transects were placed in 16 independent trackway verges, each adjacent to thicket-aged coupes (11-20 years old). Individual trackway elements (i.e. running adjacent to a single planting event) were rarely long enough to permit placement of more than one transect in an element. Sampled trackways were a mean of 0.78 km (SD ± 0.25 km) from the nearest other sampled trackway. To minimise shading effects, the northern-most verge was sampled in trackways running east-west and in north-south oriented trackways the widest of the two verges was sampled. Trackway transects are referred to as ‘linear elements’ hereafter.

In 2009, spider assemblages were sampled in each transect on two occasions representing the peak period of spider abundance and activity, May and June. 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 along each transect, were opened for seven consecutive days. Traps in each transect were pooled and data from the two sampling months were combined giving one composite sample per transect. Adult spiders were identified to species following Roberts (1987, 1996); juvenile and sub-adult specimens were not identified due to the lack of developed reproductive structures.

In August of 2009 we measured the following habitat variables at 40 points along each transect: vegetation height in each transect was assessed using a sward stick (diameter 90 mm, weight 250 g, following Dolman and Sutherland (1992)) and frequency (summed incidence) of pine needles, debris (brash and vegetation litter) and percentage of bare substrate was visually estimated in a 20 x 20 cm area at each point. Canopy cover was assessed using a spherical densitometer at six evenly spaced locations in each transect.

Geographical clustering of chronosequence sites was unavoidable due to the forestry felling regime which targets mechanical operations in specific forest areas (Fig. 5.1). We recognize that some of the response to the chronosequence may be due to spatial autocorrelation of these sampling sites. However, it is likely that the major differences in species composition in the sampled chronosequence are attributed to differences in the growth stage of the tree crop and hence differing levels of shade and ground vegetation, rather than geographical location. Distances between chronosequence sites were kept to a minimum by selecting locations within the central forest blocks; the maximum distance separating sites was 10.7 km.

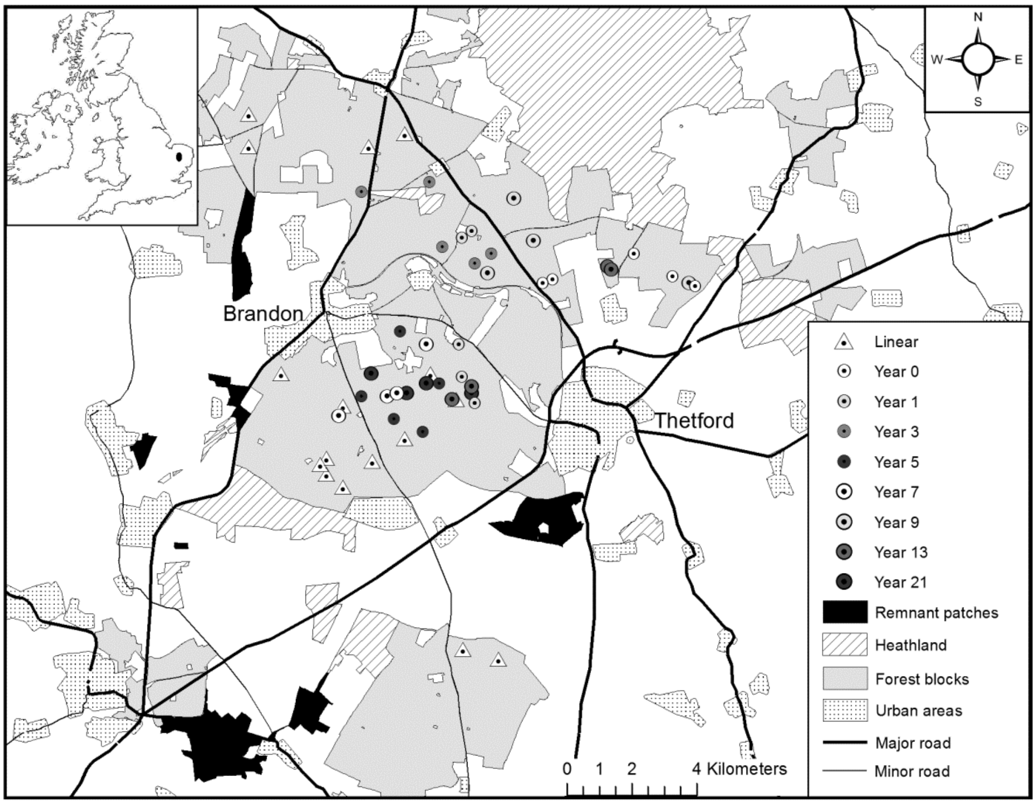

Fig. 5.1. Sample locations within Breckland showing the distribution of sampled remnant patches, linear elements and different aged ephemeral patches (year numbers indicate planting age of coupes).

5.2.3 Functional traits

In order to understand ecological factors that determined assemblage responses to different habitat elements, we selected life history traits that were considered to indicate dispersal ability, rarity and habitat affinity. Traits were chosen for which detailed information was available at the individual species level from published literature (Table 5.1). To ensure ordinal variables had a useable number of species per category, uncommon sub-categories were merged into broader classes. The habitat affinities of species were classified as those associated with shaded woodland habitats (hereafter 'woodland'), eurytopic species associated with many habitat types or with any mesic habitat type (hereafter pooled as 'generalists') and those associated with dry calcareous and acidic grassland, dry heathland, dunes, sand or gravel pits (hereafter 'dry-open').

Aerial dispersal by ballooning (passively floating on silk threads) is thought to be an effective mechanism for both long and short distance dispersal to colonise suitable habitat (Bell et al. 2005; Duffey 1998). We assigned species as ballooners if they had a published record of ballooning in the review by Bell et al. (2005), following Lambeets et al. (2008) and Langlands et al. (2011).

Table 5.1. Description of spider traits.

Type	**Trait**	**Code**	**Data Type**	**Attribute**
Physiological	Body size	Size	quantitative	Female body size in mm (Roberts 1996)
	Moisture preference	Aridity	quantitative	Standardised niche parameters between 0 and 1. Niche position is 0 for the species which prefer the moistest habitats and 1 for the species which prefer the driest habitats (Entling et al. 2007)
	Shade preference	Shade	quantitative	Standardised niche parameters between 0 and 1. Niche position is 0 for the species which prefer the most open habitats and 1 for the species which prefer the most shaded habitats (Entling et al. 2007)
	Ballooning	Flight	1 nominal	Flight=exact species listed as ballooning in Bell et al. (2005)
	Active hunter	Act.Web	2 nominal	Active hunting; web spinning (Uetz et al. 1999)
Ecological	Niche breadth	Niche	3 ordinal	Habitat specifity 1='narrow' 2='medium' 3='wide'. Calculated from Harvey (personal data)
	Habitat association	Hab.Ass	3 nominal	open-dry habitat species ('dry-open'); generalist and open-mesic species ('generalists'); shade tolerant species ('woodland'). Taken from descriptions in Harvey et al. (2002) and Roberts (1996)
	Distribution	UK10km	quantitative	Number of 10 km squares in which the species has been recorded in the UK. Taken from Harvey (personal data)
	Designated species	Threat	1 nominal	Species has designation in the UK (Na, Nb). Taken from Harvey et al. (2002)

5.2.4 Analysis

Data was analysed using individual transects (pooled pitfall traps over two sampling months) as the sampling unit. We acknowledge that transects in linear elements may capture greater beta diversity than pairs of transects within individual remnant or ephemeral patches, that were only separated by 50 m. Species accumulation with increasing sampling effort (Gotelli and Colwell 2001) was examined separately for linear elements, remnant patches and different aged ephemeral patches, using random permutation of the sampling data with the vegan package (Oksanen et al. 2010) within R v.2.15.1 (R Development Core Team 2012).

Assemblage composition across sampled transects was examined using non-Metric Multidimensional Scaling (NMDS) performed on a matrix of Bray-Curtis dissimilarities of spider abundance data (square root transformed and Wisconsin double standardization) using the vegan package in R. Centroids for each habitat type were plotted to visualise assemblage differences. Environmental variables were fitted as vectors to the ordination; only those significant at $P<0.01$ were displayed. The two vegetation structure variables (sward height and bare ground) were also fitted as a surface to better illustrate patterns between sites.

To examine linkages in the trait data, a trait dissimilarity matrix (taking traits as variables and species as samples) was calculated using the Gower coefficient (Gower 1971). The Gower coefficient handles mixed data types, including traits that are nominal, ordinal or continuous; continuous traits were first standardised to zero mean and unit variance across species. Principal Coordinates Analysis (PCoA) was conducted on the dissimilarity matrix using the vegan package in R. Associations among traits were then visualised by plotting trait vectors based on the Spearman rank correlation of the trait in relation to the first two PCoA ordination axes, following Langlands et al. (2011).

Trait-specific responses to habitat types were analysed using fourth-corner analysis (Dray and Legendre 2008). Fourth-corner procedure tests the link between all combinations of species traits and environmental attributes (in this case landscape elements; remnant patches, linear and ephemeral forest patches). It uses a three data-table analysis where matrix ‘R’ (environmental attributes x site) is indirectly related to matrix ‘Q’ (trait x species), via a third matrix ‘L’ (species x site). Extension of fourth-corner analysis now allows the use of species abundance data (Dray and Legendre 2008) where previously only species presence/absence data could be considered (Legendre et al. 1997). The fourth-corner procedure uses a generalised statistic S_{RLQ} that can analyse quantitative variables, qualitative variables or a mixture of both. When both the trait (Q) and environment (R) variables are quantitative the test statistic is equal to the Pearson correlation coefficient r, when both are qualitative χ^2 is calculated and when data are mixed the correlation ratio η^2 is used (Dray and Legendre 2008).

Whether the observed linkage among traits and environmental attributes differs significantly from that which may be attributed to chance, is assessed against null models determined by the observed structure of the data matrices , using randomisation and permutation (Dray and Legendre 2008). We applied permutation Model 1 to test the null hypothesis (that R is not linked to Q) when examining links between the fixed traits of the species and fixed characteristics of the sites, mediated by the observed data of table L (Dray and Legendre 2008). Model 1 randomises presence-absence of individual species relative to site characteristics (permuting within each column of matrix L), but does not re-sample the species-trait relationship (matrix Q) or the environment-site relationship (matrix R). This was appropriate (Dray and Legendre 2008) as traits were determined from the literature and not by empirical sampling, and the environment matrix was determined *a priori* by the experimental design. Prior to analysis spider abundance data were square root transformed to reduce the effect of dominant species. As fourth-corner uses repeated testing, results were adjusted using Holm’s correction (Holm 1979) following Aubin et al. (2009). To assist interpretation of fourth-corner results, abundance-weighted mean trait values for each habitat type were plotted, showing significant fourth-corner results. Fourth-corner analyses were calculated with 9999 permutations using the ade4 package (Dray and Dufour 2007) in R.

5.3 Results

We sampled a total of 14 338 adult individuals from 143 species. Trapping successfully sampled the species assemblages, as shown by species rarefaction within each habitat (Fig. 5.2). Species richness was highest in the linear elements (83 species) and lowest in the 21 year old coupes (43 species) and remnant patches (53 species). Species richness combined over the chronosequence of ephemeral patches recorded 131 of the 143 recorded species; 43 species were unique to the ephemeral patches, nine species unique to remnant patches and three to linear elements. We compiled species-specific traits for 133 spider species which were used in the subsequent analysis; insufficient data were available to characterise traits of the remaining ten species.

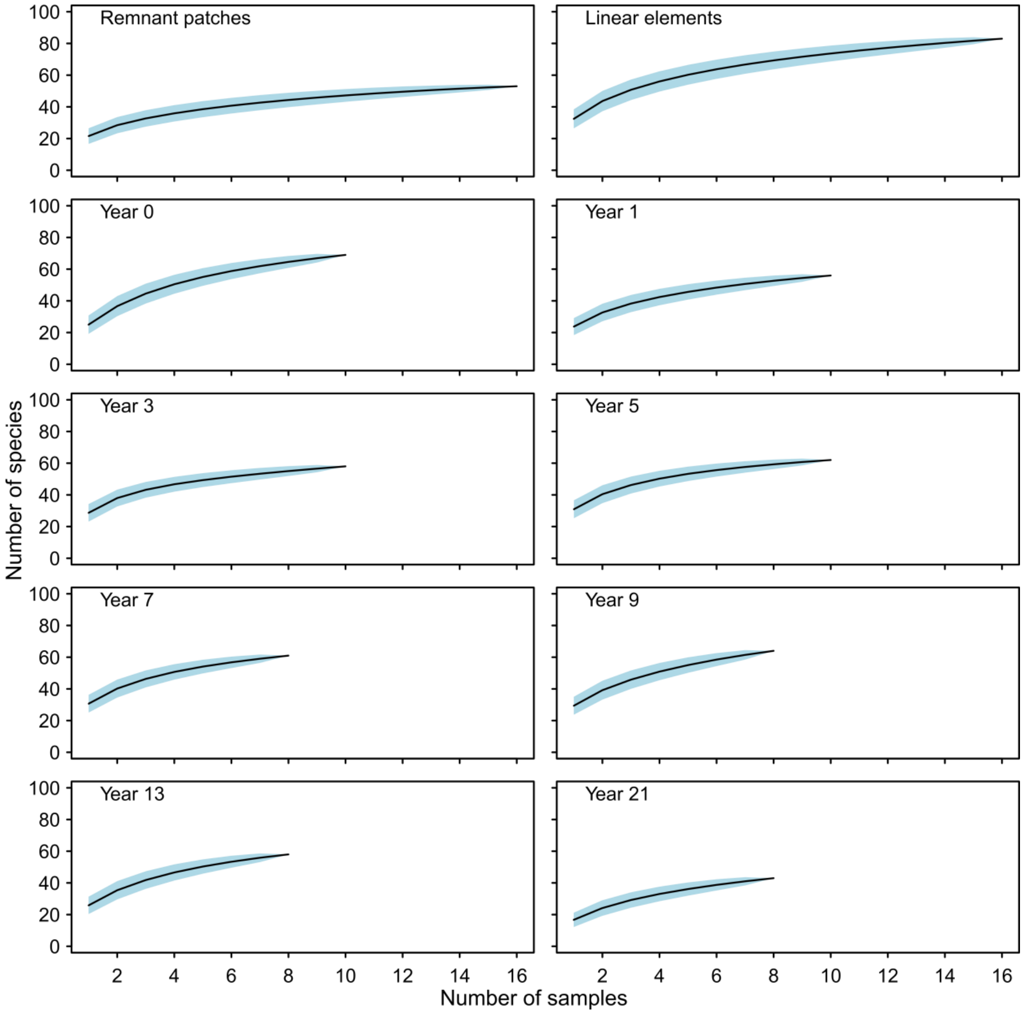

Fig. 5.2. Species accumulation (± SD) for spider assemblages collected by pitfall trapping in remnant patches, open habitat linear elements and ephemeral patches (numbers indicate planting age of coupes).

5.3.1 Community analysis

NMDS successfully represented the assemblage structure of the sampled transects with a stress value of 0.17 (Fig. 5.3). Spider assemblages differed between the remnant patches and all other habitat types; no forestry element resembled the community composition of remnant patches of semi-natural open habitat. Separation of remnant patches was predominantly along axis one of the ordination, with remnant patches and 21 year old coupes showing the greatest division (Fig. 5.3a). Axis two separated recently opened coupes (cleared-unplanted and one year old coupes) from older coupes and remnant patches. Assemblage composition of linear elements resembled that of five, seven and nine year old ephemeral patches.

The direction of environmental variable vectors indicated the degree of physical disturbance and shading experienced at each transect. Axis one was positively associated with bare substrate and negatively associated with canopy cover and pine needle ground cover (Fig. 5.3b). Canopy cover and ground cover of pine needles increased with tree age, and was therefore strongly associated with older ephemeral coups. Although sward height was low in 21 year old coups (Fig. 5.3c), the pine needle ground cover prevented substrate being exposed. Large amounts of debris (brash and litter) were associated with transects predominately from sites that had been recently cleared. Greater extent of bare substrate was associated with remnant patches, which are exposed to regular small-scale physical disturbance.

Species associated with dry-open habitats were found in all three landscape elements, ephemeral patches, linear forest elements and remnant patches (Fig. 5.4). All dry-open species found in linear elements were also found in ephemeral patches. No dry-open species were recorded in 13 and 21 year old coupes. Of the 23 species recorded in younger coupes, all were found in one, three and five year old ephemeral patches. Three dry-open species were unique to the ephemeral patches and an additional five were unique to remnant patches.

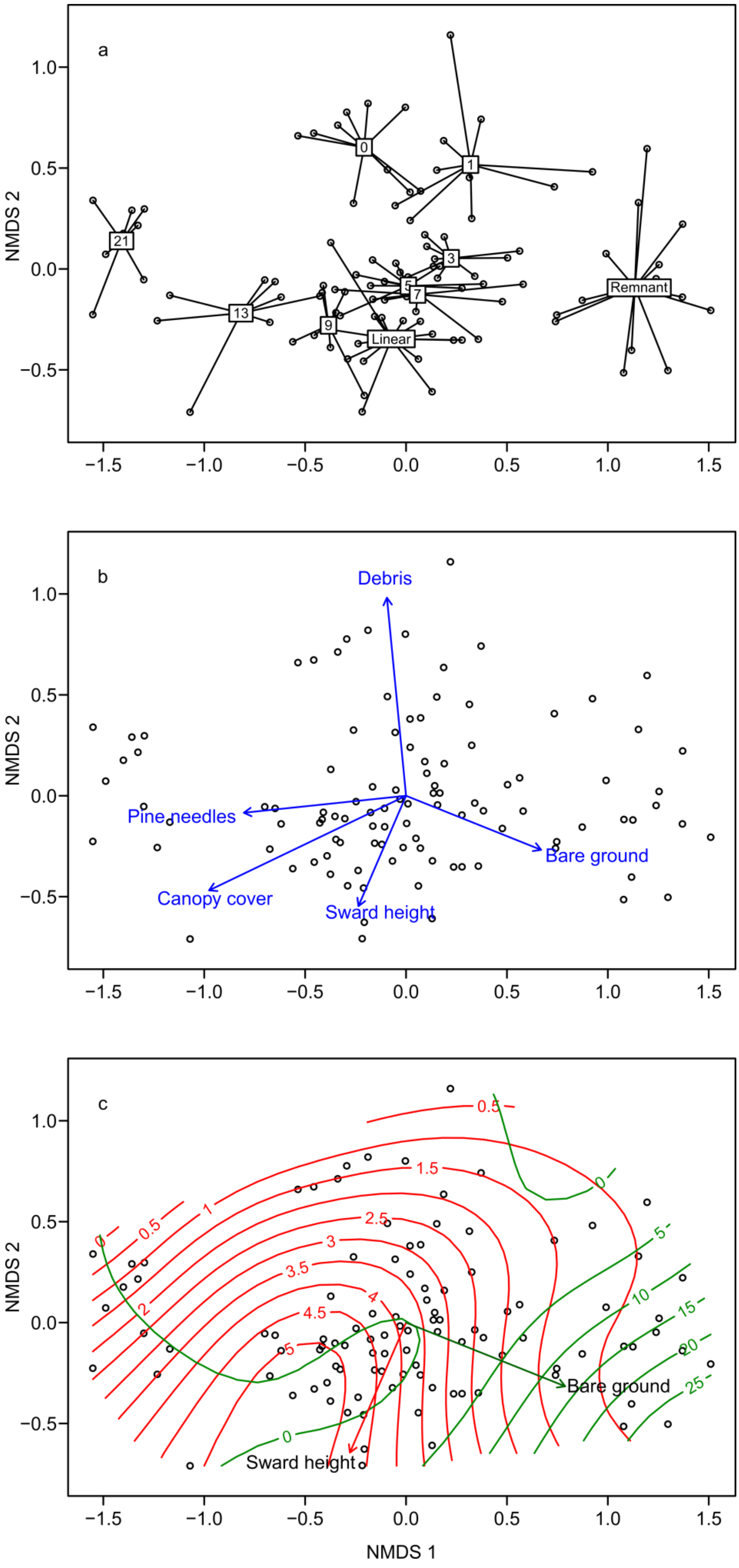

Fig. 5.3. Non-metric multi-dimensional scaling (NMDS) of spider assemblages collected by pitfall trapping (stress = 0.17). Open circles represent sampled transects. a) Displays assemblage separation with centroids denoting sampled landscape element; remnant patches (Remnant), open habitat linear elements (Linear) and numbers indicating planting age of coupes, b) environment variables displayed as vectors, c) surface showing arrangement of sward height and bare ground for sampled transects.

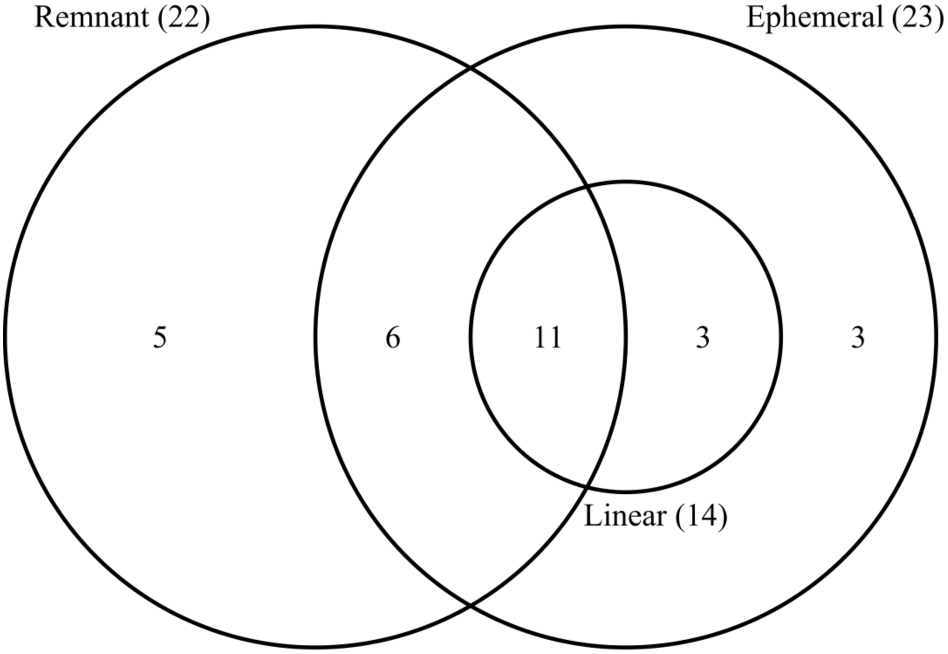

Fig. 5.4. The incidence and overlap of dry-open habitat associated species recorded from remnant patches, ephemeral patches and linear elements. Numbers in parentheses are total species number recorded.

5.3.2 Linked traits

The first two PCoA axes represented 60% of the variation in life history traits among spider species (Fig. 5.5), indicating considerable covariance among different traits. Greater scores on axis one were associated with species that have a larger UK range, wider niche breadth and use a web hunting strategy; while active hunting, large-bodied and dry-open species were negatively associated with axis one. High positive values for axis two represented woodland species and low values were associated with greater UK range, wider niche breadth, generalist habitat association and larger body size. Trait vector positions in the PCoA indicate strong correlation existed between large body size and an active hunting strategy. Not surprisingly, dry-open habitat association and greater aridity scores were strongly correlated, both attributes were also strongly associated with threatened species. Wider niche breadth, greater distribution, generalist habitat association and ballooning proficiency were also correlated.

The PCoA ordination also showed clear clustering of the main families (Fig. 5.5). The small web-spinning Linyphiidae were grouped to the right of the ordination along with the web-spinning Therididae. Both Linyphiidae and Therididae were divided on axis two of the ordination, species in the upper ordination space were shade-tolerant woodland species, whereas, species towards the bottom tended to be generalists. The large, active-hunting Lycosidae, Gnaphosidae and Clubionidae were grouped to the left part of the ordination but were distributed on the second axis, with species in the upper-left associated with dry-open habitats, and those toward the bottom being more generalist species.

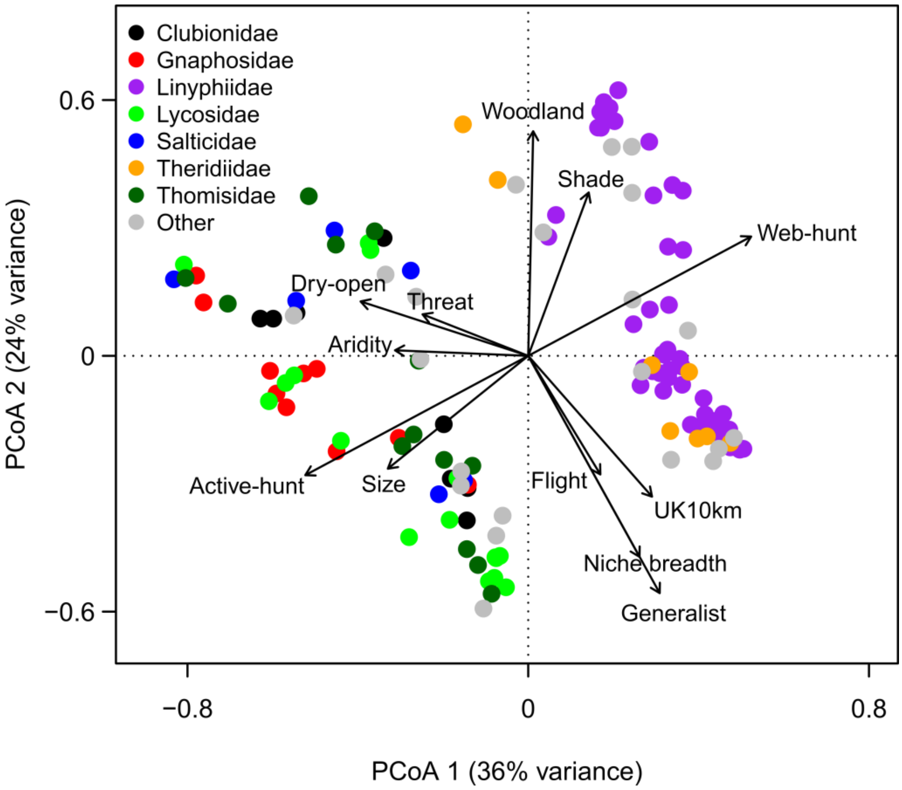

Fig. 5.5. Principal coordinate analysis (PCoA) of the similarity based on 12 traits of 133 spider species (see Table 5.1 for trait details). Trait vectors represent the Spearman correlation, with the length and direction indicating the relationship with PCoA axes.

5.3.3 Species traits

All nine traits tested were significantly linked with at least one landscape element in the fourth-corner analysis (Table 5.2). Mean body size was significantly associated with assemblages found one and three years after planting, when mean body size was greatest, and again in 9, 13 and 21 year old coupes when mean body size was lowest (Fig. 5.6a). The abundance of ballooning individuals was highest in the remnant patches and lowest in the 13 and 21 year old coupes, which corresponded with the significant fourth corner results (Fig. 5.6b). More active-hunting spiders were found in the one and three year old coupes, whereas the abundance of web-spinning spiders was greatest in the three oldest age classes of coupe (Fig. 5.6c). Spiders with the smallest UK range (number of UK 10 km squares occupied) were found in the remnant patches and one and 21 year old coupes (Fig. 5.6d). Species with the largest range were found in the nine year old coupes. The abundance of threatened spiders was greatest in the one and three year old coupes (Fig. 5.6e). The abundance of narrow-niche species was greatest in the remnant patches and the one year old coupes; these sites also had low abundance of medium and wide-niche species (Fig. 5.6f). Linear elements had high abundances of wide-niche species and low abundance of narrow-niche species, as did the five, seven and nine year old coupes. Mean species-based aridity scores were highest in the reference sites and for assemblages from the one and three year old coupes; lowest values were found in the cleared-unplanted, nine, 13 and 21 year old coupes (Fig. 5.6g). As expected, mean species-based shade scores were highest in the oldest coupes and lowest in the remnant patches (Fig. 5.6h). Aridity and shade scores matched the response pattern of habitat association, with the abundance of dry-open habitat species highest in the remnant patches, one, three and five year old coupes, and lowest in the cleared-unplanted, nine and 13 year old coupes (Fig. 5.6i). The abundance of woodland spiders was highest in the nine, 13 and 21 year old coupes.

Table 5.2. Fourth-corner test results in which different landscape elements are related to species traits (see Table 5.1 for trait details). Fourth-corner analysis used permutation Model 1 and 9999 permutations. For each trait the test statistic is given and the test values for each habitat type (*P < 0.05, **P < 0.01)

Trait	Test Statistic	Remnant	Linear	Year 0	Year 1	Year 3	Year 5	Year 7	Year 9	Year 13	Year 21
Size	F	1.8	7.9	3.8	64.0**	38.8**	25.3**	6.8	22.7**	84.6**	81.0**
Flight	Chi	24.2*	0.3	5.1	5.0	1.8	3.4	1.2	5.4	29.3**	52.3**
Active	Chi	2.4	4.6	13.1	40.9**	38.7**	8.8	12.5	24.3**	88.7**	156.1**
UK10km	F	140.4**	20.2	11.3	4.9	3.8	3.7	3.7	25.5**	1.2	5.7
Threat	Chi	4.3	15.8	1.7	83.9**	27.5*	5.6	2.1	10.5	13.2	11.3
Niche	Chi	36.7**	36.1*	7.2	123.5**	11.3	16.2	13.7	20.3	17.3	90.5**
Aridity	F	327.0**	13.4	69.6**	26.3**	65.0**	13.9	0.0	57.9**	128.8**	109.8**
Shade	F	465.2**	0.5	2.0	8.2	15.8	4.8	1.2	47.3**	170.2**	521.7**
Habitat	Chi	385.5**	49.6**	49.9**	50.3**	68.0**	19.7	2.3	73.8**	134.9**	289.4**

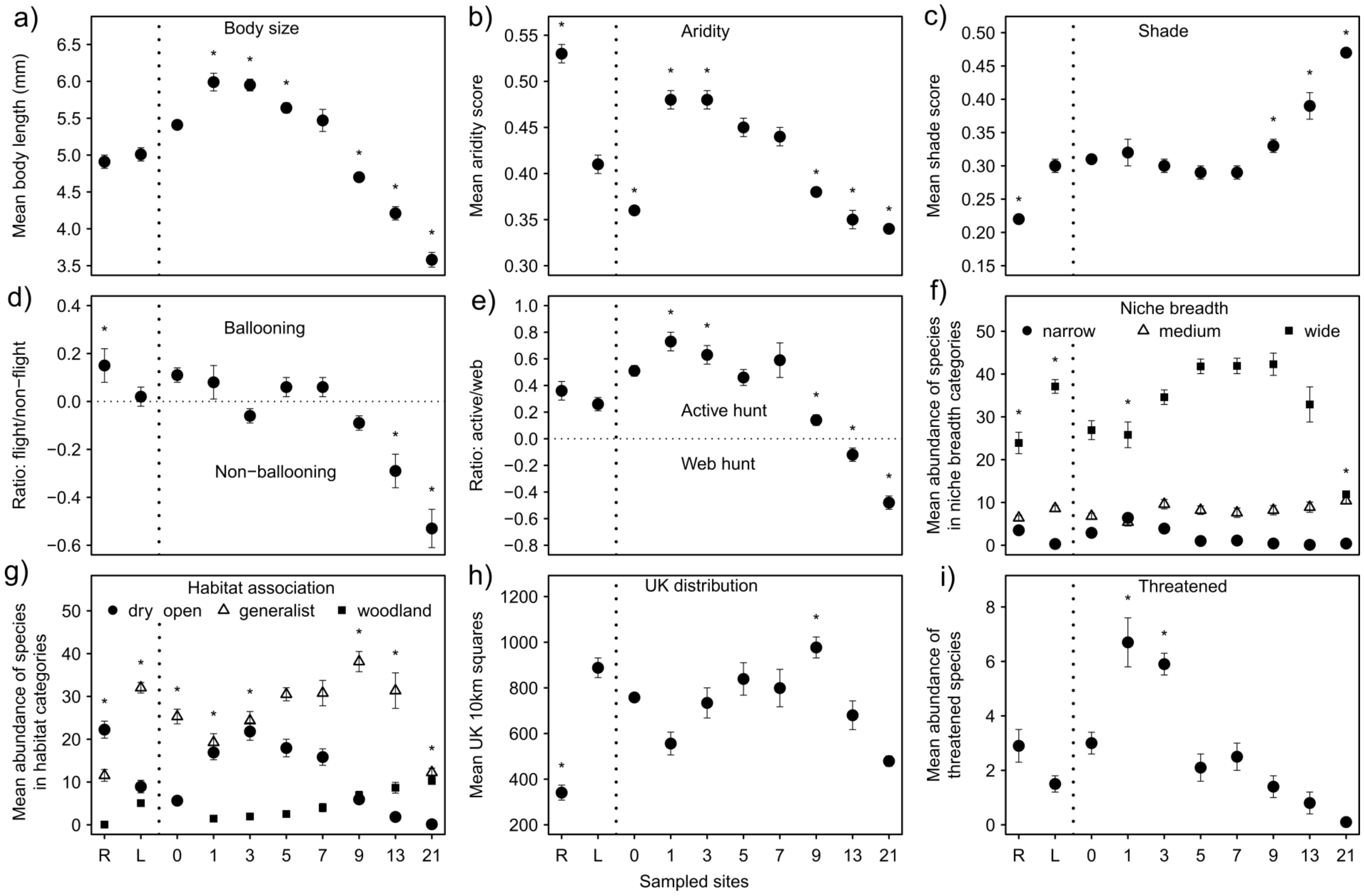

Fig. 5.6. Mean abundance (sqrt) or ratio ± SE of spider traits against each habitat type. Asterisk indicates significant fourth-corner results. Dotted line used to separate remnant and linear habitat from the sampled chronosequence. R=remnant patches, L=linear elements, 0=cleared unplanted, 1=one year old, 3=two year old, 5=five year old, 7=seven year old, 9=nine year old, 13=thirteen year old, 21=twenty one year old coupe.

5.4 Discussion

The epigeic spider assemblages in open-habitat remnant patches were dissimilar to both open-habitat linear elements and ephemeral patches within the plantation forest landscape. Clear-cut harvesting had a major impact on the spider assemblages inhabiting the forested coupes and assemblage composition changed throughout the sampled chronosequence. Although different to reference communities the assemblage composition of young ephemeral patches (one and three years after planting) contained many individuals and species associated with dry-open habitats. In contrast, the linear elements contained a more generalist community, likely due to edge effects enabling vagrants to populate from adjacent habitat (Webb and Hopkins 1984). Traits associated with the young ephemeral patches were mostly large-bodied active hunters, differing from our predictions of small-bodied highly dispersive colonists, and also from findings of other arthropod groups colonising after disturbance (Malmstrom 2012; Mullen et al. 2008)

5.4.1 Contrasting species composition of remnant patches, linear elements and the ephemeral patch chronosequence

The species composition in the chronosequence rapidly changed in the years leading up to canopy closure. The assemblage was relatively species-rich in the cleared-unplanted sites and contained predominantly generalist individuals. Woodland species were also found at this stage and may have persisted through the felling and timber harvesting operations. Niemela et al. (1993) found that the mixing of persisting woodland species with open habitat species elevated species richness following clear-cutting in North American plantations and it is likely that this explains the relatively high species richness in our cleared-unplanted sites. At this unplanted stage a thick cover of needle litter and debris remained from felling operations and this may provide cover for persisting woodland species.

The community composition of one and three year old coupes was most similar to the remnant patches. These young ephemeral patches contained the largest proportion of dry-open habitat individuals compared to other non-remnant patches. At this early stage in the plantation regeneration, woodland and generalist spiders were reduced in the assemblage. We recorded more dry-open habitat species in ephemeral patches (23 species) than in remnant patches (22 species) and in linear elements (14 species); however it should be noted that combined sampling effort was greater for the chronosequence than in remnant patches and linear elements. All dry-open species recorded in linear elements were also recorded in the chronosequence.

Rapid change within nine years after planting changed the composition of the assemblage back to one dominated by generalists, with reductions in abundance of dry-open habitat species and increases in woodland individuals. Mean species-based aridity and shade scores for the landscape elements clearly showed the transition from open to closed habitats. In addition to the loss of open habitat species, the closed canopy 21 year old sites had greatly reduced spider abundance. General patterns of increased species richness directly after clear-felling, followed by a brief dominance of open-habitat species found for spiders in this system, are consistent with both carabids (Mullen et al. 2008; Niemela et al. 1993) and staphylinids (Pohl et al. 2007) in regenerating plantations. Oxbrough et al. (2010) found that after canopy closure spider composition changed little in maturing plantation forest and suggested that canopy cover and ground layer homogeneity were the main drivers of arthropod composition. Therefore, it is expected that the spider composition in coupes older than 21 years will change little in our study system until the canopy re-opens at very mature stages allowing light penetration and the growth of ground layer vegetation.

Shifting species dominance within the chronosequence typified assemblage patterns following regeneration. In older coupes, the damp habitat species *Pirata hygrophilus* was dominant, whereas in the cleared unplanted coupes *P. hygrophilus* was the third most numerous species after two generalist wolf spiders, *Pardosa prativaga* and *Pardosa pullata*. One year after planting, two dry open habitat species, *Xerolycosa nemoralis* and *Pardosa monticola* (also the dominant species in remnant patches) were the most dominant spiders in the assemblage. Spiders colonising in the first summer after felling would have had one year to reproduce and in which time each female *P. monticola* may have produced two cohorts (Bonte and Maelfait 2001), with brood sizes of over 70 spiderlings possible (Bonte et al. 2007). Pedley et al. (2013) surveyed forest trackways in the same system and found that the dominant three species of wolf spiders differed among trackways set in different plantation ages, comprising a gradient related to shade tolerance. Shading due to canopy closure affects ground vegetation and litter layer by reduced structural heterogeneity and decreased temperature that results in changing spider compositions (Ziesche and Roth 2008) and hence shifting species dominance in the current study system.

Linear landscape elements, such as trackways and roadside verges have been advocated as dispersal conduits for open habitat invertebrates (Bertoncelj and Dolman in press; Eversham and Telfer 1994; Vermeulen 1994). Linear trackways in this study were most similar to nine, seven and five year old coupes in the ordination. The assemblages in linear elements had low species-based aridity scores and were dominated by generalist species. The composition also contained a relatively substantial abundance of woodland individuals while also providing habitat for small numbers of dry-open habitat individuals. Species richness in the linear elements was high compared to the remnant patches; we recorded 44% more species in linear elements, although the sampled assemblage only contained three unique species not recorded in remnant or ephemeral patches. Influx of generalist and woodland species from adjacent habitat, in this case thicket coupes, likely resulted in increased species richness for open linear elements. The effect of converging species increasing overall richness at habitat ecotones (the interface of two habitats) is well documented. Webb and Hopkins (1984) found that small fragments of heathland provided greater invertebrate richness due to vagrants from neighbouring habitat. Halme and Niemela (1993) found similar patterns in carabids inhabiting small forest fragments in Finland, with high species richness attributed to the mixture of forest and open habitat species. Driscoll and Weir (2005) found linear strips of Australian mallee habitat were species-rich due to both strip-specialists and species from the matrix. The influence of edge effects at plantation boundaries is well known for spiders (Downie et al. 1996; Kowal and Cartar 2012; Muff et al. 2009) and may partly be explained by increased habitat heterogeneity at border zones, as vegetation structure is an important factor determining habitat suitability for spiders (Bultman and Uetz 1982; Gibson et al. 1992). It is likely that the narrow shape of linear elements increased edge effects and resulted in a composition very different to remnant patches. Therefore, the potential of linear elements bordered by sharply contrasting matrix habitat to functions as dispersal conduits for epigeic spiders is questionable.

As with other studies comparing spiders in forested habitat or ecotones, pitfall trapping was the only sampling method undertaken (Downie et al. 1996; Kowal and Cartar 2012; Larrivee et al. 2008; Muff et al. 2009; Oxbrough et al. 2005). Comparisons between sites did not take account of the aboveground (shrub and arboreal) invertebrate composition and only the ground-active assemblage was assessed. Kowal and Cartar (2012) suggested that the aboveground spider assemblages, especially web spinners, may respond to changes in vegetation structure more than ground-active species due to their affinity with physical vegetation structure in forest ecotones. Our focus was on open habitat species of disturbed habitat and thus catches from pitfall traps represent the ground-active assemblage well (Standen 2000). For studies focusing on forest biodiversity, especially those primarily concerned with species richness, multiple methods would be needed to assess the arboreal and shrub layer composition (Wermelinger et al. 2007), although pitfall trapping will provide comparisons of ground invertebrates.

5.4.2 Species traits of colonised ephemeral patches and permanent linear elements

Aerial dispersal via ballooning was only significantly more prevalent in remnant patches. Non-ballooning was more prevalent in older ephemeral patches, presumably because taller trees will obstruct aerial dispersal and may prevent spiders reaching the ground. The ability to disperse aerially is seen as a key trait for insects colonising unstable habitat (Ribera et al. 2001; Roff 1990). Ballooning spiders are often considered early colonists to newly open habitat, such as after volcanic eruptions (Crawford et al. 1995) and in agricultural fields where they are important predators of crop pests (Nyffeler and Sunderland 2003; Schmidt and Tscharntke 2005a). In addition, ballooning has potential to disperse individuals over vast distances; modelled flight patterns of ballooning Linyphiidae have estimated possible dispersal distances of 30 km per day given suitable weather conditions (Thomas et al. 2003). The lack of ballooning colonists in young ephemeral patches may in part be due to the composition of the surrounding landscape. The majority of the forest cycle is undisturbed habitat; during a 60-80 year growth cycle the disturbance caused by clear-felling, brash removal and ploughing only provides open disturbed habitat until the thicket stage, approximately 6-8% of the growth cycle. In agricultural landscapes, refuge and source habitat is important as regularly disturbed cropland requires recurrent colonisation after ploughing, pesticides or burning (Schmidt et al. 2005; Sunderland and Samu 2000; Thorbek and Bilde 2004). Species richness and density of ballooning spiders is increased with increased amounts of non-crop vegetation in agricultural landscapes (Schmidt and Tscharntke 2005b). In the current study, sampled ephemeral patches were all interior plantation sites and, to colonise from non-forest areas, open-habitat ballooners would need to passively float at heights in excess of 20m on favourable thermals over mature forested patches before currents dropped them into restock patches. In addition, the wind tunnel effect in forestry trackways, thought to increase wind-throw in straight and wide forest rides (Warren and Fuller 1993), may further impede passive flight from linear elements into young ephemeral patches. Given the large percentage of forested area, there is a high chance of landing in unsuitable habitat, emphasising the significance of landscape composition in influencing animal abundance.

The majority of the land outside the forest is intensive agriculture and hence frequently and repeatedly disturbed. The higher proportion of ballooners in remnant patches may reflect increased ballooning in spiders exploiting unoccupied habitat in the croplands surrounding remnant sites. Furthermore, flight was associated with generalist species in the PCoA, and generalist ballooning spiders may be more widespread in open habitat such as grasslands, scrub and mixed agricultural landscapes compared to forested habitat. To thoroughly assess the colonisation by ballooners, appropriate aerial trapping would be needed, such as suspended sticky traps or aerial suction traps (Greenstone et al. 1985; Thorbek et al. 2002).

Terrestrial movement alone may be sufficient for ground-active spiders to disperse locally (Samu et al. 2003). Wide ranges in the distances of terrestrial movements have been recorded for Lycosid spiders in open habitat (2-50m per day) (Bonte et al. 2003a; Bonte et al. 2007; Kiss and Samu 2000; Waiboonya 2010). Potential terrestrial dispersal distances of several hundred metres over a lifetime may be possible for ground-active spiders. It is likely that large active species will have greater dispersal ability than smaller active spiders. Body size and an active hunting strategy were positively correlated traits and were mostly associated with Lycosidae, Gnaphosidae and Thomisdae in this study. Both mean body size and active hunting were greater in one and three years old coupes. The presence of a few large, active dry-open habitat individuals in linear elements may allow rapid colonisation of cleared-unplanted and young ephemeral patches via terrestrial movements. This, along with a reduction in small, web-hunting woodland spiders, dominant in closed canopy forest, would explain the increase in mean body size and active hunting strategy in the assemblages of young coupes after clear-felling.

Mean body size steadily decreased in the chronosequence after peaking in the first year. While dispersal ability is commonly cited as one of the most important traits determining species response to disturbance, body size in relation the r-K continuum (see Reznick et al. 2002 for historical review of concepts) is also commonly thought to explain assemblage response (Chiu and Kuo 2012; Statzner and Beche 2010). The theory states that in stable habitat, K-selected species (larger size, slower growth rates) dominate, whereas in unstable habitat r-reselected species (small size, faster growth rates and greater fecundity) dominate. Measures of fecundity were not available for species in this study so it is unknown if differences in body size at this scale would relate directly to productivity. There is evidence that some larger-bodied spider species may take more than a year to become mature and that variation exists within species (Hendrickx and Maelfait 2003); in contrast, some Linyphiidae can reproduce in less a year (Wise 1976). Trade-offs between greater body size and number of offspring per reproductive event may not be straightforward, as some spiders invest in parental care and some small species produce only one or two eggs (Edwards and Edwards 2006). However, our results for body size contrast with the expected response from the r-K continuum and from our predictions based on increased carabids body size in response to increased canopy cover in plantation regeneration and decreasing management intensity (Mullen et al. 2008; Ribera et al. 2001). If size is related to productivity then this suggests that colonisation ability via dispersal of large active species alone, or in conjunction with productivity, is more important in filtering spider composition in the forestry system. However, covariance among traits confounded simple interpretations based on dispersal traits alone. Body size was positively associated with species-based aridity in the PCoA of traits. Entling et al. (2010) reported that spider body size increased in warm, dry environments due to increased desiccation of small species, which have a weaker cuticle and greater surface to volume ratio. The peak of body size in one year old coupes with a decline after year three was mirrored in a similar peak and decline of species-based aridity within the chronosequence. This is consistent with a response to habitat structure and microclimate, well known determinants of spider composition (Buchholz 2010; Entling et al. 2007; Muff et al. 2009; Ziesche and Roth 2008), as an alternative explanation to dispersal.

Spiders are particularly vulnerable to mechanical operations in crop fields (Thorbek and Bilde 2004) and grassland (Bell et al. 2001); the same is expected with forestry operations, where clear-felling, brash removal and ploughing will initially remove spiders through direct mortality. Following intensive management, recently clear-felled forest compartments comprised low vegetation complexity and bare substrate. Specialist narrow-niche communities, capable of tolerating the barren conditions, colonised these stressful environments. Narrow-niche spiders were found predominately in the remnant sites and one year old coupes, where the highest species-based aridity scores were recorded, and along with the 21 year old sites, had the lowest average species range scores. Specialist spiders in the study region are predominantly xerophilic species of open sand habitats (Dolman et al. 2012). Young ephemeral patches contained more threatened individuals than any other landscape element, likely due to the specialised regional assemblage containing many xerophilic species.

Twenty eight specialist species associated with dry-open habitat were recorded in this study. Of the five dry-open species that were only recorded in remnant patches, three had national conservation designations and four are known ballooners. These five species were also small bodied, ranging from 1.55 mm to 3.50 mm. The three dry-open habitat species recorded only in ephemeral patches were all large active hunting species, ranging from 4.25 mm to 8.50 mm in body size. Passive ballooning in fragmented landscapes may represent a high risk strategy for narrow-niche species. Bonte et al. (2003b) showed that specialist xerophilic spiders in fragmented sand dune habitat were less likely to balloon than habitat generalists. Although it is possible that rare heath specialists were missed from the trapping in forest sites due to their scarcity in the landscape, the trait trends in young ephemeral patches (large-bodied active hunters) highlights that terrestrial dispersal is important for heathland species.

5.4.3 Conclusions

Habitat fragmentation theory predicts that some species will be restricted by poor dispersal ability to remnant habitat, while those with good dispersal ability can take advantage of ephemeral and connecting habitat elements. In the plantation system studied, we found that the majority of dry-open habitat spiders were able to colonise ephemeral patches within five years. The assemblages in the ephemeral patches were predominately large active hunters likely to colonise by terrestrial movements, rather than small bodied ballooning species for which the prevailing landscape composition may overwhelm dispersal from small scattered patches of remnant habitat. Rapid change in spider composition following tree growth and ground vegetation succession modified the assemblages to one dominated by generalist species until canopy closure. Our results agree with others that find high overall species richness through the plantation cycle (Butterfield et al. 1995; Mullen et al. 2008; Niemela et al. 1993; Oxbrough et al. 2005), but our focus highlights how fleeting the opportunity early in the plantation cycle is for open habitat specialists.

Linear elements supported a much reduced proportion of the open heathland community. Assemblages in linear elements were mostly generalists and the composition was heavily influenced by edge effects. Linear elements may still provide movement pathways for small numbers of dry-open spiders enabling quick colonisation of ephemeral patches but this is unlikely for species requiring high quality open habitat. For epigeic spider assemblages, linear connecting elements may require increased habitat quality to combat detrimental edge effects of matrix habitat.

In contrast to our predictions, ephemeral stepping stones were not dominated by small-bodied ballooning generalists. Apart from a few heathland restricted species, most of the reference community colonised the young ephemeral patches suggesting they are not dispersal limited and are not restricted to permanent remnants. Species that were restricted were small species capable of flight, which is in contrast to predictions and highlights that passive ballooning may well be a poor strategy in highly fragmented habitat. Ephemeral stepping stones may provide suitable connectivity for all but the most restricted species.

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Chapter 6

Concluding remarks

6.1 Key findings

Habitat fragmentation in highly modernised landscapes requires innovative conservation techniques to enhance network connectivity. This can be supported through greater understanding of species filtering in response to environmental and habitat attributes, using trait-based analysis. This thesis has shown that by altering management a plantation forest landscape could usefully incorporate the requirements of many specialist open habitat species. Analysis of species-based traits explained the filtering of assemblages by experimental disturbance and landscape elements, including linear corridors and ephemeral stepping stones.

Trackways in the plantation forest were found to support a portion of the specialist heathland spider community (Chapter 2). However, assemblages were unlike those of reference heath sites (Chapter 2), with trackway assemblages becoming increasingly dominated by woodland and generalist species as tree crops matured and shade increased. Trackway widening was recommended to provide unshaded trackway habitat for the length of the rotation, enhancing trackway suitability and thus connectivity for open habitat spiders. Similar recommendations have been suggested to encourage open habitat Lepidoptera, Coleoptera and Heteroptera that also use unshaded plantation forest trackways (Greatorex-Davies et al. 1994; Warren 1985).

To create sparse vegetation structures and bare substrate suitable for regionally important species (Dolman et al. 2012), physical disturbance in forestry trackways was suggested in order to break up dense grass swards that dominant trackways, which are conventionally managed by annual cutting. Experimental treatments were established in recognition of this need for alternative management of early successional biodiversity. Using information gained from the analyses presented in Chapter 2, experimental treatments were established within plantation forest trackways to test the optimum level of disturbance to enhance specialist heathland assemblages. Specialist carabid and vascular plant species increased in abundance and richness with increasing disturbance intensity, whereas spider assemblages were left depauperate. Spider assemblages are known to be susceptible to mechanical operations due to direct mortality (Bell et al. 2001; Thorbek and Bilde 2004), which may explain this response. It is likely that intense disturbance treatments, such as turf stripping, will benefit specialist species and provide long lasting effects to vegetation structure; this will reduce the need for rapid reapplication, which would negatively affect spider assemblages. Current trackway management (annual mowing) was found to be too benign and did not produce suitable vegetation structure for heathland biodiversity.

Species-trait analysis explained the filtering of multi-taxa assemblages by the experimental gradient of disturbance. Reduced size and increased dispersal ability was predicted as a response to disturbance. Small bodied, herbivorous, macropterous carabids and small statured, annual plants with wind dispersed seed increased in abundance with increasing disturbance intensity. Results of trait filtering for carabids and plants agree with patterns of response reported for other disturbance regimes (McIntyre et al. 1995; Ribera et al. 2001), adding to the generality of predictive statements for these two taxa. For spiders, mean body size increased, as did the abundance of active hunters, but there was no evidence to indicate aerial dispersal (via ballooning) was affecting species response to disturbance intensity. While carabids and vascular plants responded in predictable ways, spider assemblages differed, illustrating that generalised predictions of response may not be possible across diverse taxa, even when the traits examined are linked to ecological processes, such as dispersal. For carabids and plants, increasing disturbance intensity enhanced the abundance of nationally threatened species, highlighting the benefit of disturbance management for the conservation of heathland species.

Community analysis, combined with trait-based analysis, highlighted the relative connectivity value of linear strips and ephemeral stepping stones for open habitat spiders. Spider assemblages in linear habitat contain relatively few heathland species, whereas relatively large ephemeral stepping stones provided suitable habitat for the majority of the heathland assemblage. Furthermore, colonisation of ephemeral patches was not by small, aerial-dispersing generalist species but by large, active-hunting species associated with dry-open habitat. Many of the dry-open habitat spiders are also species found in fragmented coastal dunes, where specialist spiders have been reported to exhibit reduced ballooning propensity compared to non-specialists (Bonte et al. 2003), as measured by tiptoe behaviour (initial flight preparation). For epigeic spiders, dispersal via terrestrial movements may be more important for colonisation in fragmented habitat than passive aerial dispersal. This builds on the knowledge gained in previous chapters illustrating that the majority of the heathland spider assemblages require suitable habitat size and quality but are not dispersal limited within the study region.

6.2 Trait plasticity

Phenotypic plasticity is expressed through changes in behaviour, physiology, morphology, growth, life history and demography due to biotic (Raimondi et al. 2000; Werner and Peacor 2003) and abiotic interactions (Ellers and Driessen 2011; Stillwell and Fox 2005). Such interactions have been described in many systems and have the potential to change community dynamics and ecosystem functions (Miner et al. 2005).

Wing polymorphism in insects is a well-studied phenotype that is believed to be associated with habitat persistence (Roff and Fairbairn 1991; Zera and Denno 1997) and has the potential to alter a species response to environmental stress. For example, Roesel's bush cricket, *Metrioptera roeselii*, has both short- and long-winged forms of which only those with long wings are capable of flight. In the UK, this species has expanded over the last 40-50 years from mainly coastal sites to numerous inland habitats, where the recently established populations exhibit increased frequencies of long-winged forms (Thomas et al. 2001). Similar dispersal plasticity has been observation in some carabid species which are able to absorb and regenerate flight muscles in changeable landscapes (Kotze et al. 2011). Both short- and long winged carabid morphs are also possible. For example, *Pterostichus melanarius*, a species to introduced Canada, displayed long-winged morphs that colonise new areas, after which short-winged forms appeared as the population becomes established (Niemela and Spence 1991). In spiders, the propensity to disperse aerially via ballooning is also believed to be plastic, dependant on habitat stability (Entling et al. 2011) and food availability (Bonte et al. 2008; Mestre and Bonte 2012). Plasticity involving dispersal related traits are also likely to have trade-offs with other traits such as those relating to breeding success (Zera and Denno 1997).

Where species-specific information is available, such as wing dimorphism, then this should be incorporated into trait analyses. Caution should be used where there is the possibility for plasticity to cause sampled populations to express different proficiencies compared to non-sampled populations. For example, fecundity measures taken from populations at the edge of their range may be very different to interior populations (Angert and Schemske 2005). The fine scale observations and experiments required to study phenotypic plasticity means that only relatively simple systems, and interactions between only several species within a system, are generally studied. For community studies on invertebrates where hundreds of species are examined, it is unlikely that detailed species-specific information and inter-species interactions are available to incorporate plasticity for the sampled assemblage. Therefore, as with all ecological studies, caution is needed if data are to be extrapolated to other habitats and systems. If plasticity in physiological traits varied the functional responses in this thesis, trait shifts may not be applicable to other habitats. However, where species-rich community data are used to examine trait patterns within a taxonomic group, such effects of plasticity may be moderated over the entire assemblage in comparison to trait effects on species poor guilds.

6.3 Evaluation of analytical methods

Chapters 2 and 3 of the thesis used ordination and habitat associations to interpret assemblage patterns. These methods have been used extensively to analyse species-rich invertebrate and plant communities. Although this was successful in describing community structure in the plantation landscape it does not provide information on why, or how, communities are arranged. To overcome this and allow generalised statements based on the functional traits of species, trait-based analysis was applied in Chapters 4 and 5. Several methods can be used to explore the link between functional traits and environmental stressors. Both fourth-corner and RLQ procedures (Doledec et al. 1996; Legendre et al. 1997) test this link directly as opposed to the emergent group techniques (Lavorel et al. 1997) which uses indirect methods to select sets of species with similar traits. Emergent group methods call for species to be placed in discrete sets; however, traits often overlap which makes drawing distinctions between groups problematic.

The two direct methods use a three data matrix design to test the link between species traits (matrix Q) and environmental variables (matrix R) via a set of species occurrence across sites (matrix L). RLQ is a multivariate analysis that relies primarily on ordination and interpretation (Barbaro and van Halder 2009; Hausner et al. 2003). Separate ordinations are first conducted for the R, L and Q matrices with the resulting scores being used for weightings linking matrices in the RLQ analysis. RLQ is a doubly constrained ordination; the variance explained can be compared to the original unconstrained ordination of matrix L which would indicate how much variation is associated with the environment and traits data. Permutation tests are used to assess the significance of relationships between the environmental variables and species traits. Thus RLQ analysis explains to what extent observed species incidence among sites arises from the link between a multivariate ordination of traits and the multivariate ordination of site environmental attributes. It does not provide understanding of which traits relate to which environmental variables. In contrast, the fourth-corner procedure tests the significance of the strength of links between all combinations of species-traits and environmental attributes. It tests whether the observed degree of linkage among traits and environmental attributes differs significantly from that expected by chance, given the observed structure of species incidence or abundances, and environment measures across sites using randomisation and permutation. Extension of fourth-corner analysis from solely species presence/absence data (Legendre et al. 1997) now incorporates species abundance data (Dray and Legendre 2008). The fourth-corner approach has recently been tested against both emergent groups (Aubin et al. 2009) and RLQ (Brind'Amour et al. 2011) and found to be a robust tool for detecting trait relationships with environmental factors. Outputs indicate the paired comparison of each individual trait character to individual variables, in this case a single gradient of disturbance intensity.

The fourth-corner procedure uses a generalised statistic S_{RLQ} that is equal to either Pearson correlation coefficient (when both the trait Q and environment R variables are quantitative), χ^2 (when both are qualitative) or the correlation ratio η^2 when data are mixed (Dray and Legendre 2008). As the reference distribution of the fourth-corner statistic is unknown, null models are used to examine whether the strength of the observed link differs from that which may be attributed to chance, given the observed structure of the data matrices (Dray and Legendre 2008).

Five different randomisation permutation models are available to generate a null distribution of the fourth-corner statistic; appropriate model choice depends on the hypothesis being tested (Dray and Legendre 2008). We applied Model 1, that randomises presence-absence of individual species relative to site characteristics (permuting within each column of matrix L); but does not re-sample the species-trait relationship (matrix Q) or the environment-site relationship (matrix R). This model is appropriate to test the null hypothesis (that R is not linked to Q) when examining links between the fixed traits of the species and fixed characteristics of the sites, mediated by the observed data of table L (Dray and Legendre 2008). This fits our premise of examining trait responses from an *a priori* manipulated environmental gradient, designed to affect species composition from a single habitat type and hence species pool; rather than measuring environmental parameters when sampling species (Model 2: permutating site vectors, or entire rows within L; equivalent to permuting rows of table R). Furthermore, because our trait data were fixed (i.e. obtained from the literature and not from direct observations) it was not necessary to resample to control for error in species traits, as is required when these have been measured from a sample of individuals during the study (Model 4: permuting species vectors, or entire columns within L, equivalent to permuting rows of table Q)(Dray and Legendre 2008). Using simulated data, Dray and Legendre (2008) showed that the power of the fourth-corner procedure to find trait/environment patterns increases with both the number of sites and species tested.

Fourth-corner analysis successfully identified significant trait links in relation to the experimental disturbance gradient in Chapter 4 and landscape attributes (linear, remnant and ephemeral) in Chapter 5. However, fourth-corner procedures suffer from several issues, including the inability to incorporate trait linkages and failure to control for spatial autocorrelation and phylogenetic patterns (Dray and Legendre 2008). The use of principal coordinate analysis (PCoA) based on trait-species data tables has provided some understanding of linked traits and phylogenetic connections in the thesis, but to date no single analytical methods resolves these collective issues. The PCoA showed covariance among traits such that functional interpretations of responses to disturbance or landscape configuration are not straightforward.

In addition, trait-based analysis is only suitable for those species where sufficient morphological, behavioural and ecological trait information is available. The effectiveness of analysis to provide generalisation is reduced when traits are assumed from related taxa. Only those species that had sufficient trait data were used in the thesis to avoid inferring data from related species. For many species and geographical regions where taxonomical knowledge is scarce, there may be insufficient information to carry out trait-based analyses. Conversely, where autoecology and life-histories of species assemblages are well characterised, use of trait-based analyses rather than community classification permits functional predictions relevant to other, less well characterised regions.

The functional mechanisms filtering species were identified for a range of diverse taxa, permitting general statements regarding responses to environmental stress. However, for spiders, improvements in the coding and measurement of dispersal and fecundity traits, particularly the relative capabilities of both terrestrial and aerial dispersal, would strengthen predictive ability and functional understanding for this group.

6.4 Conservation implications and recommendations

6.4.1 Landscape connectivity

Most often connectivity is thought of as habitat corridors linking two core patches (Simberloff et al. 1992) and large amounts of literature support the use of corridors for enhancing dispersal (Beier and Noss 1998; Gilbert-Norton et al. 2010). The corridor literature is often focussed on whether the movement of animals through continuous linear strips will benefit isolated populations. Much less importance has been placed on the benefit of alternative types of connecting elements that differ in configuration and function, such as stepping stones and habitat mosaics, or the percolation of breeding population over generations. The importance of restoring network connectivity has been embedded in strategic policy and planning (Lawton et al. 2010; Mitchell et al. 2007; Natural England 2011), however, there is little agreement as to what this involves for different species and how practitioners should implement mitigation actions on the ground.

The results of this thesis conclude that connectivity enhancement of early successional networks requires a variety of management techniques and habitat configurations to incorporate specialist early successional assemblages. For dry-open habitat spiders, narrow linear strips represent low suitability due to strong edge effect increasing vagrant species from the matrix. However, larger open patches representing connectivity in the form of stepping stones support a substantial amount of the heathland spider assemblage. Although the colonisation method (either ballooning or cursorial movements) in ephemeral patches was not directly tested, it is unlikely that the specialist heathland spiders colonised fragmented patches by ballooning. This is supported by findings from spider assemblages in fragmented dune habitat (Bonte et al. 2004; Bonte et al. 2003) and by the functional traits of colonists, which indicate large spiders associated with an active hunting strategy, and not small ballooning species, were able to colonise. If dry-open habitat spiders did colonise by cursorial movements it is likely they did so via dispersal along trackways, even though sampling of trackways indicates low abundance of heath associated species. However, small abundance in linear trackway assemblages may still deliver colonists to large ephemeral patches where rapid reproduction within the first year could account for the dominance of dry-open habitat species in ephemeral recently replanted forestry patches.

6.4.2 Plantation forest

Conservation activities within plantation landscapes should target species of regional importance and where plantations are on non-forest habitat then open-habitat species should be considered. Conversely, where natural forest was replaced then conservation efforts should be focused on species typical of old growth forest, such as mixed planting, selective logging, leaving dead wood on forest floors and maintaining some mature coupes (Brockerhoff et al. 2008; Fuller et al. 2008; Niemela 1997). Providing open habitat for early successional species is often more problematic as it requires regular disturbance to recharge successional processes.

The vast majority of the plantation landscape is continuous closed canopy forest, and, for any one coupe, open ephemeral habitats are available for less than five years within the 60-80 year growth cycle. To benefit species dispersal, landscape heterogeneity should be increased, as has been recommended for agricultural systems (Benton et al. 2003). The results for the thesis show that without significant widening, trackways will suffer from substantial edge effects and may not support a heathland spider assemblage even with improved vegetation structures. In contrast, specialist carabids and vascular plants appear to suffer less from edge effects and are likely to benefit from any level of soil disturbance, with the greatest benefit coming from turf removal.

For spiders, stepping stones of ephemeral habitat may be sufficient to provide connectivity in the plantation landscape for most heathland species. This corresponds with results for heathland carabids, which are also able to colonise young ephemeral coupes (Bertoncelj 2010). Conversely, Eycott (2005) found that many open habitat plants were dispersal limited and required permanent open space, such as trackways, to persist within the plantation landscape. For maximum benefit, disturbance management combined with trackway widening would provide increased early successional habitat for heathland biodiversity, while also increasing network connectivity for dispersal limited species.

Recommendations from the thesis have already fed into forestry management plans aimed at enhancing open habitat with Thetford Forest. Trackway widening has commenced and there are plans for greater disturbance in permanent open habitat. It is likely that the forest landscape provides a better opportunity to re-establish connectivity for lowland heath than the highly modified agricultural landscape, where problems of eutrophication and spray drift confound the quality of linear elements. Plantation forest soils on former heathland area remain relatively nutrient poor and can retain a viable heathland seed bank for many years (Pywell et al. 2002; Walker et al. 2004). With the addition of regular disturbance, open habitat within lowland plantation forests could add significant enhancements to biological networks.

6.4.3 Lowland heath

Disturbance is a fundamental management tool in the maintenance and restoration of heathland, grassland and dune biodiversity (Buchholz 2010; Dolman and Sutherland 1994; Schirmel et al. 2011). Creating the appropriate vegetation structure for lowland heath species is critical. Although the management treatments in this thesis were conducted on open plantation soils, the rapid benefit gained and variable responses of contrasting grass-heath taxa are relevant to management of degraded heathland habitat.

Agricultural runoff and increased atmospheric nitrogen deposition accelerates successional processes, which results in the loss of characteristic heathland vegetation (Barker et al. 2004; Hardtle et al. 2007). Traditional management techniques of dry heaths, such as mowing and grazing, may need to be augmented with high intensity disturbance, such as turf removal, to compensate for atmospheric nitrogen deposition (Hardtle et al. 2006). Creating heavily disturbed patches within reserves will benefit many early successional species that require bare substrate and sparse vegetation, while untreated patches will provide refugia for species vulnerable to mechanical disturbance. Although this thesis did not analyse soil nutrient levels, the increase in specialist heath carabids and vascular plants associated with physically disturbed, low-nutrient soils, highlights the rapid benefits of high intensity disturbance management for lowland heath.

The Breckland heaths have long been acknowledged as having a unique assemblage and supporting species not found elsewhere in the UK (Dolman et al. 2010; Duffey et al. 1957; Watt 1971). However, recent data on the status of invertebrate populations on Breckland heaths are rare and there have been no recent systematic surveys. The invertebrate surveys of remnant Breckland heath in this thesis are therefore an important resource and have been reported to land managers. For most of these sites the important fauna remain, but suitable vegetation structure is often restricted to small heavily rabbit-grazed or mechanically disturbed areas. It is likely that a decline in rabbit numbers and/or increased nutrient levels will result in an increased demand for physical management of sites if the characteristic xerophilic and arenicolous fauna are to be conserved.

6.5 Future research

The assessment of corridor use for open habitat invertebrates has predominately been based on behavioural studies of aerial dispersing species (Haddad 1999; Haddad and Baum 1999; Haddad and Tewksbury 2005; Ockinger and Smith 2008; Sutcliffe and Thomas 1996). Movement data for ground-active heathland species would help parameterise dispersal models that may better represent other heathland fauna. During this study, mark-recapture observations were attempted in order to determine if there was enhanced dispersal in linear trackways as opposed to primary open heath habitat (Waiboonya 2010). However, weather conditions during replicate observations confounded results; heavy rain during one observation period saturated vegetation and effectively reduced the suitable linear environment from approximately 20 m to 3-4 m. The narrowing of suitable linear habitat funnelled movements and consequently increasing step lengths compared to observations in dry weather. The collection of further data could be used to parameterise random walk or simulation models, which would assist in developing landscape networks facilitating metapopulation dynamics.

The comparison of the relative benefit of different types of connectivity for different species will improve generalisations for other taxa and ecosystems. Pitfall trap sampling for spiders within the different forestry landscape elements resulted in the capture of carabids. The identification and analyses of these samples could provide valuable and potentially contrasting results. Exploring functional trait responses for other diverse taxonomic groups would also lead to greater predictive power.

As pressure grows to further intensify crop production and expand urban areas in already fragmented landscapes, conservation will need to rapidly predict outcomes of alternative management solutions for species preservation. Experimental testing of management options, followed by robust sampling programs, taxonomic identification, analyses and reporting is a long process. New techniques such as biomonitoring with DNA barcoding (Hajibabaei et al. 2011; Yu et al. 2012) are being developed and will shorten the reaction time for conservation decisions. Currently, samples from the thesis are being used to validate these techniques. Spatially explicit dispersal models that can simulate population changes for different management options will also considerably cut down decision time (Jongejans et al. 2008). Plantation forest systems that offer replicated blocks of habitat incorporating corridors, stepping stones and contrasting matrix habitat provide an excellent opportunity to test these techniques.

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