Spatial Dynamics of Ground Beetle (Coleoptera: Carabidae) Assemblage in a Forest and Open Habitat Mosaic Landscape

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Abstract

This thesis explores the relative importance of within-patch habitat quality, the temporal persistence and spatial connectivity of habitat patches, for heathland ground beetle assemblages in a forested and open habitat landscape mosaic of Breckland, Eastern England. Comparison of the carabid fauna of two distinct landscape elements: remnants of once extensive lowland heathland and the pine plantations of Thetford Forest managed by rotational clear-felling, showed the high value of the forest landscape for carabid species restricted to grassland, heathland and sandy habitats (GHS). Within the forest landscape, temporal changes in carabid community in planted stands are determined by management and succession, with conditions suitable for GHS species persisting for just seven years after replanting. For persistence of GHS species within Thetford Forest permanent open space, representing approximately ten percent of the area, is essential. Habitat quality, particularly greater cover of bare sand, lower sward and shallow soil litter, were more important predictors of patch suitability for GHS species than patch size. Suitability of linear trackway elements within the plantation was determined by the surrounding matrix, with high GHS species richness in trackways surrounded by younger plantations (<20 years) and very few GHS in those surrounded by older plantations. Behaviour of the model arenicolous species *Harpalus rufipalpis* differed between these two types of trackways, with greater levels of activity and more leakage in poor quality trackways surrounded by older trees; thus only a subset of trackway elements will serve as corridors for conduit. Despite the interrupted nature of this network, colonisation of newly created clear-fells by GHS species was not affected by their isolation, at least at the current scale of management. Almost all GHS species recorded in permanent open habitats were shown to successfully colonise ephemeral open patches: colonists did not represent a subset of GHS species and were not filtered by dispersal ability.

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Chapter 1: Introduction

Population dynamics in heterogeneous landscapes

Since ecologists became aware of spatial heterogeneity its effects on population dynamics and interactions have been the focus of population studies (Turner 1989). Two main aspects of spatial heterogeneity of landscapes have been put forward: composition (differences among landscapes, in the amount or proportions of specific habitat types of interest) and configuration (differences among landscapes, in the structural organisation or the spatial pattern of specific habitat types of interest) (Dunning *et al.* 1992). Spatial complexity has mostly been considered in its simplest form, in terms of the spatial pattern of patches set in a background matrix (Wiens 1995).

Considering spatial composition, configuration and patch-matrix organisation of landscapes, and the relative importance of the birth / death ratio compared to the immigration / emigration ratio for population persistence, a range of types of populations have been described (Hanski 1997, Thomas & Kunin 1999, Fahrig & Nuttle 2005). For example, populations have been described as a “spatially extended population” (Freckleton & Watkinson 2002) or a “patchy population” (Harrison 1991) with high degree of movement among local populations, as a “metapopulation” (Hanski 1991, Hanski 1998) with intermediate movement relative to patch spacing that is sufficient to allow local population reinforcement or recolonisation of vacant patches, but not sufficient to synchronise the dynamics of sub-populations, and as a “regional ensemble” or “remnant population” (Freckleton & Watkinson 2002) comprising separate unconnected local populations.

Another division of population types giving more weight to habitat quality and birth / death ratio are “sources”, “sinks” and “pseudo-sinks” as suggested by Pulliam (1988) and Watkinson & Sutherland (1995). Such classification of populations has received much attention as defining type of population could give clear implications for optimal management for its persistence. However, according to Thomas & Kunnin (1999) such categorisation is illusory as any one species does not belong to any of these types throughout its range but rather each local population within spatially structured population could be assigned to any of the above mentioned types.

Despite such warnings, the metapopulations have been by far the most influential in population and conservation studies (Hanski 1999). The concept of a metapopulation developed from the island biogeography theory (McArthur & Wilson 1967) and is based on population persistence across a group of unstable local populations that exist in a balance between local extinctions and the establishment of new population at unoccupied sites (Hanski 1998). For a metapopulation to persist, the replacement condition should be met, which implies that a smaller network of local populations comprising fewer patches is necessarily more threatened than metapopulations comprising large and well connected networks (Hanski 1998). This conclusion has led to a great increase in the importance given to landscape configuration and habitat connectivity in conservation biology, such that connectivity has been described as the third measure of landscape structure (in addition to landscape composition and configuration) (Taylor *et al.* 1993). In metapopulations therefore the regional processes (immigration / emigration) are more important than local dynamics (birth /death rates) and empirical studies confirmed such dynamics in the pool frog in ponds along the Baltic coast of Sweden (Sjogren-Gulve 1991) and the Glanville Fritillary in Southwest Finland (Hanski *et al.* 1994). However, Harrison (1994) found that few species fit the classic metapopulation model and Baguette's review (2004) shows classic metapopulations are likely to be found either on the edge of species distribution, in species with very small local populations or species which are declining in the study area.

By focusing on immigration and emigration, the metapopulation paradigm neglects the processes within habitat patches (Thomas *et al.* 2001) which are mostly connected with habitat quality and its potential to reduce or increase growth rates or carrying capacities (Davies *et al.* 2001). In fact the "habitat quality approach" to population ecology developed in parallel to the metapopulation approach (Armstrong 2005) and only recent theory suggests that far from being alternative, these processes are linked (Wiegand *et al.* 1999, Thomas *et al.* 2001). Empirical studies comparing effects of within-patch habitat quality, patch size and patch isolation showed that it is at least as important to maintain high habitat quality as it is to maintain connected populations within a landscape (Dennis & Eales 1997, Davies *et al.* 2001, Thomas *et al.* 2001, Bauerfeind *et al.* 2009). Thus metapopulation theory has usefully introduced the processes on the landscape scale into conservation planning, but it should not be used as a substitute for management of within-patch habitat quality (Harrison 1994, Harrison & Bruna 1999, Margules & Pressey 2000).

In addition to heterogeneity on spatial scale, habitats are subject to changes in time due to disturbance or succession. In a simulation experiment Fahrig (1992) found the effect of temporal variability (patch longevity) far outweighed the effect of spatial variability (isolation) of habitat in determining the population stability. Fahrig concluded that in very ephemeral habitats, spatial variability may be unimportant. Similarly, Matlack & Monde (2004) found that prediction of decline of slow moving species in landscapes with high frequency of habitat destruction cannot be predicted by static description of habitat connectivity. Analysing data from two metapopulations of the butterfly *Plebeju argus*, Hodgson and colleagues (2009) found that an increase in spatial connectivity of habitat patches in dynamic habitat (with high temporal variability) did not increase patch occupancy. Therefore observations of habitat of different ages should be used to determine the scale of temporal variability of habitat of interest within studied landscape to be able to assess its importance for population persistence.

Closely connected with temporal changes and succession is also formation of species assemblages. As the metapopulation theory only relates to populations of one species it does not include effects of relationships among species. To broaden the metapopulation theory to the level of community the concept of metacommunity as a set of local communities that are linked by dispersal of multiple potentially interacting species evolved was developed (Wilson 1992). Several models of metacommunity functioning have been proposed which focus on different processes determining distribution and abundance of species (reviewed in Leibold etal. (2004)). Two main and opposing interpretations of the role of biological interactions were developed. According to the niche theory each species occupies only those sites to which it is well adapted and from which it is able to exclude competitors (Vandermeer 1972). The second interpretation is the neutral theory which most species belonging to the same guild are able to grow at most sites and the community composition is determined largely by the accidents of dispersal (Caswell 1976, Bell 2001).

Studies of effects of habitat fragmentation on biodiversity are a good example of how intertwined and often inseparable are effects on populations of landscape composition, configuration and within-patch quality. Habitat fragmentation was defined by Wilcove and colleagues (Wilcove *et al.* 1986) as "process during which a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original". There are three separate processes included in this definition of which the first is habitat loss (change in landscape composition) which has been proven to have large and consistently negative effects on the original biodiversity (Tilman *et al.* 1994, Pimm *et al.* 1995, Sih *et al.* 2000, Dirzo & Raven 2003). The second process is change in spatial configuration of habitat (also called fragmentation *per se*) which results in an increase in the number of patches, a decrease in patch sizes and increase in isolation of patches, without any change in the overall amount of habitat (Haila 2002, Tscharntke *et al.* 2002, Fahrig 2003, Ewers & Didham 2006). Fragmentation *per se* when separated from habitat loss, has much weaker effects on biodiversity that are as likely to be positive as negative (Harrison & Bruna 1999, Fahrig 2003). The third process are the so called "edge effects", through which landscape composition affects the quality of remaining habitat patches, either physically (e.g. microclimate at woodland edges) or through effects on species interactions as seen with increased activity by generalist predators intruding from the matrix (Saunders *et al.* 1991, Collinge 1996, Fagan *et al.* 1999, Ries *et al.* 2004). These processes affect biodiversity in different ways and because researchers often explore effects of only one or two of them, the results of empirical studies of fragmentation effects on natural populations are widely contrasting (Fahrig 2003, Ewers & Didham 2006). Fragmentation is expected to give rise to multiple, even contradictory responses, depending on the species characteristics (dispersal ability, habitat specialisation, trophic level), geographic regions and type of environment. Therefore the effects of habitat fragmentation should be considered in specific places at specific times for specific species, at relevant temporal and spatial scales (Haila 2002, Ewers & Didham 2006).

Influenced mostly by biogeography and metapopulation theory, several authors suggest that the way to mitigate negative effects of fragmentation is to improve connectivity within the landscape, for which implementation of corridors and stepping stones have been suggested (Beier & Noss 1998, Rosenberg *et al.* 1999). In this sense, corridors are defined as "linear landscape elements that provide for movement between habitat patches, but not necessarily reproduction" (Rosenberg *et al.* 1999). This facilitation of movement would reduce probability of extinction of spatially structured populations by decreasing inbreeding depression and increasing fitness of local populations (Brown & Kodric-Brown 1977, Palstra & Ruzzante 2008), or by increasing recolonisation of empty habitat patches (Hanski 1991, Hanski 1994, Hanski 1998). The term corridor has been used in the literature also to describe elements which would facilitate access to resources within an individual's home range (Nielsen *et al.* 2004), for seasonal migrations (Mazerolle 2005) and/or movement across barriers such as highways (Braden *et al.* 2008) but these functions will not be considered here. Stepping stones are patches of remnant vegetation within the matrix that were suggested to increase connectivity by reducing the distance that individuals have to travel at once through the matrix (Forman 1995, Uezu *et al.* 2008), but these have received far less attention in the literature than corridors.

The use of corridors in conservation has been disputed from the beginning (Hobbs 1992, Mann & Plummer 1995) with reviews that are either strongly supportive (Noss 1987, Beier & Noss 1998), or strongly skeptical (Simberloff & Cox 1987, Simberloff *et al.* 1992), pointing out potential negative effects of corridors such as transmission of diseases, fires or introduced predators. Additional potentially negative effect of "outbreeding depression" as a decrease in the fitness of progeny resulting from outcrosses between genetically differentiated populations (Pusey & Wolf 1996) could be a consequence of increased connectivity by corridors. Results of empirical studies of the use of corridors are also contradictory. Measure from which movement rates among patches of habitat could be inferred were positively affected by corridors for butterflies (Sutcliffe & Thomas 1996, Haddad 1999, Haddad *et al.* 2003, Varkonyi *et al.* 2003, Haddad & Tewksbury 2005), moths (Monkkonen & Mutanen 2003), crickets (Berggren *et al.* 2002), flies (Fried *et al.* 2005), small mammals (Bennett 1990, Coffman *et al.* 2001, Mech & Hallett 2001, Haddad *et al.* 2003), birds (Haas 1995), bears (Dixon *et al.* 2006) and plants (Tewksbury *et al.* 2002, Damschen *et al.* 2006). However, movement rates among habitat patches were not affected by the presence of corridors for soil fauna (Rantalainen *et al.* 2004), for community of over 300 open-habitat insect species (Collinge 2000), for grassland butterflies (Ockinger & Smith 2008), for some forest interior insect species (Hill 1995), two species of rodents (Horskins *et al.* 2006) and forest birds (Hannon & Schmiegelow 2002).

As Chetkiewicz and colleagues (2006) suggest in their recent review the important impediment to the effective use of corridor is the gap between the composition and spatial configuration of habitats (pattern) and the ways animals actually move within landscapes (process). Similarly such a dichotomy was described as structural *versus* functional connectivity of landscapes (Taylor *et al.* 2006). The designation of corridors is often based on patterns of remaining habitat that appear (to human observers) to be connected without evaluation of their use by the target species. Behavioural studies of movement have shown that general dispersal patterns are affected by edge-specific behaviour (Ovaskainen 2004), by gender and environmental heterogeneity (Rudd & McEvoy 1996), by different micro-habitat selection depending on habitat type (Bowne *et al.* 1999) and by differences in movement among individuals (Morales & Ellner 2002). Chetkiewicz and colleagues (2006) conclude that even with more attention given to processes of habitat selection and movement of organisms, we are unlikely to be able to produce general prescriptions for corridor designs for multiple species, locations and scales.

Furthermore, the debate about corridors has had a narrow focus on corridors as continuous linkages on a small local scale among local populations, where corridors should enable continuous dispersal movements. For example, the length of corridors in studies of their effects on invertebrate dispersal were 5m (Berggren *et al.* 2002), 10m (Collinge 2000), 150m (Tewksbury *et al.* 2002, Fried *et al.* 2005, Haddad & Tewksbury 2005), between 64 and 384m (Haddad 1999, Haddad *et al.* 2003) and up to 500m (Sutcliffe & Thomas 1996). Most of the above described studies on the use of corridors also examine their use by one or two species and very few consider assemblage or communities. Bennett (2003) suggests the scope should be broadened to the issue of management of linkages at the landscape or regional scale with arrangement of habitats that would ensure ecological connectivity for species, communities and ecological processes.

However, even though functional connectivity of the landscape is important, we cannot assume it will in itself guarantee long tem persistence of species populations (Taylor *et al.* 2006). Biodiversity studies of population persistence should explore effects of several ecological processes and not assume connectivity and spatial configuration of habitat to be of primary importance (Fahrig & Nuttle 2005).

In conservation of mosaic anthropogenic landscapes in Europe, where traditional farming practices created semi-natural early successional habitats, considering the relative importance of spatial arrangement, temporal dynamics and habitat quality for persistence of plant and animal populations is essential. The habitat type which is the focus of this thesis, is lowland heathland, a semi-natural habitat characterized by dwarf shrubs growing on relatively nutrient poor, acidic soils (UK Biodiversity Action Plan 2005). Heathland was created by human management such as burning, cutting and rabbit and sheep grazing and regular disturbance is essential for persistence of this habitat (Price 2003). Due to land-use changes such as conversion of grazing land to arable land, agriculture intensification or abandonment, areas once dominated with heathland are increasingly more fragmented. Changes in management of remaining heathland such as reduction in grazing and disturbance and eutrophication have lead to changes in vegetation structure (Dolman & Sutherland 1992) and habitat suitability of these areas for typical invertebrate species (Telfer & Eversham 1996). This thesis examines effects of fragmentation, temporal dynamics and differences in size and habitat quality of heathland remnants on assemblage of ground beetles.

Ground beetles as study organisms

Ground beetles (Coleoptera: Carabidae) are one of the most diverse and well studied insect families (Holland 2002). Several characteristics make this group very useful in the study of landscape ecology.

Different species of ground beetles have diverse habitat requirements ranging from eurytopic to stenotopic species (Holland 2002). Habitat choice is so specific that they can be relied upon to provide consistent habitat related information and used to characterize habitats (Lovei & Sunderland 1996) even to the extent that fossil beetle remains could be used for interpreting the past climate conditions (Ponel *et al.* 2003). The larval stage in ground beetles is the most sensitive for environmental factors due to poor mobility and weak chitinisation which makes them sensitive to desiccation, starvation, parasites and diseases (Lovei & Sunderland 1996). Therefore soil moisture is likely to be the most influential of all their environmental requirements (Holland 2002).

Species in this family also vary according to their dispersal ability, which can be roughly estimated from their ability to fly (de Vries *et al.* 1996). Species can be macropterous (winged) or brachipterous (wingless), with some species being dimorphic (some individuals are macropterous and some brachipterous). Flight ability varies little between the sexes (Roff 1994). Distances that carabids can walk are limited. Some of the larger species can possibly walk for more than 1000m (den Boer 1970), but for most species a distance of 500m is very exceptional (Baars 1979). In his experiment with radioactive marked beetles Baars (1979) showed movement of two ground beetle species (*Poecilus versicolor* and *Calathus melanocephalus*) was a combination of alternating random walk and directed movement, thus resulting in only small displacement in a random direction within a 24h period. He estimated that *Poecilus versicolor* can move on average 160m in a season. Vermeulen (1994) estimated *Pterostichus lepidus* and *Harpalus servus* can move on average 50-150m in a season.

Ground beetles can be easily and cost-effectively collected using pitfall traps, which are the most commonly used field method (Spence & Niemela 1994). Even though pitfall traps have some disadvantages as the catch is a function of both density of the population and activity of individuals (Greenslade 1964), pitfall trapping has been shown to reliably reflect variation in carabid assemblages and their habitat associations (Dufrene & Legendre 1997, Lin *et al.* 2005). However, despite these biases, when comparing carabid assemblage collected in different habitat types within Thetford Forest using pitfall traps and hand searching, Lin and colleagues (2005) found both methods gave a quantitatively similar ordination of community composition.

Characteristics mentioned above make Carabids highly suitable for studies of environmental changes associated with land-use and succession and for studies of changes in habitat configuration. Carabid assemblages have been shown to respond quickly to forest felling (Butterfield 1997, Koivula & Niemela 2003, Pihlaja *et al.* 2006), land-use change from arable to grassland (Purtauf *et al.* 2004), use of different crops in arable fields (Kinnunen & Tiainen 1999) and the intensity of management in gradient from intensive arable fields to upland grassland and moorland (Ribera *et al.* 2001). In a study of 32 heathland remnants in the Netherlands, ranging in size from <0.4 to >1600ha, de Vries (1996) found carabid assemblages were sensitive to patch size with smaller patches supporting fewer heathland specialised species. Comparing number and abundance of species in 22 patches of farmland of similar size that were divided into two categories according to the amount of farmland within different distance buffers, Kinnunen and colleagues (1996) found isolated patches to have fewer species. The effect of habitat quality of patches however was not considered in this study. A comparison of the number of forest specialist carabid species in 15 sites of different size, shape, altitude and distance from the continuous “mainland” deciduous forest in Hungary, showed smaller and more isolated patches to have fewer forest specialist species (Magura *et al.* 2001).

Overall study of decline of species in Europe within the last 50-100 years (Kotze & O'Hara 2003) showed that large bodied carabid populations have declined more than smaller ones, possibly because of their lower reproductive output and lower powers of dispersal. Habitat specialists have also decreased more than habitat generalist species.

Thesis outline

This survey was conducted in the Breckland region, in eastern England (at 52° 27’N, 0° 42’E) which was historically dominated by heathland of which approximately 7,000ha now remain (Lambley 1990). Since 1920 approximately 20,000ha of abandoned fields and heaths have been converted to pine plantation, now called Thetford Forest. Plantation is managed by rotational clear-felling and replanting of stands, providing a heavily replicated series of patches at different successional stages connected by a linear network of trackways. The forest also includes open habitats, potentially suitable for heathland species. Open habitats within the plantation vary in size, isolation and longevity with some of them being permanent and some ephemeral. Such heterogeneous mosaic landscape is an ideal model system for studies of temporal and spatial dynamics of assemblages and effects of habitat quality and spatial organisation of habitat on local assemblages.

The initial data chapter (Chapter two) is an overview and comparison of the ground beetle fauna present in larger and continuous protected heaths and smaller and more fragmented mosaic of open spaces and open disturbed habitats within Thetford Forest plantations. Characteristics of species associated with grassland, heathland and sandy habitats (GHS) such as body size and wing presence are compared between the two landscape elements with the aim to explore potential dispersal limitations of species restricted to protected heaths. The analysis then focuses on carabid assemblage composition of permanent open spaces and of different growth stages within conifer plantation, to determine the scale of temporal variability of habitats and their relative value for species associated with open habitats within forested mosaic landscape.

Chapter three focuses on carabid assemblage in permanent open spaces within the plantation, comparing narrow linear open habitat along the network of trackways ("corridors") and larger open patches embedded within forest stands ("stepping stones"). Relative importance of habitat quality (vegetation structure and height, soil characteristic), patch longevity and patch size for the presence of GHS species is tested. The age of plantations surrounding trackways was expected to affect conditions within trackways and consequently carabid assemblage. The effectiveness of current management of trackways for conservation of heathland species is examined.

In the fourth data chapter, early colonisation of newly created clear-felled stands and recently replanted or "restocked" stands by carabids absent from mature forest stands is explored. Following paradigm of island biogeography theory, smaller and more isolated patches would host fewer species due to reduced probability of colonisation. Clear-felled and young restocked stands were selected to eliminate the effects of differences among patches in habitat quality, as within these areas environmental conditions are homogenised by spraying of vegetation and ploughing.

The last data chapter examines behaviour of an arenicolous ground beetle *Harpalus rufipalpis* in trackways surrounded by two types of matrix: younger plantations with approximately 7m tall trees and mature plantations with approximately 14m tall trees. The differences in environmental conditions in these two types of trackways was expected to effect direction and speed of dispersal of individuals with individuals travelling faster in areas with unfavourable conditions (trackways surrounded by mature forest). Behaviour was studies using mark-release-recapture method in a grid of pitfall traps.

The final chapter summarises and synthesises the results of all data chapters, examines weaknesses and unanswered questions and gives recommendations for the use of these results in management of afforested landscapes for the conservation of heathland species.

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Chapter 2: Landscape scale carabid assemblage composition; species functional groups and habitat associations among linear ephemeral and source areas

Abstract

Within the area of Breckland in Eastern England conservation interests focus on lowland heathland, a high maintenance secondary habitat that has been reduced greatly in the last 200 years throughout Western Europe due to landuse changes. Remnants of heathland habitats now occur as protected heaths but also as patches of open space within pine plantations of Thetford Forest. Thirty seven heathland, grassland and sandy habitat associated carabid species (hereafter referred to as ‘GHS’ species) are still found in Breckland of which more than half are also present within the forest landscape. The absence of the remaining 40 percent of GHS species from the forest landscape could not be explained by a lack of dispersal ability (winged versus unwinged) or size of the species. Within the forest landscape very few GHS species are found within the closed canopy plantations but they are present in both permanent and ephemeral open areas. Most of the GHS species recorded from permanent open areas were also found in newly created clear-fells and young replanted stands therefore connectivity does not seem to present a problem in this landscape, under current management. However, the carabid community structure in ephemeral open areas is different from that in permanent open areas, mostly due to very pronounced dominance of the two most abundant species *Harpalus rufipalpis* and *Nebria salina*.

Introduction

Lowland heathland is a man made cultural landscape in Western Europe where secondary succession is manipulated by traditional agricultural practises no longer applied these days. It encompasses a range of early successional and shade intolerant plant communities which are typically dominated by ericaceous dwarf shrubs and are restricted to acidic, mineral based and infertile soils below 300m altitude (Webb 1986, Gimmingham 1992). Heathlands support distinctive insect fauna of which some species are specialised for utilising plant species characteristic of heaths and other species require physical conditions provided by heathlands that are not found in the surrounding landscape (Webb 1986).

In the region of Breckland in Eastern England habitats have been altered by human activities for at least 5000 years most pronounced of which was intensive sheep and rabbit grazing and various forms of physical disturbance including chalk and flint mining, episodic arable cultivation, turf and litter cutting (Dolman & Sutherland 1992). This, combined with the semi-continental climate and sandy soils characteristic of the region, resulted in a unique mixture of lowland heathland, steppe, coastal dune and Mediterranean communities (Watt 1971, Dolman & Sutherland 1991). The Breckland region has undergone significant changes in land use within the last 200 years, the most pronounced of which is the reduction in the area of lowland heathland estimated at about 76% (from 29000ha in 1900 to 7000ha currently) (Lambley 1990). In the 1920s more than 20 000ha previously covered with heathland and abandoned fields were planted with trees (now called Thetford Forest). Following the severe reduction of rabbit populations by myxomatosis in the 1950s, most remaining heathland became densely vegetated (Dolman & Sutherland 1992).

Similar reduction in the area of heathland occurred in other countries in Western Europe (Gimmingham 1992, Webb 1998), therefore heathland is now considered a rare and threatened habitat that is protected by EC Habitats Directive. Within the UK, the Biodiversity Action Plan (BAP) requires the remaining lowland heathland to be maintained in favourable condition and a further 6000 ha of this habitat to be recreated by 2005 (Biodiversity Steering Group 1995). Numerous threatened or vulnerable invertebrate species associated with, or dependent on, lowland heathland and lowland acidic grassland habitats are priority species included within the UK Biodiversity Action Plan (UK Biodiversity Partnership 2007).

Within the Breckland region heathland today exists as protected remnants of heaths (Sites of Special scientific interest) but also as open areas within Thetford Forest plantations which support populations of heathland-associated species (Lin *et al.* 2007). A comparison of presence and absence of heathland associated species between these two components of Breckland will give important information about the conservation value of Thetford Forest for heathland species. As dispersal ability of ground beetle species can roughly be estimated by its ability to fly (in other words the presence or absence of wings) (de Vries *et al.* 1996) a comparison of characteristics (such as body size and presence of wings) for species living in heathland remnants in the wider landscape, and those also recorded within the plantation can be used to estimate the importance of connectivity for persistence of heathland species in the landscape.

Thetford Forest is managed by clear-felling which creates a mosaic of different successional phases. High importance of temporal dynamics in comparison with spatial arrangement of habitat for patchy populations has been shown in several modelling studies (Fahrig 1992, Matlack & Monde 2004, Hodgson *et al.* 2009) therefore it is important to first explore the temporal dynamics within the forest landscape and determine which successional stages are suitable for heathland species and which heathland species manage to colonise them. In addition, I explore the carabid community of permanent open areas within the forest landscape especially in comparison with ephemeral open areas, to determine the relative roles of these different types of open habitat patches for the persistence of populations of heathland species within the landscape.

Methods

STUDY AREA

I identified 25 remaining heathland sites within Breckland of which 20 are designated as Sites of Special Scientific Interest with area between 13 and 4678ha (average 389ha ± 1022 SD). Thetford Forest is divided into 12 management units or blocks (Hemami *et al.* 2005, Eycott *et al.* 2006) (Figure 2. 1). Management by clear-felling and replanting of large even-aged stands creates distinct successional stages, which were defined in previous studies (Ratcliffe & Mayle 1992, Hemami *et al.* 2004) and were used in present study (Table 2. 1). Due to the annual rotational pattern of management, there is continuous production of new patches of recently created open habitat, which then develop into habitat unsuitable for open-ground species as the tree crop ages. Thus these patches provide an ephemeral window of opportunity for open habitat fauna. In addition to these ephemeral and short lived open habitat patches, there are also two types of permanent open habitats: a network of linear trackways and larger unplanted patches with an average area 7.7ha ± 10.2 SD (hereafter referred to as open patches). Throughout, I refer to these differing landscape elements as ephemeral and permanent open habitat.

Table 2. 1; Successional stages used in present study, following Ratcliffe & Mayle (1992) and Hemami and colleagues (2004). In the first summer season after being ploughed and replanted in winter, restocks are zero years old.

Stage	Age of trees	Grouping
Felled-unplanted	No trees, area not ploughed	Ephemeral open areas
Restocks	0-5 years	
Pre-thicket	6-10 years	Closed canopy
Thicket	11-20 years	
Pole	21-30 years	
Pre-fell	>30 years	

Originally the forest was planted in a regular grid of polygonal compartments divided by a network of linear trackways. Following forestry guidelines for diversification of landscape (UK Forestry Standard 2004) replanting units are now of irregular shape that straddle the original compartment boundaries and form groups of even-aged trees, which represented individual sampling sites in the present study (hereafter referred to as patches). The original network of trackways of different width (approx. 5-50m) and surface structure (sand, gravel) remains. The middle part of each trackway (track) is used by forestry vehicles and the verges of equal width on each side of the track are occasionally swiped to prevent tree growth. In selected trackways approximately 100m long strips including the track and the verges represented individual sampling sites in the present study.

Each selected patch or trackway represented an individual sampling site. In all sampling sites the basic unit of replication was a transect. Survey was conducted in Lynford, Croxton, High Lodge and Elveden blocks (Figure 2. 1) of which the latter two form a large core area of the forest abutting a large heathland remnant with deep sandy soil over large part of it. Within these blocks the comparison of different landscape elements was spatially very well replicated, with a total of 109 sites sampled.

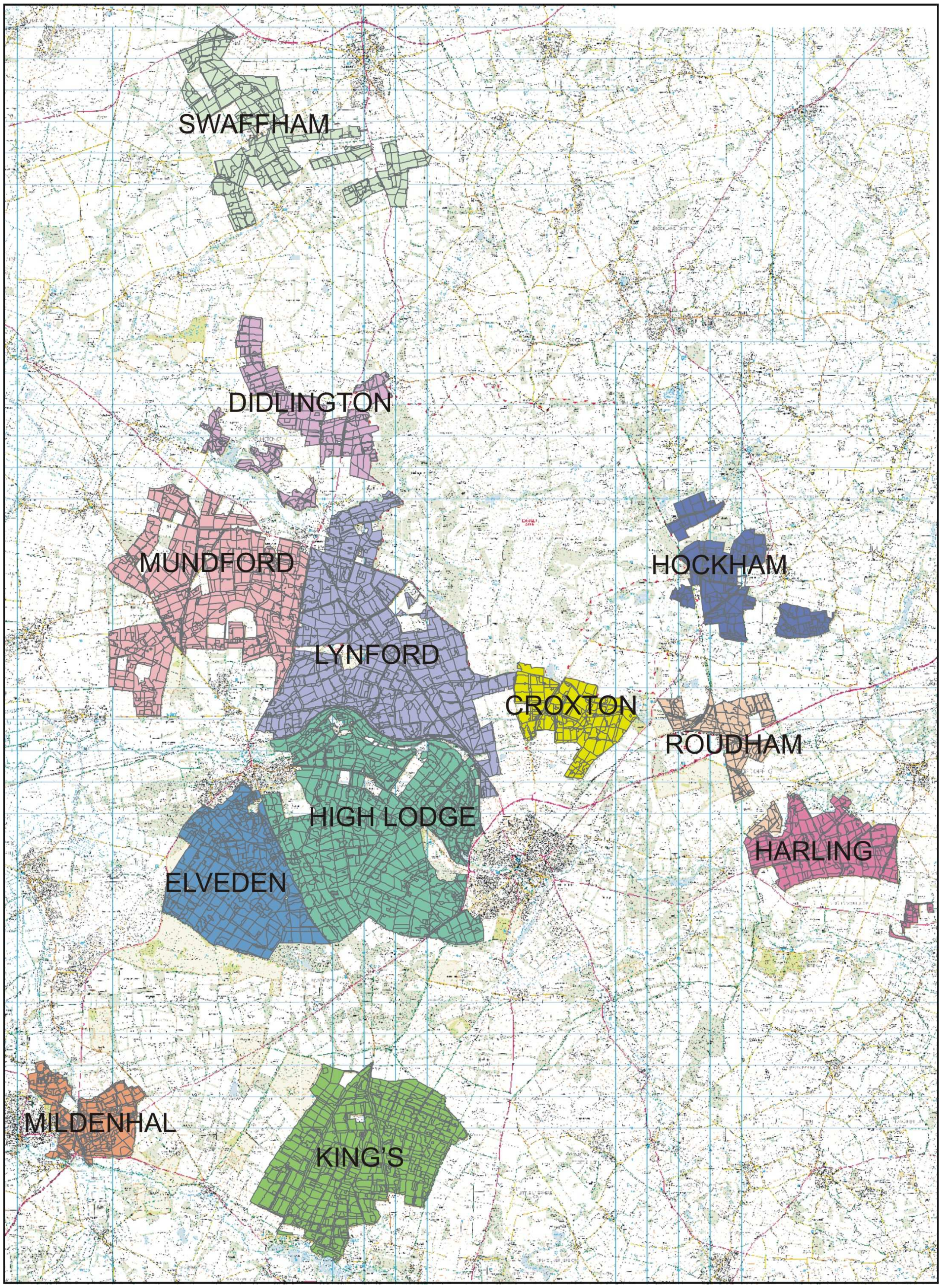

Figure 2. 1; Twelve management blocks of Thetford Forest located within the region of Breckland.

GROUND BEETLE FAUNA

For information about presence of ground beetles species in remaining heaths and arable land within Breckland I used a published review of carabid fauna in Breckland (Lin *et al.* 2007). From this review I also used information about presence of carabid species within Thetford Forest caught in previous studies conducted in this area. To further explore the forest component of Breckland an extensive sampling of ground beetles using pitfall traps was conducted in two main periods: 2001-2002 (Lin 2005) and 2005-2006 (present study). A total of 109 different sites were sampled of which 42 were sampled in more than one year resulting in 151 site/year combinations with 365 sampled transects (Table 2. 2).

In 2001 0-4 year old restocked patches were sampled and resampled in 2002 with one zero year restock added. Two prefell patches were sampled in 2001 of which one was resampled in 2002 and four other prefell patches were added. Trackways and open patches were sampled in 2005 and all open patches were resampled in 2006. Three replicates of each of: pre-thicket, thicket and pole stages, were sampled in 2006. Felled-unplanted patches were sampled in 2002 and 2005; zero year old restocks were sampled in all four years.

In both study periods two transects (apart from those exceptions stated in Table 2. 2) each comprising five pitfall traps were set up in each of the sampled sites. Pitfall traps were open for five consequent days on each of the four sampling occasions during spring/summer months (mid May, mid June, end of July and end of August). In trackways one transect was set in the middle of the track and one in the verge (1-2m away from the track, depending on the width of the verge). There were three trackways where it was not possible to sample the track due to extremely hard surface so only the verge was sampled. Pitfall traps were transparent plastic cups, 7.5cm deep and 6.5 cm in diameter filled with approximately 50ml of ethylene glycol as killing and preserving chemical. Traps in transect were approximately 30m apart to ensure their independence (Digweed *et al.* 1995) and on each sampling occasion captures from each of the five pitfalls in transect were pooled prior to identification.

Table 2. 2; Number of sampled sites of eight different habitat types within Thetford Forest in different sampling years and unique number of sampling sites for each habitat. Numbers in superscripts indicate the number of transects per site where the number of transects was different from two.

	2001	2002	2005	2006	Number of unique locations
Open patches	/	/	12^3	11^3; 1^6	12
Trackways	/	/	36; 3^1	/	39
Felled-unplanted	/	5	12^3	/	17
Restocks (0-5 years)	16; 1^4; 4^5	22	4^3	7^3; 1^6	26
Pre-thicket (6-10 years)	/	/	/	3	3
Thicket (11-20 years)	/	/	/	3	3
Pole (21-30 years)	/	/	/	3	3
Pre-fell (>30 years)	2^1	5	/	/	6

Carabids collected were identified to species level according to Lindroth (1974), while nomenclature followed Luff (2007). Information about habitat preferences, wing morphology and species size were derived from Luff (2007). Text descriptions and key words in the literature were summarised and interpreted as described in Table 2. 3. Habitat preference classification of species followed a hierarchical order of habitats from woodland, open woodland, arable, moorland, grassland, heathland and sandy habitats with species that can occur in all habitats classified as eurytopic. For example species that can be found in grassland and arable would be classified as arable since this habitat is higher on the hierarchical scale. Grassland, heathland and sandy habitats are the lowest on the scale, thus carabid species classified as GHS species are exclusive and restricted to these habitats (Table 2. 3). For information about species distribution within the UK (number of $10km^2$ occupied by the species) I downloaded information about squares from the National Biodiversity Network web page (National Biodiversity Network 2008). Biodiversity conservation status of nationally scarce species was given to all Red Data Book (RDB), Biodiversity Action Plan (BAP) and to all notable A (hereafter Na: known from 30 or fewer $10km^2$ within the UK) or notable B (hereafter Nb: recorded from 31 to 100 of the 1698 $10km^2$ within the UK) species (Hyman & Parsons 1992). All species found in 2001-2002 and 2005-2006 survey of Thetford Forest and their characteristics are given in Appendix 2. A.

Table 2. 3; Habitat preference and wing morphology groups used in the present study and their descriptions as found in the literature.

Habitat preference group	**Description in the literature**
Eurytopic (E)	Species described as living in most habitats.
Woodland (W)	Species associated with woodland and possibly other habitats hierarchically lower than woodland.
Open woodland (OW)	Species associated with open woodland or semi-open habitats but not woodland. Possibly also found in habitats hierarchically lower than open woodland.
Arable (A)	Species associated with arable land and gardens but not found in woodland or open-woodland. Possibly also found in habitats hierarchically lower than arable, including heathland or gravel pits etc.
Moorland (M)	Species associated with moorland, upland grassland and upland heaths but not included in any of the previous three categories. Possibly also found in habitats hierarchically lower than moorland.
Dry grassland, heathland and sandy habitats (GHS)	Species exclusively associated with one or more of: lowland dry grassland (G), heathland (H), sand dunes, gravel pits or sandy habitats (S) and not included in any of the previous categories.
Wing morphology group	**Description in the literature**
MA = macropterous	Winged.
BR = brachipterous	Wingless or flightless.
DI = dimorphic	Dimorphic; some individuals are winged, some are not.
MA+	Dimorphic, but mostly winged.
BR+	Dimorphic, but mostly wingless.
(MA)	Probably winged.
(BR)	Probably wingless or flightless.

DATA ANALYSIS

For overall comparison of presence of carabid species in remaining heaths, arable land and forest landscape within Breckland compiled data from the review of Lin and colleagues (2007) and the present study were used. Out of 89 species recorded from Thetford Forest eight species (*Asaphidion curtum* (GHS), *Paradromius linearis* (A), *Calathus micropterus* (W), *Carabus arvensis* (M), *Carabus glabratus* (M), *Laistus rufomarginatus* (W), *Pterostichus oblongopunctatus* (W) and *Carabus violaceus* (E)) were only found in previous studies conducted in this area (Collier 1995, Doberski & Lyle 1997, Humphrey *et al.* 1999, English Nature 2003) as reviewed by Lin and colleagues (2007), but were not found in the present systematic survey and were therefore omitted from further detailed analysis of incidence and assemblage composition among forest landscape elements.

Pitfall trap samples from different months were pooled for each transect, to provide a single aggregate sample for each year/transect combination, based on consistent protocols in terms of trap numbers and sampling periods across all years. Species richness and abundance of specialist GHS species in zero year old restocks sampled in both periods were compared in a general linear model (GLM) using SPSS for Windows 16 in order to validate comparison of data collected in the two periods.

Transects of all habitat types within Thetford Forest were combined to calculate an overall sample based rarefaction curve using EstimateS 8 (Colwell 2007) with number of species plotted as a function of number of individuals as recommended by Gotelli & Colwell (2001). Separate rarefaction curves for each habitat type were calculated using data for all carabid species in five different habitat types within the forest landscape (felled-unplanted, restocks, open patches, trackways and closed canopy forest) and using data for GHS carabid species in four open habitat types within the forest landscape (felled-unplanted, restocks, trackways and open patches).

The nestedness of the species presence-absence matrix, based on pooled data of all species found in all habitat types within the forest landscape, was calculated using Nestedness Temparature Calculator (Atmar & Patterson 1995) as recommended by Atmar & Patterson (1993). The same analysis was used for pooled data of all species found in all samples excluding closed canopy forest and for pooled data of GHS species found in all open habitats within the forest landscape. In the Nestedness Temperature Calculator the probability that a perfectly nested design might arise randomly is estimated from combinatory mathematics using unordered sampling without replacement (Patterson&Atmar, 86) which can result in extremely low probability values which have also been reported from studies with similar types of datasets (Lees & Peres 2006, Urquiza-Haas *et al.* 2009). Even though in their recent paper Ulrich & Gotelli (2007) argue that Brualdi and Sanderson discrepancy index and Cutler's index of unexpected presences performed better, the nestedness temperature calculator is widely used in the literature and online calculators for other indexes are not yet available.

Species heterogeneity in five main habitat types within the forest landscape was compared using Simpson's index (that gives more weight to common species) following equation:

$$1 - D = 1 - \sum (p_i)^2$$

1-D = Simpson's index of diversity
p = proportion of individuals of species i in the community

and Shannon-Wiener function (which gives more weight to rare species (Krebs 1989)) following equation:

$$H = \sum_{i=1}^{s} (p_i)(\log_2 p_i)$$

H = index of species diversity
s = number of species
p_i = proportion of total sample belonging to ith species

Carabid community structure was analysed by Principal Component Analysis (PCA) using CANOCO for Windows 4.5 (ter Braak & Smilauer 1997). Data were square-root transformed before the analysis. Average sample score was calculated for each site using scores of all transects at the site. In cases where sites were sampled in more than one sampling year an average sample score of all transects at the site was calculated for each year separately. Scores of species in different habitat preference groups (sqrt(n+1)transformed data) and scores of samples of different habitat types (non-transformed data) were compared using GLMs. For multiple comparisons among habitat preference groups and habitat types Tukey post-hoc test was used.

Number and abundance of species per site for each of the habitat preference groups of species were compared among six habitat types (felled-unplanted, restocks, pre-thicket, trackways, open patches and mature forest, that combines all thicket+pole+pre-fell sites) using pooled data from two transects. At sites where more than two transects were sampled, I consider just two randomly selected transects from each site to standardise sampling effort. Sites where only one transect was sampled were excluded from this analysis. GLMs with normal distribution and Tukey post-hoc test for multiple comparisons were used to examine the number of species. Non-parametric Kruskal-Wallis tests with Steel-Dwass multiple comparisons tests were used to analyse abundance.

Results

All species of ground beetles found in Breckland were grouped according to their habitat preference into eurytopic (13 species), woodland (15 species), open woodland (4 species), moorland (8 species), grassland (10 species), heathland (14 species), sandy habitat (14 species) (together, 21 GHS species) and arable (33 species) associated species.

Comparison of species composition of remaining protected heaths, arable land (Lin *et al.* 2007) and the forest landscape (Lin and colleagues (2007) and present survey) within Breckland showed that out of 111 species of ground beetles recorded in the region, 89 (79.4%) are present in the forest landscape (Figure 2. 2).

Twenty-two (60.0%) of 37 GHS species recorded within Breckland were also found in the forest landscape (Figure 2. 2). Fourteen GHS species restricted to heaths (i.e. recorded from heathland sites but not recorded from within the forest landscape) were recorded from fewer heathland sites in Breckland (mean 1.8 ± 1.3 SD) than GHS species also found within the forest landscape (mean 4.5 ± 2.5 SD; Mann-Whitney test *U*=58.0; *P*=0.002) but there was no difference between these two groups of species in distribution within the whole of UK (species restricted to heaths mean 128.1 ± 153.5 SD 10km^2; species also in the forest 183.3 ± 192.5 SD 10km^2; Mann-Whitney test *U*=106.0; *P*=0.119). There was also no difference between the GHS species restricted to heaths and those also found within the forest landscape in body size (species restricted to heaths mean 7.5cm ± 4.1 SD; species also in the forest 7.4cm ± 2.1 SD; Mann-Whitney test *U*=14.0; *P*=0.661) and in presence of wings (among species found only in heaths there are three brachipterous species but within the forest there is only one brachipterous species; Fisher’s Exact Test, *P*=0.283).

Of 22 GHS species recorded from the forest landscape eight are nationally scarce species, while seven nationally scarce GHS species have been recorded solely from the remaining heaths and one solely from arable land (Figure 2. 2). The seven nationally scarce GHS species (3RDB, 3 Na, 1 Nb) only found on heaths were significantly more restricted in their UK distribution (mean 13.0 ± 8.8 SD 10km^2) than eight nationally scarce species also recorded from the forest (mean 66.9 ± 35.5 SD 10km^2; Mann-Whitney test *U*=4.0;

P=0.005). Species only found in heaths were also more restricted in distribution within Breckland being found in fewer heathland sites (mean 2.4 ± 1.6 SD) than species also recorded from the forest (mean 5.5 ± 2.4 SD; Mann-Whitney test *U*=7.5; *P*=0.016). However there was no difference between these two groups of species in average size (species restricted to heaths mean 8.1cm ± 1.4 SD; species also in the forest 7.6cm ± 1.9 SD; Mann-Whitney test *U*=25.0; *P*=0.728) and presence of wings (each group has one brachipterous species).

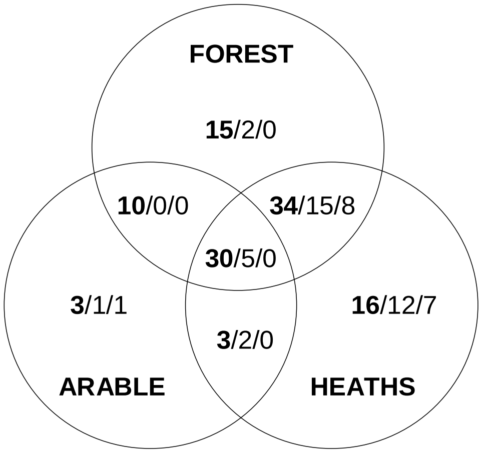

Figure 2. 2; Total number of species / number of GHS / number of nationally scarce GHS species of ground beetles in heaths, arable land and the forest landscape within Breckland and the number of species that overlap between the habitats.

Out of 89 species recorded from Thetford Forest eight were only found in previous studies conducted in this area and reviewed by Lin and colleagues (2007) but were not found in the present systematic survey and were therefore omitted from further analysis comparing assemblages among landscape elements within the forest.

During present systematic survey of different habitat types within Thetford Forest a total of 22,382 individual ground beetles belonging to 81 species were collected and identified. 8,450 individuals belonging to 55 species were collected in the 2001-2002 survey and 13,932 individuals belonging to 78 species were collected in the 2005-2006 survey. Three species were only recorded in the 2001-2002 survey and 26 species were only recorded in 2005-2006 survey.

There was no difference in the number of species and pooled abundance of GHS species recorded per transect in zero year stands sampled during the 2001-2002 and the 2005-2006 surveys (Table 2. 4). Therefore I assumed results of both surveys are consistent and I pooled the data from these two surveys.

Table 2. 4; Comparison of mean ± SD number and abundance of GHS species per transect in zero year old stands in 2001/2002 and 2005/2006 surveys.

	2001/02	2005/06	*F*	df	*P*
Number of GHS spp	2.9±1.1	3.3±1.3	1.51	64	0.224
Abundance of GHS spp	36.3±22.2	37.7±29.6	0.04	64	0.835

Sampling of ground beetles in Thetford Forest during the present systematic survey was thorough as the rarefaction curve approaches the asymptote (Figure 2. 3). Separate rarefaction curves for five habitat types within the forest landscape show these habitat types were sampled thoroughly with the exception of closed canopy forest where the total number of individuals caught was very low (Figure 2. 34).

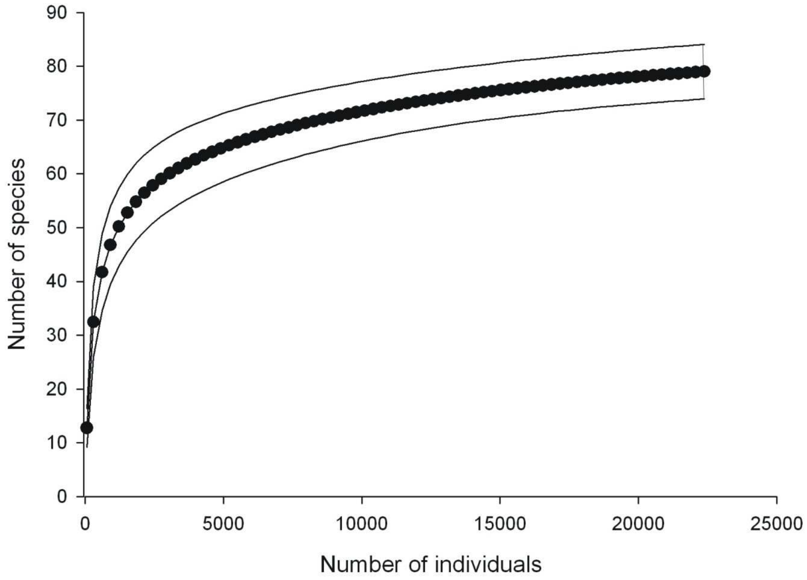

Figure 2. 3; Species richness rarefaction curve (Mao Tau function) with 95% confidence interval lines of carabid species collected in different habitat types within Thetford Forest in a systematic survey. Every fifth sample is plotted on the graph.

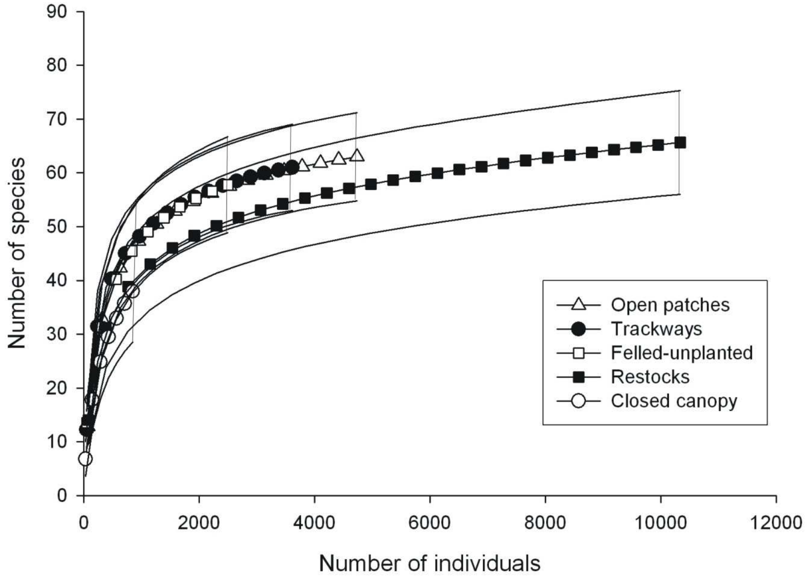

Figure 2. 4; Carabid species richness rarefaction curves (Mao Tau function) with 95% confidence interval lines in the five different habitat types within Thetford Forest. Every fifth sample is plotted on the graph.

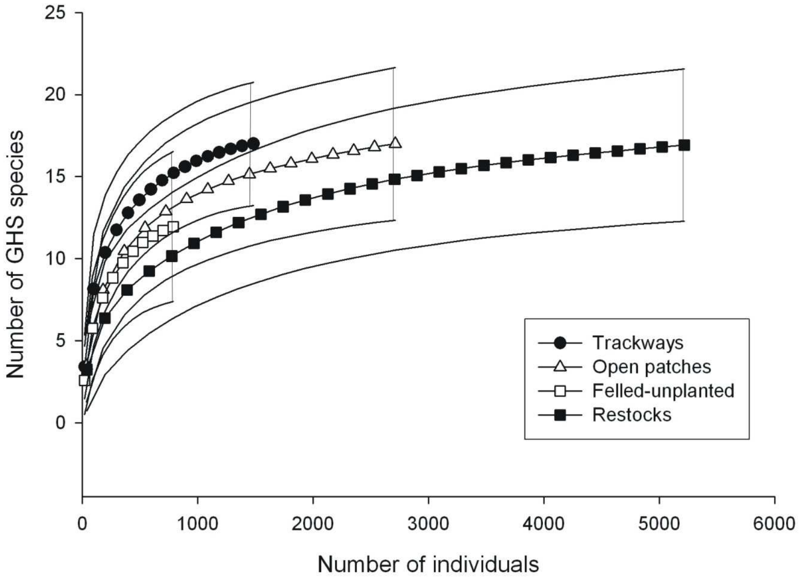

Figure 2. 5; Sample-based rarefaction curves (Mao Tau function) with 95% confidence interval lines of the number of species classified as dependent on dry grassland, heathland or sandy ground (GHS) compared among the four open habitat types within Thetford Forest. Every fifth sample is plotted on the graph.

Rarefaction curves of all species in five habitat types within the forest landscape showed that trackways, open patches and felled-unplanted areas had similar and the highest rates of species accumulation. Restocks had slightly lower rates of species accumulation but approached a similar asymptotic species richness and were within the confidence intervals of the other habitats. Closed canopy forest stands, for which fewer individuals were sampled, followed a similar initial trajectory to that of restocks (Figure 2. 4). Similarly, considering solely GHS species, rates of species accumulation were the highest in trackways followed by open patches and felled-unplanted areas, with restocks having the lowest rates of GHS species accumulation among open space habitats (Figure 2. 5). However, all open habitats approached similar asymptotic species richness.

According to Simpson’s and Shannon-Wiener indexes, trackways had the highest diversity followed by felled-unplanted, open patches and restocks. Closed canopy forest had the lowest diversity (Table 2. 5).

Thus the lower rates of species accumulation in felled unplanted and restocked patches (when scaled by the number of individuals sampled; Figure 2. 5) relate to lower equitability and dominance by a few species, within an assemblage that is still highly speciose, rather than to lower species richness.

Table 2. 5; Ground beetle species richness and diversity in five habitat types in Thetford Forest (all transects were pooled).

	Closed canopy	Felled-unplanted	Restocks	Trackways	Open patches
Number of transects	30	46	139	75	75
Number of species	39	58	66	61	63
Number of individuals	845	2552	10642	3611	4732
Simpson's index	0.733	0.880	0.829	0.917	0.841
Shannon-Wiener index	2.918	3.883	3.654	4.391	3.896

Ground beetle species within the forest landscape exhibited a nested distribution pattern, with a matrix temperature of 16.2°. The Monte Carlo probability (*P*) of obtaining a similar or a higher degree of nestedness by chance alone (in 50 runs) was infinitesimally small **(**$P = 1.7 \times 10^{-193}$). When closed canopy samples were removed from the analysis the nestedness temperature increased very little to 18.8° (probability of obtaining higher nestedness by chance in 50 runs was again very small: $P = 3.7 \times 10^{-178}$). For GHS species within open habitats within the forest landscape the nestedness was even higher with a matrix temperature of 5.5° (probability of obtaining higher nestedness by chance in 50 runs was small: $P = 4.2 \times 10^{-80}$).

An overview of species occurrence among the three main habitat types (closed canopy forest, ephemeral open habitats and permanent open habitats) within the forest landscape showed that out of 81 species, 34 (42.0%) occur in all habitats (Figure 2. 6). Fourty-two species (51.9%) (17 arable, 15 GHS, 4 moorland, 3 woodland, 2 open woodland and 1 eurytopic species) were found exclusively in open areas and only two species (3.7%) (both eurytopic) were found exclusively in closed canopy forest stands. Out of 21 GHS species, six (28.6%) were found in all three habitat types and 15 (71.4%) were only found in open areas (whether permanent or ephemeral, or both). Six GHS species found in all forest habitats were significantly more abundant in our samples (mean number of individuals caught per species 1676.2 ± 2710.8 SD) than 15 GHS species only found in open habitats (mean number of individuals caught per species 22.7 ± 26.6 SD; Mann-Whitney test U=0.0; P<0.001) but there was no difference between these two groups of species in distribution within UK (Mann-Whitney test U=30.0; P=0.243), body size (Mann-Whitney test U=23.5; P=0.094) or presence of wings (more restricted group has one brachipterous species; Fisher's Exact Test, P=0.714). There were eight nationally scarce GHS species found in the forest landscape of which only one was found in all habitats and seven were restricted to open areas (Figure 2. 6).

Focusing on open habitats within the forest landscape, both permanent open habitats (open patches, trackways) and ephemeral open habitats (felled-unplanted and restocked areas) I found 21 GHS species (Figure 2. 7). Two GHS species were exclusive to ephemeral open habitats (felled-unplanted and restocked areas) and two to trackways. None of the GHS species were restricted to open patches.

Of the eight nationally scarce GHS species found within Thetford Forest, four (all Nb species: *Amara equestris*, *Amara fulva*, *Amara lucida*, *Panageus bipustulatus*) were recorded from all open habitats (open patches, trackways and ephemeral open areas). These four species had an average 87.8 ± 26.9 SD 10km^2 distribution in UK and on average 99.3 ± 145.7 SD individuals per species were caught in this study. Out of four more restricted species *Amara consularis* (Nb) was exclusive to ephemeral open areas, *Harpalus pumilus* and *Masoreus wetterhalli* (both Na) were exclusive to trackways and *Calathus ambiguous* (Nb) was found both in open patches and ephemeral open areas. These four more restricted species had on average 46.0 ± 32.4 SD 10km^2 UK distribution (did not differ significantly from four less restricted species, Mann-Whitney test U=2.0; P=0.083) and 5.5 ± 5.7 SD individuals per species were caught (differ significantly from four less restricted species, Mann-Whitney test U=1.0; P=0.042). All four of the less restricted nationally scarce GHS species are macropterous whereas only two of the more restricted species are macropterous, one is dimorphic and one is brachipterous. Species in these two groups do not differ in average body size (Mann-Whitney test U=7.0; P=0.773).

Excluding those more generalist species, i.e. those recorded in closed canopy forest habitats, the ratio of GHS species found solely within permanent open elements, to those found in both permanent and ephemeral elements, to those found only in ephemeral elements (felled and restocked) was 2:17:2 for all GHS species, but 1:5:2 for nationally scarce GHS species. Considering this in terms of GHS species that are not nationally scarce versus GHS species that are nationally scarce produces ratios of 1:12:0 and 1:5:2 respectively. Considering this further, in terms of element exclusivity (only one of the two landscape elements) versus generality (both permanent and ephemeral landscape elements) 1:12 and 3:5. Thus, this suggests that a greater proportion of the nationally scarce GHS species are found exclusively in only one of the landscape elements. However, a Fisher Exact test of the final contrast is non-significant (P=0.252). An alternative explanation is that, the nationally scarce species are represented by very few individuals, and thus their apparent restriction to only one or other landscape element could have arisen by chance sampling artefacts.

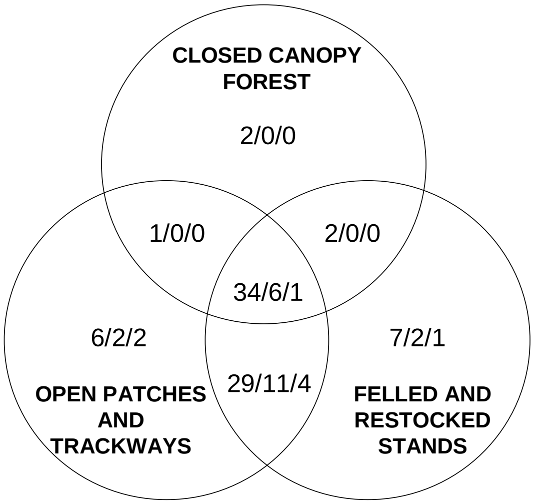

Figure 2. 6; Total number of species / number of GHS species / number of nationally scarce GHS species of ground beetles in three main habitat types (closed canopy forest, felled and restocked stands and open patches and trackways) and the number of species that overlap between different habitat types.

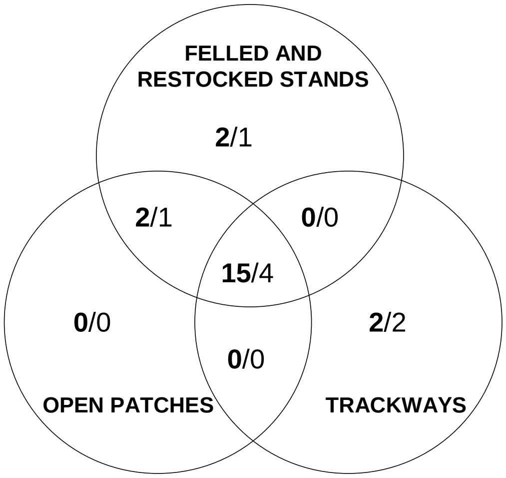

Figure 2. 7; Total number of GHS species / number of nationally scarce GHS species in three different types of open habitat within Thetford Forest and the number of species that overlap between different habitat types.

Principal component analysis of the assemblage showed scores of GHS associated species were the highest on both axes and differed significantly from the location of eurytopic species on the first axis and from the location of eurytopic and woodland species on the second axis (Figure 2. 8). GHS and eurytopic species did not differ significantly from open woodland, moorland and arable associated groups on either of the axes (Figure 2. 8; Table 2. 6 A).

Significant differences in PCA axis 1 and 2 sample scores for five habitat types (Table 2. 6 B) show that carabid community composition differs among these habitat types. Overall, the primary contrast captured by the first PCA axis (explaining 26.5% of the variance in the data) is between closed canopy samples, and all open habitats (Figure 2.9). The secondary contrast, captured by the orthogonal second axis (explaining 12.3% of the variance) is among the different open habitats, primarily between the permanent (trackways and open patches) *versus* ephemeral (felled unplanted and restocked stands) patches (Figure 2. 9). Closed canopy forest transects have low scores on axis one and intermediate scores on axis two (Figure 2. 9, polygon A) and were significantly different from all other habitat types on axis 1 and from trackways and open patches on axis 2. Low scores of closed canopy forest correspond with low species scores on both axes for eurytopic and woodland species (Figure 2. 8 A). Ephemeral open habitats (felled-unplanted and restocked areas) are located in the lower right hand side of the bi-plot, while permanent open habitats (open patches and trackways) are located in the upper right hand side of the bi-plot. On the first axis felled-unplanted and trackways had lower scores compared to restocks with open patches having intermediate values. Scores of restocks and felled-unplanted on the second axis are similar and both lower than those of trackways and open patches (Table 2. 6 B).

Table 2. 6; Principal component analysis of forest landscape dataset. A) Species habitat preference group’s scores (average ± SD) compared on axis 1 and 2 of the species PCA. B) Axis one and two sample scores (average ± SD) compared among five habitat types. Results of GLMs are shown; means with different superscript letter differ significantly according to Tukey post-hoc test ($P<0.05$).

A

	Eurytopic	Woodland	Open woodland	Arable	Moorland	GHS	*F*	*P*	R^2
Axis 1	-0.10±0.13 ^{a}	0±0.13 ^{ab}	0.12±0.30 ^{ab}	0.06±0.12 ^{ab}	0.15±0.19 ^{ab}	0.14±0.25 ^{b}	3.16	0.012	0.119
Axis 2	-0.14±0.28 ^{a}	-0.15±0.23 ^{a}	0.04±0.18 ^{ab}	0.06±0.20 ^{ab}	0.05±0.19 ^{ab}	0.11±0.19 ^{b}	3.73	0.005	0.146

B

		Ephemeral open habitats		*Permanent open habitats*				
	Closed canopy	Felled-unplanted	Restock	Trackways	Open	*F*	*P*	R^2
Axis 1	-1.38±0.23 ^{a}	-0.31±0.65 ^{b}	0.51±0.81 ^{c}	-0.40±0.80 ^{b}	0.14±0.91 ^{bc}	22.16	<0.001	0.361
Axis 2	-0.30±0.52 ^{a}	-0.51±0.55 ^{a}	-0.43±0.64 ^{a}	0.95±0.65 ^{b}	0.49±0.80 ^{b}	33.13	<0.001	0.461

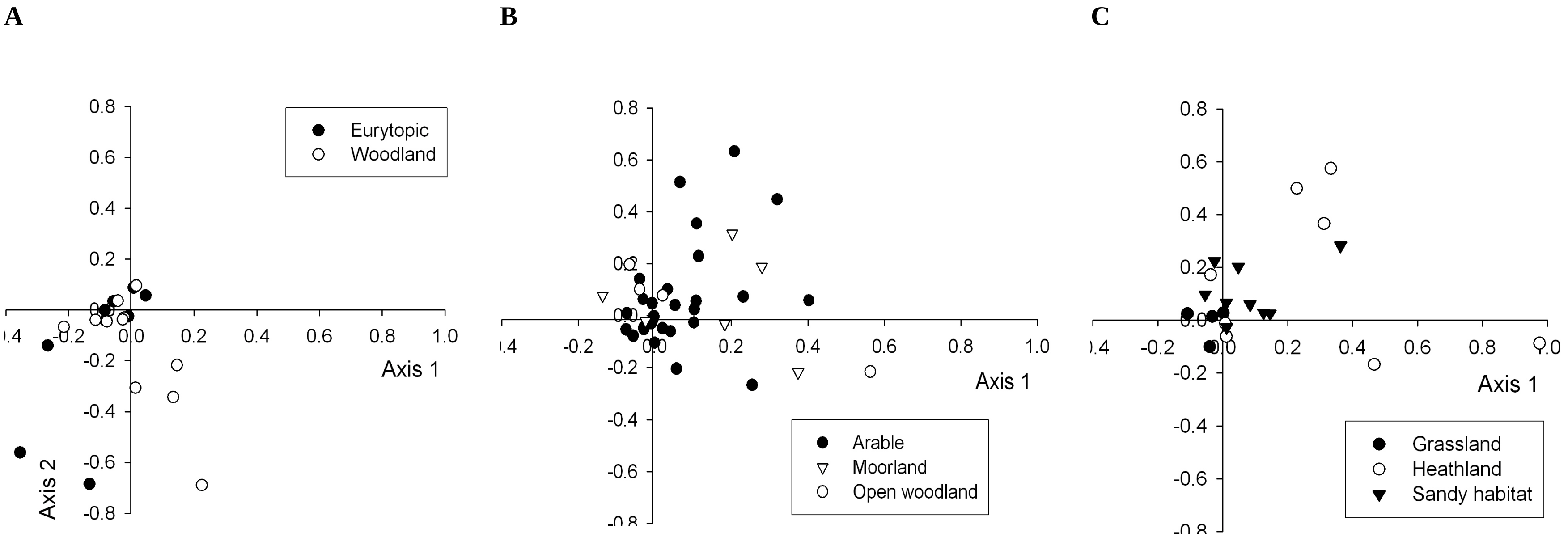

Figure 2. 8; Species scores of Principal component analysis grouped according to their habitat preference: A) eurytopic and woodland, B) arable, open woodland and moorland, C) grassland, heathland and sandy habitat.

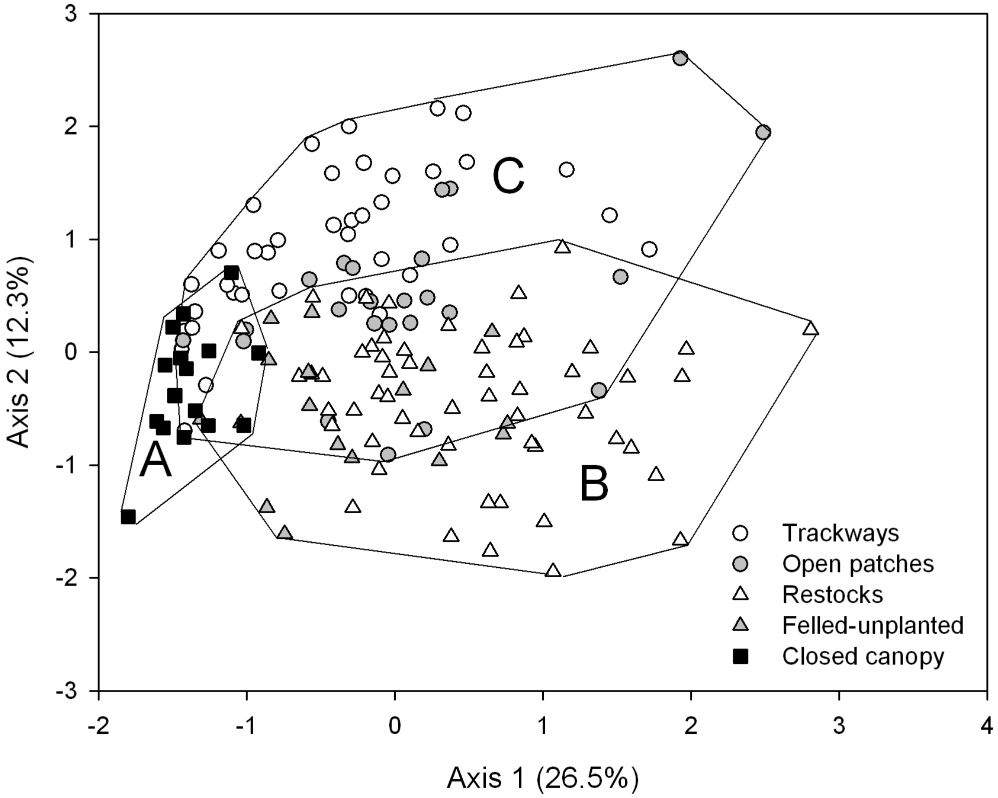

Figure 2. 9; Principal component analysis of carabid beetle composition (performed on square root transformed data) of samples from five habitat types within Thetford Forest. Each symbol represents a pooled value of all transects in a site/year combination. Minimum convex polygons are shown for A=closed canopy forest, B=ephemeral open habitats (felled-unplanted and restocks), C=permanent open habitats (open patches and trackways).

Comparison of number and abundance of different habitat preference groups of carabids between habitat types confirms the differences in carabid community apparent within the PCA analysis. Closed canopy habitats (pre-thicket, thicket, pole and prefell) had the lowest overall number and abundance of species especially due to very low number and abundance of GHS and arable associated species (Table 2. 7). Pre-thicket stands are a clear intermediate stage of succession between open areas and mature forest as they have intermediate number of eurytopic, arable, moorland and open woodland species and low number of woodland species. In felled-unplanted and restocked areas there is still a relatively high number and abundance of woodland species (higher than in permanent open habitats). Felled-unplanted areas also support a relatively high number and abundance of eurytopic species which decline in restocks. There is also a high number and abundance of arable, moorland and GHS associated species in these patches which increase in restocked patches reaching similar values as in permanent open habitats (open patches and trackways). Permanent open patches like restocks have a lower number of eurytopic species than felled-unplanted areas. Number and abundance of woodland species in permanent open areas is even lower than in restocks and it is similar only to pre-thicket patches (Table 2. 7).

Pooling all GHS species found in open forest habitats (total number of individuals caught is 10,371), the abundance was dominated by *Harpalus rufipalpis*, with 7,155 individuals captured, 69.0% of the total number of GHS individuals captured, and *Nebria salina* (1,218 individuals, 11.7%). These two were followed by *Calathus erratus* (521 individuals, 5.0%), *Amara convexior* (497 individuals, 4.8%), *Amara tibialis* (328 individuals, 3.2%) and *Amara equestris* (316 individuals, 3.0%). Fifteen GHS species with the lowest abundance represent only 3.2% of individuals caught. Out of these 15 rare GHS species seven species were represented by fewer than 10 individuals. Number of individuals of each GHS species in open habitats within the forest landscape was not correlated to the number of heathland sites in Breckland where the species was recorded (Rs=0.096; P =0.680, n=21) but it was marginally correlated to the species distribution range within UK with more abundant species having larger distribution ranges (Rs=0.417; P =0.060). GHS species with larger body size were also more abundant in open landscape elements within the forest landscape (Rs=0.527; P =0.014).

Abundance of GHS species (other than *H.rufipalpis* and *Neb.salina*) reached its peak in two year old restocks and gradually decreased in older restocks (Figure 2. 10 A). Abundance of *Nebria salina* was highest in two year old restocks and abundance of *Harpalus rufipalpis* was highest in three year old restocks (Figure 2. 10 A). Dominance of *Harpalus rufipalpis* and *Nebria salina* was much more pronounced in felled-unplanted and restocked stands than in permanent open areas (open patches and trackways) (Figure 2. 10 B). Although the total abundance of GHS species restocked stands exceeds that in trackways, this is largely due to their dominance by abundant *Harpalus rufipalpis* and *Nebria salina*. Excluding these two species, mean abundance of GHS species other than *H.rufipalpis* and *Neb.salina* is significantly higher in permanent open areas than in ephemeral open habitats (both clear-felled unplanted and restocked stands) (Table 2. 7, B).

Table 2. 7; Mean ± SD number of A) species and B) individuals (per site, 2 transects pooled) for each carabid habitat preference group, compared among six habitat types or landscape elements within Thetford Forest. Results of A) GLM performed on non-transformed data, or B) non-parametric Kruskal Wallis tests are shown; means with the same super-script letter do not differ significantly (tested by A: Tukey, or B: Steel-Dwass multiple comparisons, $P<0.05$).

	Felled-unplanted	**Restocks**	**Pre-thicket**	**Thicket, Pole, Prefell**	**Open patches**	**Trackway**	*F*	df	*P*
N	17	55	3	11	24	36			
A: No. Species									
Eurytopic	4.0 ± 0.9^{b}	2.8 ± 0.9^{a}	3.0 ± 1.0^{ab}	3.7 ± 1.0^{ab}	2.7 ± 1.3^{a}	2.5 ± 1.4^{a}	5.7	5	<0.001
Woodland	3.7 ± 1.3^{a}	3.3 ± 1.2^{a}	0.7 ± 0.6^{b}	2.5 ± 1.5^{ab}	1.7 ± 1.4^{b}	2.0 ± 1.1^{b}	11.0	5	<0.001
Open woodland	1.2 ± 0.5^{ab}	1.0 ± 0.3^{a}	1.3 ± 0.6^{ab}	0.2 ± 0.4^{c}	1.5 ± 0.7^{b}	1.4 ± 0.9^{a}	9.0	5	<0.001
Arable	5.5 ± 2.7^{a}	6.1 ± 2.3^{a}	4.7 ± 3.8^{ab}	1.1 ± 1.5^{b}	6.1 ± 2.8^{a}	6.4 ± 2.1^{a}	9.5	5	<0.001
Moorland	1.4 ± 0.9^{ab}	1.6 ± 1.0^{a}	1.0 ± 1.0^{ab}	0.5 ± 0.5^{b}	1.6 ± 0.9^{a}	1.6 ± 0.9^{a}	3.3	5	0.008
All GHS	3.4 ± 1.7^{b}	4.3 ± 1.6^{ab}	2.0 ± 1.0^{abc}	1.0 ± 1.2^{c}	4.9 ± 2.0^{ab}	5.0 ± 2.2^{a}	10.3	5	<0.001
GHS excl. *H.rufipalpis* & *N.salina*	1.9 ± 1.5^{ab}	2.3 ± 1.6^{ab}	0.3 ± 0.6^{a}	0.4 ± 0.5^{a}	3.4 ± 1.7^{b}	3.4 ± 1.9^{b}	9.5	5	<0.001
TOTAL	19.2 ± 5.1^{a}	18.9 ± 4.3^{a}	12.7 ± 5.5^{ab}	8.9 ± 4.2^{b}	18.5 ± 4.9^{a}	18.9 ± 4.0^{a}	11.3	5	<0.001
B: No. individuals									
Eurytopic	30.5 ± 25.0^{a}	14.4 ± 13.7^{b}	28.3 ± 27.2^{ab}	39.3 ± 36.5^{a}	12.7 ± 15.4^{b}	10.5 ± 11.6^{b}	30.0	5	<0.001
Woodland	11.5 ± 8.3^{bc}	18.4 ± 13.4^{c}	0.7 ± 0.6^{ab}	7.6 ± 6.6^{ab}	3.5 ± 3.6^{a}	3.3 ± 2.6^{a}	73.0	5	<0.001
Open woodland	13.1 ± 11.0^{ab}	10.8 ± 8.5^{a}	2.0 ± 1.0^{abc}	1.1 ± 2.8^{c}	11.0 ± 10.2^{ab}	7.2 ± 8.4^{b}	32.1	5	<0.001
Arable	18.2 ± 27.5^{b}	22.0 ± 19.2^{ab}	7.3 ± 8.4^{abc}	1.5 ± 2.2^{c}	24.8 ± 17.2^{ab}	33.5 ± 27.4^{a}	39.6	5	<0.001
Moorland	1.8 ± 1.3^{a}	6.6 ± 7.7^{b}	2.3 ± 2.0^{ab}	1.2 ± 1.7^{a}	4.4 ± 4.5^{ab}	3.6 ± 2.7^{ab}	19.5	5	<0.001
All GHS	35.5 ± 29.2^{b}	75.9 ± 58.4^{a}	3.3 ± 2.3^{bc}	1.3 ± 1.7^{c}	79.1 ± 96.9^{ab}	40.7 ± 41.0^{b}	48.6	5	<0.001
GHS excl. *H.rufipalpis* & *N.salina*	4.2 ± 4.2^{b}	6.8 ± 8.4^{b}	0.3 ± 0.6^{ab}	0.4 ± 0.5^{a}	29.5 ± 58.4^{c}	15.2 ± 13.3^{c}	49.0	5	<0.001
TOTAL	110.5 ± 37.8^{a}	148.0 ± 75.3^{a}	44.0 ± 27.9^{ab}	51.9 ± 37.2^{b}	135.5 ± 105.7^{a}	98.7 ± 57.3^{b}	24.4	5	<0.001

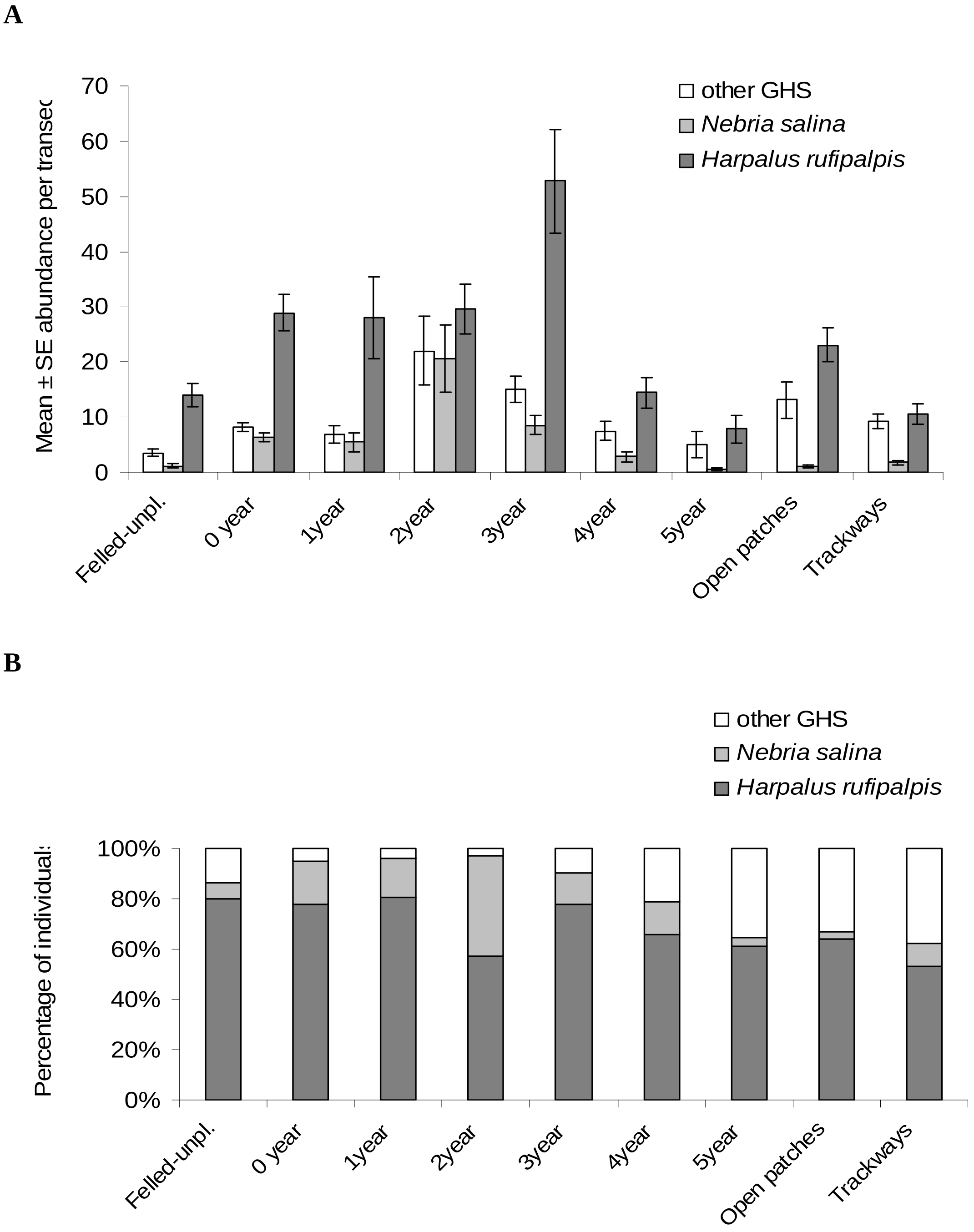

Figure 2. 10; A) Mean ± SE abundance per transect and B) percentage of individuals of *Harpalus rufipalpis*, *Nebria salina* and other GHS species (excluding *Harpalus rufipalpis* and *Nebria salina*) in felled-unplanted, 0-5 years old restocks, open patches and trackways.

Discussion

This study represents a very thorough summary of spatial and temporal distribution of ground beetles among differing landscape elements within a diverse mosaic landscape. With 22,382 individuals caught in 109 sampling sites, this is to my knowledge the largest study of its kind in Europe, in terms of both sampling effort and number of individuals collected (Butterfield *et al.* 1995, Antvogel & Bonn 2001, Jukes *et al.* 2001, Koivula & Niemela 2003, Magura *et al.* 2003, Matveinen-Huju *et al.* 2006, Pihlaja *et al.* 2006, Barbaro *et al.* 2007, Mullen *et al.* 2008). In combination with review of data on ground beetles collected in Breckland hethland reserves (Lin *et al.* 2007) it gives a good overview of presence and abundance of ground beetle species in different landscape elements and habitat types within this region.

The results show that 14 species (32%) of all GHS specialist species found in Breckland are restricted to remnant heathland sites outside the afforested landscape, while seven of these species are of special concern for conservation (nationally scarce species). Some of these species have specific habitat requirements with *Broscus cephalotes, Calathus mollis* and *Harpalus servus* found in sand dunes (Telfer & Eversham 1996), *Cymindis axillaris* and *Cymindis macularis* associated with dry sandy soil (Welch & Hammond 1995) and *Amara infima* and *Anisodactylus nemorivagus* living in *Calluna* heathlands (Telfer & Eversham 1996). As these species also have limited distribution within the UK I assume they are absent from the forest due to specific habitat requirements which are not present within the forest landscape. I found no evidence that these species absence from the forested landscape was due to dispersal limitation. Another potential reason for this difference in occupancy between heaths and the forest landscape could be more comprehensive information for species on heaths as a result of combining data from different sources including records from the Invertebrate Site Register, with a bias towards rare species. Information for carabid species within the forest landscape was obtained solely by intensive pitfall trapping, which has an inherent bias towards larger and more active species (Greenslade 1964, Spence & Niemela 1994, Lin *et al.* 2005).

Within the forest landscape the number and abundance of carabids and the composition of carabid community differed greatly among habitat types. The diversity indexes and rarefaction curves show the lowest species richness in closed canopy forest compared to other habitat types. Also the average abundance of individuals in pre-thicket, thicket, pole and prefell stages is the lowest compared to other habitats. The community of these habitats is dominated by eurytopic and woodland species and GHS species practically disappear from these areas. Thus I can conclude that closed canopy patches represent a barrier for the dispersal of heathland species. Carabid species associated with arable, moorland, open woodland, grassland, heathland and sandy habitats dominate the community of open areas within the plantation.

The rapid change in carabid community composition after felling due to colonisation by open habitat specialist species has been observed in plantation of *Picea sutchensis* in Northeast UK (Butterfield 1997), in plantation of *Picea abies* in Southern Ireland (Mullen *et al.* 2008) and in clear-fells of natural forest in boreal region of Finland (Heliola *et al.* 2001). In present study there was no evidence that very many GHS species were restricted either to just the permanent open landscape elements (open patches and trackways) or to ephemeral open areas (felled-unplanted and restocks). However, dominance of two most abundant GHS species (*Harpalus rufipalpis* and *Nebria salina*) was more pronounced in ephemeral elements and abundance of other GHS species was higher in permanent open areas. Both *Harpalus rufipalpis* and *Nebria salina* are winged species associated with heathy and sandy habitats which seem to benefit from management of clearfells before replanting (ploughing) by fast reproduction.

From this a number of important conclusions can be drawn. Firstly, ephemeral open habitats are not serving as a stepping-stone system independent of the permanent open habitats. Secondly, there is little or no evidence that GHS species found in permanent open habitats are dispersal limited; instead most of the GHS species found within the forest manage to colonise newly created open habitat within five years after felling. Open patches and trackways are not refugial habitats for these species, as the GHS populations within these habitats are not static relictual populations and also occur in other emphemeral landscape elements. Rather, open patches and trackways probably represent a constant source of colonisers for felled-unplanted and restocked patches.

Low nestedness temperature of the carabid assemblage within the forest suggests that species are not distributed randomly and that those present in species-poor samples are a subset of species found in species-rich samples. I expected that the temperature would increase considerably when species-poor samples of closed canopy forest were excluded but this was not the case.

This result and the relatively large variation in carabid community structure among sampled sites within the same type of open habitat in plantation suggest there is a large effect of habitat quality on the carabid beetles. Heterogeneity among trackways surrounded by trees of different age and differences among open patches of different size, isolation and vegetation structure will be explored further in the following chapters.

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Appendix 2. A; Eighty-one species of ground beetles found during systematic survey in Thetford Forest and their characteristics: wing morphology, habitat preference as summarised from literature, habitat description from three different sources (1: (Luff 2007); 2:(Luff 1998); 3:(Lindroth 1974)) are provided, with classification of habitat preference giving priority to the habitat description of (Luff 2007), minimum and maximum body size (mm) and the number of $10km^2$ in which the species is found in UK. Species are arranged according to their habitat preference.

Abreviations used in the table:

Wing morphology: MA: Winged; BR: Wingless or flightless; DI: Dimorphic; MA+: Dimorphic, but mostly winged; BR+: Dimorphic, but mostly wingless; (MA): probably winged; (BR): probably wingless or flightless

Habitat Preference: E: Eurytopic; W: Woodland; OW: Open-Woodland / Semi-Open habitats; A: Arable / Gardens; M: Moorland / Upland Grassland / Upland Heath; G: Dry Grassland; H: Heath; S: Sandy / Sand Dune / Gravel pit

Status: Na & Nb: Nationally Scarce A or B (Hyman & Parsons 1992);

SPECIES	**Wing**	**Habitat pref.**	**Habitat description**	**Min size**	**Max size**	**Nu of $10km^2$**	**Status**
EURYTOPIC SPECIES							
Bradycellus harpalinus	MA	E	1 wide range of dry habitats incl. gardens, grasslands, heath, arable and woodlands 2 open country on sandy or peaty heaths and grassland, some woods 3 sandy soil, often under *Calluna*	3.8	5.0	546	
Carabus nemoralis	BR	E	1 gardens, fields and most habitats that are not exceptionally wet 2 wide range of habitats, including urban gardens 3 in forests, parks, open country, farmland	20.0	26.0	475	

SPECIES	Wing	Habitat pref.	Habitat description	Min size	Max size	Nu of 10km^2	Status
Leistus terminatus	DI	E	1 damp grasslands, woodland and gardens 2 in all except the driest habitats, esp. in long grass and woodland 3 the most hygrophilus species in genus, moist, shady places among wet leaves, often under alders	6.0	8.0	613	
Loricera pilicornis	MA	E	1 grasslands, damp woodland, cultivated fields, gardens and near standing or running fresh water 2 in all except the driest habitats 3 on moist, more or less shaded ground, usually near water	6.0	8.0	1153	
Nebria brevicollis	MA	E	1 almost all habitats, esp. woodland, gardens and agricultural grasslands 2 in almost any habitat which is not exceptionally dry 3 eurytopic, in deciduous forests and parks and in open country	11.0	14.0	1280	
Notiophilus biguttatus	DI	E	1 gardens, woodland, grasslands and arable 2 almost all habitats, especially woodland 3 in somewhat shady but dry places	5.0	6.0	1213	
Pterostichus madidus	BR	E	1 woodlands, gardens and dry grasslands 2 almost all habitats, esp. woodland, gardens, grassland 3 in open country, arable, gardens	14.0	18.0	1289	
Pterostichus strenuus	DI	E	1 almost all habitats except at high altitudes, esp. grasslands 2 most habitats which are not too dry, lowland grassland, gardens and woods 3 shady places, mostly in damp deciduous forests on clayish soil, among moss and leaves	6.0	7.2	995	

SPECIES	Wing	Habitat pref.	Habitat description	Min size	Max size	Nu of 10km^2	Status
WOODLAND SPECIES							
Laemostenus terricola	BR	E	1 woods, gardens, buildings and associated with mammalian burrows 2 occurs in a variety of habitats, both indoors and in woods and open country, where may be associated with the underground runs of small mammals 3 in and around houses, in cellars, stables etc.	13.0	17.0	188	
Notiophilus rufipes	MA	W	1 gardens and deciduous woodland where there is leaf litter 2 woodland species found especially in the litter of deciduous trees 3 habitat as *N.biguttatus* but somewhat moister places (among leaf litter)	5.5	6.5	180	
Badister sodalis	DI	W	1 litter in damp woodlands, usually on heavy soils 2 in damp areas with abundant litter within woodland on clay soils 3 among leaves and moss on moist, shaded places	3.8	4.6	159	
Calathus rotundicollis	DI	W,A,S	1 woodlands, also sometimes in gardens and coastal dunes 2 almost exclusively in woodland, sometimes on coastal dunes 3 forests, usually under deciduous trees, also in gardens	8.5	10.5	452	
Leistus spinibarbis	MA	W,A,S	1 woods, gardens and near the coast 2 woodland, also on dunes 3 under trees in somewhat moist places	8.0	10.5	357	
Notiophilus palustris	MA	W,G	1 damp grasslands, woodland on heavy soils and other shaded habitats 2 prefers damper or more shaded habitats than *N.germinyi* 3 in more shaded and somewhat moister spots than *N.germinyi*, also in open country if the vegetation is dense	4.5	5.5	415	

SPECIES	**Wing**	**Habitat pref.**	**Habitat description**	**Min size**	**Max size**	**Nu of 10km^2**	**Status**
Stomis pumicatus	BR	W,G	1 woodland, grassland and disturbed ground 2 in damp, shaded habitats, woodland, unmanaged grassland, riverside vegetation 3 meadows and fields, gardens where soil is rich in humus	6.5	8.5	382	
Carabus problematicus	BR	W,G,M	1 woodland, rough grasslands and moorlands 2 many habitats, esp. long grassland, woodland, heaths 3 open, dry country, mostly on heaths, but also in thin forests	20.0	28.0	712	
Licinus depressus	BR	W,G,S	1 open and shaded habitats on dry, sandy or calcareous soils, also in gravel pits 2 dry, usually calcareous soils in grassland or woodland, also chalk and gravel pits 3 on dry sand, gravel or chalk	9.0	11.5	68	Nb
Pterostichus quadrifoveolatus	MA	W,H	1 woodlands and on lowland heaths 2 burnt ground, recent records from unburnt heaths on sandy or peaty soils, woodlands or wetlands 3 on burnt soil, rarely on heaths without evidence of burning	9.5	11.5	70	Nb
Cychrus caraboides	BR	W,M	1 woods and upland grasslands and on peaty moors 2 mainly woodland, also damp moorland and grassland 3 woodland, shady, rather moist places	14.0	19.0	697	
Pterostichus niger	MA	W,M,G	1 woodland, damp grasslands and moorland 2 woodland and damp grassland and upland moors 3 parks, thin forests etc. on not too dry soil	16.0	21.0	939	
OPEN WOODLAND SPECIES							
Synuchus vivalis	MA+	OW,A,G	1 gardens, grassland, open woodlands and arable land 2 wide variety of open not too dry habitats, gardens, grassland, arable, open woodland 3 in open not too dry habitats, usually on sand or gravel	6.0	8.5	250	

SPECIES	Wing	Habitat pref.	Habitat description	Min size	Max size	Nu of 10km^2	Status
Agonum muelleri	MA	OW,A,G	1 damp grasslands, fields, gardens, open woodland and dune slacks 2 in many habitats that are not too wet nor too dry, gardens, arable, grasslands, open woodland, dunes near freshwater 3 on open, clayish, moderately dry, often arable	7.0	9.0	701	
Syntomus truncatellus	BR+	OW,A,S	1 open ground in fields, pasture woodland and dunes 2 open, fields, open woodland, grassland 3 open, dry soil, usually with sparse vegetation	2.8	3.3	83	
Amara lunicollis	MA	OW,M,G	1 in most open or semi-open habitats, esp. if well drained yet not too dry 2 moorland, grassland, some arable, open woodland on rather dry sandy or peaty ground 3 meadows, gardens, open forests	7.5	9.0	359	
ARABLE SPECIES							
Bembidion lampros	DI	A	1 all dry, sunny habitats, esp. gardens and agricultural land 2 open, sunny sites, arable fields 3 dry, open soils of different kinds	3.0	4.0	905	
Leistus ferrugineus	BR	A	1 fields, gardens and open, moderately dry places 2 woodland and grassland, often dry situations 3 more open country and drier places than other member of the genus, often in moss and grass tufts	6.0	8.0	543	
Platyderus depressus	(MA)	A	1 fields, gardens and waste ground in open situations and dry soils 2 dry, sandy or chalky soils, in open situations 3 open country among leaves and moss, seems to prefer sandy or chalky soil	6.0	8.5	137	Nb
Trechus quadristriatus	MA	A	1 most habitats, esp. agricultural fields, gardens and other disturbed, open and dry situations 2 in most open habitats, including arable 3 in open rather dry country with short vegetation	3.6	4.1	688	

SPECIES	**Wing**	**Habitat pref.**	**Habitat description**	**Min size**	**Max size**	**Nu of 10km^2**	**Status**
Bembidion quadrimaculatum	MA	A	1 fields and gardens on open dry soils 2 open, dry soils, including arable fields, where it may be the dominant species 3 on open, rather dry soil with no or thin vegetation	2.8	3.4	496	
Amara apricaria	MA	A	1 open, often cultivated land, and where there is ruderal vegetation 2 dry, open and sandy soils, incl. arable especially if weedy 3 on open, dry places, usually with weed vegetation	6.5	8.5	339	
Clivina fossor	BR+	A	1 almost all open habitats, esp. arable land, pasture and gardens 2 widespread species, subterranean, living in most soils 3 on all kinds of open, not too dry and more or less vegetated ground	6.0	6.8	705	
Acupalpus meridianus	MA	A	1 gardens and fields on open clay or peat soils 2 only member of genus not tied to water, open, sunny ground, esp. on clay or peat, may be in heavy arable land 3 open, often arable on clayish or sandy soil	3.0	3.7	182	
Ophonus rufibarbis	MA	A	1 partly vegetated dry habitats on almost all soils 2 partly shaded habitats, on clay soils with humus, often in gardens and agricultural land 3 in open or somewhat shaded places with humus-mixed soil	6.5	9.5	282	
Amara similata	MA	A	1 open fields and gardens, often near water 2 open habitats on moderately dry soils (coexists with *Amara ovata*, but less xerophilous) 3 on open, moderately dry ground with Cruciferous plants and other weeds	8.0	9.5	342	

SPECIES	**Wing**	**Habitat pref.**	**Habitat description**	**Min size**	**Max size**	**Nu of 10km^2**	**Status**
Amara ovata	MA	A,G	1 open, dry fields and gardens 2 open, moderately dry ground; arable, gardens, grassland 3 open, rather dry, gravely ground with sparse but often tall vegetation	8.0	9.5	311	
Amara plebeja	MA	A,G	1 in damp grasslands and other well vegetated moist habitats incl. arable fields on heavy soil 2 humid vegetated soils, arable clay, intensively managed grassland 3 on firm clay, often near water among grass	6.0	7.8	704	
Anchomenus dorsalis	MA	A,G	1 arable fields, gardens and on waste ground with dry soils 2 dry, open habitats, grasslands, gardens, arable 3 open meadows, grassland on gravely or clayish often chalky soil	6.0	8.0	681	
Calathus fuscipes	BR	A,G	1 open grasslands, arable fields and gardens 2 habitats with well draining soil, gardens, grassland, arable 3 moderately dry meadows and grassland, cultivated soil, also in thin forests	10.0	14.0	781	
Poecilus cupreus	MA	A,G	1 dry habitats and fields 2 open, moderately dry and warm habitats (short grass and agricultural fields) 3 open, not too dry meadows and fields, sometimes near water	11.0	13.0	387	
Pterostichus melanarius	BR+	A,G	1 gardens, grassland and esp. agricultural fields 2 widespread and common, prefers more open habitats than *P.madidus*, is commoner in non-basic grassland and arable 3 in all kinds of open, not too dry country	13.0	17.0	843	

SPECIES	Wing	Habitat pref.	Habitat description	Min size	Max size	Nu of 10km^2	Status
Anisodactylus binotatus	MA	A,G	1 damp meadows and marshy habitats, as well as arable land on poorly-draining soils 2 in damp, open habitats, including clayish arable fields, grassland near water, and some marshes 3 rather hygrophilous, occurring in open grassland on clayish soil, mostly near water	10.0	13.0	133	
Curtonotus aulicus	MA	A,G	1 almost all open, dry habitats where there is herbaceous vegetation in seed 2 dry, well-vegetated habitats 3 meadow ground with abundant Compositae plants	11.0	14.0	491	
Calathus melanocephalus	BR+	A,G,H	1 grasslands, heaths, gardens and arable 2 open habitats ranging from coastal dunes and lowland heaths to upland grassland and moors 3 all kinds of open, moderately dry soil with grass, meadow or weed vegetation	6.0	8.5	904	
Harpalus smaragdinus	MA	A,G,H	1 dry heaths, sandpits, grassland and arable fields 2 heaths, dry grassland and arable land, sand pits 3 in open, dry country on sandy soil	9.0	10.5	29	Nb
Syntomus foveatus	BR	A,G,H	1 dry heaths, waste ground, grasslands, arable land and dunes 2 dry, sandy heaths, grassland, coastal dunes and sometimes on arable and gardens 3 on sandy, dry fields with sparse vegetation	3.2	3.8	316	
Amara aenea	MA	A,G,S	1 dry grasslands, gardens, dunes and waste land 2 dry open sunny, often seen running on paths and gardens 3 open, usually sandy ground with sparse vegetation	6.5	8.8	701	
Harpalus affinis	MA	A,G,S	1 gardens, waste ground, arable fields and almost all open dry situations 2 open, dry soils, common in gardens, arable land, dry grassland and coastal dunes 3 in all kinds of open country	9.0	12.0	640	

SPECIES	**Wing**	**Habitat pref.**	**Habitat description**	**Min size**	**Max size**	**Nu of 10km^2**	**Status**
Harpalus rubripes	MA	A,G,S	1 open dry sandy and chalky habitats 2 usually on the coast, also dry, sandy soils on arable land, grassland, sand pits and dunes 3 on dry, gravely or sandy soil with sparse vegetation	9.0	11.5	247	
Harpalus tardus	MA	A,G,S	1 dry, open habitats incl. dunes, grassland, gardens and arable land 2 fields and gardens on dry soils 3 sandy and gravely, rather dry soil	8.5	11.0	197	
Poecilus versicolor	MA	A,M,G	1 grasslands, moors and arable land, esp. if wet 2 open habitats, grassland, upland moors, arable 3 more xerophilous than *P.cupreus* in all kinds of open fields	10.5	12.5	316	
Trechus obtusus	BR	A,M,H	1 fields, gardens, moorland and dry heaths 2 in most non-wooded habitats 3 in open rather dry country with short vegetation	3.6	4.0	689	
Amara eurynota	MA	A,S	1 in arable, dunes and other open, rather dry situations 2 open ground in dunes and weedy bare soil; has benefited from agricultural cultivation 3 on open, light often cultivated ground among weeds	9.6	12.5	134	
Asaphidion stierlini	MA	A,S	1 gardens, chalk pits and other open situations on light soils 2 drier habitats including sand and chalk pits 3 NOT INCLUDED	3.8	4.5	28	
Harpalus rufipes	MA	A,S	1 open, dry situations on light soils, esp. arable fields 2 open, dry situations, esp. arable fields on sand or chalk and on waste ground 3 open country, cultivated fields and on waste places	11.0	16.0	667	
MOORLAND SPECIES							
Amara communis	MA	M,G	1 grasslands and moorlands, even if wet 2 in mainly open habitats such as grasslands, cultivated gardens and open woodland 3 eurytopic, in all kinds of moderately dry, open country and thin forests	6.0	8.0	333	

SPECIES	**Wing**	**Habitat pref.**	**Habitat description**	**Min size**	**Max size**	**Nu of 10km^2**	**Status**
Harpalus latus	MA	M,G	1 dry grasslands and upland heaths 2 any habitat moderately dry, woodland, upland grassland and bracken, dry heaths 3 all kinds of open or slightly shaded ground	8.5	10.5	400	
Cicindela campestris	MA	M,G,H	1 open grassland and moorland on sandy or peaty soils 2 open, dry heaths and moors 3 unfastidious species, with preference for sandy and heathy ground	12.0	17.0	630	
Notiophilus germinyi	DI	M,G,H	1 moorland, heaths and dry grasslands 2 heaths, moors, dry grassland 3 open, rather dry country, among grass, mosses etc.	4.5	5.5	319	
Notiophilus aquaticus	DI	M,G,S	1 open habitats such as grassland, dunes, moorland and by rivers 2 open heaths, dunes, moors and short grassland 3 in all kinds of open, moderately to pronouncedly dry country	5.0	6.0	467	
Olisthopus rotundatus	MA	M,H,S	1 dry moors and heaths, usually where there is *Calluna* but also on coastal dunes 2 dry heath with *Calluna*, also found in dry grassland and on dunes 3 dry, open, often sandy ground, under *Calluna*	6.5	8.0	406	
GRASSLAND, HEATHLAND AND SANDY HABITAT SPECIES							
Amara lucida	MA	G,H,S	1 sand dunes and dry grassland, mostly costal 2 mainly costal, found locally in sand dunes and dry grassland, inland in sandy grassland and heaths 3 dry grassland, sand dunes	4.7	6.5	87	Nb
Amara familiaris	MA	G,H,S	1 open grasslands, heaths and dunes 2 in most open, sunny and moderately dry habitats 3 on all kinds of open ground (meadows, waste) among weeds	5.5	7.3	687	

SPECIES	Wing	Habitat pref.	Habitat description	Min size	Max size	Nu of 10km^2	Status
Badister bullatus	MA	G,H,S	1 most habitats, esp. open, dry often sandy situations such as lowland heaths, grasslands and dunes 2 on open, dry, sandy soils, usually at low altitudes (in the north on sand dunes) 3 most erytopic *Badister*, in dry as well as rather moist, open and rather shaded (under bushes, open forests)	4.8	6.3	588	
Panagaeus bipustulatus	MA	G,S	1 open, well-drained grasslands and dunes, also chalk and gravel pits 2 dry, sandy or calcareous grassland and dunes, also in sand, chalk and gravel pits 3 almost xerophilus, open, sandy or gravely ground with short meadow vegetation, often in chalky districts	6.5	7.5	105	Nb
Amara consularis	MA	H,S	1 dry sand and gravel pits with vegetation, also lowland sandy heaths 2 open, often humus-rich sandy or gravely soil, gravel pits 3 in open habitats, on sand and gravel, sometimes with mixture of humus, often gravel pits	8.0	9.5	75	Nb
Amara tibialis	MA	H,S	1 sand pits, dry heaths, dunes and well drained open ground 2 open, sandy areas of grass and heath on coastal sand dunes or inland 3 dry, open, sandy country with low vegetation	4.5	5.9	257	
Calathus cinctus	DI	H,S	1 on coastal dunes and dry lowland heaths 2 coastal sand dunes, lowland heaths 3 dry, sandy ground with sparse vegetation, especially near the coast	6.0	8.5	48	
Calathus erratus	DI	H,S	1 open, dry sandy sites and coastal dunes 2 dry sandy habitats, both on coastal dunes and inland on heaths 3 dry, usually sandy ground with sparse vegetation	8.5	11.5	218	

SPECIES	**Wing**	**Habitat pref.**	**Habitat description**	**Min size**	**Max size**	**Nu of 10km^2**	**Status**
Harpalus anxius	MA	H,S	1 dunes and inland sand pits and sandy heaths 2 coastal sand dunes, inland on sandy heaths and sand pits 3 sandy soil, usually on the coast	6.5	8.0	90	
Harpalus rufipalpis	MA	H,S	1 sandy places, heaths, dunes and sand pits 2 sandy soils, heaths, dunes and in sand pits 3 in open sandy soil	7.5	10.5	116	
Nebria salina	MA	H,S	1 sandy or unproductive soils and lowland heaths 2 in less-productive habitats, heaths, sand dunes, upland grassland 3 drier and more open country then *Nebria brevicollis*	11.0	14.0	523	
Masoreus wetterhalli	BR+	H,S	1 sand and gravel soils, usually near the coast, often under low vegetation 2 mainly on the coast (dunes, shingle), also on dry heaths in Norfolk 3 on sand and gravel with sparse vegetation	4.5	6.0	21	Na
Amara bifrons	MA	S	1 open sites on well drained soils 2 sandy soils with little vegetation 3 xerophilus species, on sand with very sparse vegetation	5.5	7.3	267	
Amara convexior	MA	S	1 dry, well drained sites with ruderal vegetation 2 open sunny sites such as gravel pits 3 gravely soil in gravel pits	6.5	8.2	124	
Amara equestris	MA	S	1 dry, sandy places, dunes and gravel pits 2 open, dry, sandy or calcareous, gravel pits 3 on dry soil, open or lightly wooded country, at roots of grass or under dry leaves	7.5	10.5	50	Nb
Amara fulva	MA	S	1 sandy and gravely sites often near water, as well as dunes 2 open, dry, sandy or gravely habitats 3 dry sand, sometimes mixed with gravel or clay	8.2	10.5	109	Nb

SPECIES	**Wing**	**Habitat pref.**	**Habitat description**	**Min size**	**Max size**	**Nu of $10km^2$**	**Status**
Amara montivaga	MA	S	1 open, sandy or chalky sites with ruderal vegetation 2 sandy sites, gravel and chalk pits, weedy vegetation 3 dry gravel, chalk and sand with weed vegetation	7.8	9.1	51	
Calathus ambiguus	MA	S	1 open, dry sandy sites, both inland and on the coast 2 little-vegetated sandy habitats, both on the coast and inland in sand pits 3 on dry, usually sandy ground with sparse vegetation, chalk pits	8.5	11.5	73	Nb
Harpalus attenuatus	MA	S	1 dunes and dry, sandy soils 2 coastal dunes and dry, sandy places inland 3 open, sandy or chalky soil	7.0	9.0	68	
Harpalus pumilus	BR	S	1 open, dry sandy sites 2 dry, open slopes, usually south-facing with little vegetation 3 in open places with sand or gravel	5.0	6.4	15	Na
Notiophilus substriatus	MA	S	1 open, dry, often sandy habitats 2 on dry soils with little or open vegetation 3 in open rather dry country	4.5	5.5	379	

Chapter 3: Relative value of permanent open habitat arranged as linear strips or large patches for conservation of heathland carabids within a forest landscape

Abstract

To comply with the UK forestry standard approximately ten percent of the area within pine plantations in lowland England are left unplanted. Where plantations have been established on former heathland on sandy soil, as in Dorset, Hampshire, Surrey, Suffolk and Norfolk, conservation interests focus on open areas within these plantations. Permanent open habitats can be arranged as distinct patches of different size, and as linear network of trackways separating plantations of different age. To assess and compare the value of both types of open space for conservation of heathland species within Thetford Forest, Breckland, Eastern England an extensive pitfall trap survey of carabid fauna was carried out in spring/summer months in 2005 and 2006. Permanent open areas within the plantation support important carabid fauna associated with dry grassland, heathland and sandy habitats, including seven nationally scarce species. Overall comparison of species present in open patches and trackways did not show any difference between these two habitat types, but there were considerable differences among sampled sites. For both habitats quality plays a more important role than the size of the area, with heathland carabids favouring areas with low swards and greater cover of bare sand, moss and lichen. Conditions within trackways are greatly affected by the age of surrounding plantation with heathland carabids only present in trackways surrounded by young plantations (<20 years). Current management of trackways for conservation (vegetation is cut and removed once a year) does not seem to have any effect on heathland associated carabids and should be reconsidered.

Introduction

Since the development of the theory of island biogeography (McArthur & Wilson 1967) the importance of spatial arrangement and size of habitat patches has remained a major concern in species conservation studies. Consequent development of metapopulation theory (Hanski 1991) further stressed the importance of these characteristics of habitat remnants in patchy landscapes. These theories are especially important in the light of increasing habitat loss and habitat fragmentation due to human activities and the consequences these processes have on natural populations. Habitat loss has typically large negative effects on biodiversity (Tilman *et al.* 1994, Dobson *et al.* 1997, Sih *et al.* 2000). Effects of fragmentation *per se* however are difficult to tease apart from habitat loss and are as likely to be positive as negative (Harrison & Bruna 1999, Debinski & Holt 2000, Fahrig 2003). A threshold value of 10-30 percent of remaining habitat within the landscape has been suggested, below which the species loss or decline in population would be greater than expected from the random sample hypothesis (Andren 1994, Fahrig 1997, 2002, Ovaskainen *et al.* 2002, Radford *et al.* 2005). Below this threshold distances between patches of original habitat increase exponentially, thus an extra loss of habitat would suddenly disrupt landscape connectivity.

Structures that would enhance connectivity such as corridors and stepping stones have been suggested to balance potential negative effects of fragmentation. Corridors as linear elements connecting patches of habitat may enable and enhance movement of individuals between isolated patches of habitat (Beier & Noss 1998, Rosenberg *et al.* 1999). Stepping stones are patches of remnant vegetation within the matrix that may increase connectivity by reducing the distance individuals have to travel at once through the matrix (regardless of whether these elements function as habitat) (Forman 1995, Uezu *et al.* 2008). Implementation and function of corridors and stepping stones has been much discussed in the literature (Simberloff & Cox 1987, Mann & Plummer 1995, Beier & Noss 1998, Chetkiewicz *et al.* 2006), but there are no simple answers and their usefulness in maintaining connectivity will depend on life history strategies of different species (Ewers & Didham 2006).

Although for large or mobile taxa, such as mammals or birds, corridors and stepping stones may both represent opportunities for ephemeral use while individuals are dispersing within a season or lifetime, for other taxa such as amphibians, reptiles and many ground dwelling invertebrates, such landscape elements may instead represent habitat for resident populations (Rosenberg *et al.* 1999). Most individuals may persist their entire lifetime within a patch or corridor, but dispersal and colonisation may occur by percolation (linear corridor) or occasional long-distance dispersal events (stepping stones). Thus it is important to consider whether the relative configuration of large patches, versus narrow linear strips (with high edge to area ratio), affects their suitability as habitat for resident populations. If strips with high exposure to edge are not suitable would it be more appropriate to arrange open habitat as a series of larger patches or stepping stones?

Investments in such structures are costly therefore optimal solutions should be considered when planning areas for conservation (Mann & Plummer 1995). In my study in Thetford Forest in Breckland UK, I evaluated the relative value of linear strips of habitat and stepping stones of different size for the conservation of open area specialists within a forest landscape. I also considered the importance of habitat quality as a consequence of management, which is especially important for the conservation of open habitats of early successional stages.

The Breckland region was historically dominated by lowland heathland and was a stronghold for rare, localised or otherwise coastal species in the UK (Dolman & Sutherland 1992). Due to agriculture intensification and planting of Thetford Forest, areas of heathland were reduced by 76 percent within the last century (Lambley 1990). Because similar reduction of heathland happened in other European countries this is now a threatened habitat protected by the EC Habitats Directive (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora). Negative effects of fragmentation of heathland have been shown as reduced number of heathland restricted ground beetle species with low powers of dispersal in smaller fragments of heaths in the Netherlands (deVries *et al.* 1996), and as lower diversity of several heathland associated invertebrate taxa in smaller and more isolated heathland remnants in Dorset, UK (Webb 1989).

To comply with UK forestry standard about 10 percent of the area of Thetford Forest is open space, the purpose of which is to encourage the development of wildlife, enable structural diversity and greater flexibility in future management. These areas represent potential refuges for heathland plants and animals therefore conservation interests focus on open areas within the plantation. Within Thetford Forest permanent open space occurs in two different forms: as connected linear strips of habitat along the network of trackways and as relatively isolated open patches of different shape and size.

The main questions I attempted to answer in this study were:
Can 10 percent of open space within a forest landscape support populations of typical heathland ground beetle species? What is the relative value of linear strips and open patches for heathland species? How important is habitat quality in relation to patch size? Is current management for conservation of open spaces positively affecting presence and abundance of heathland species?

The results of the current study will contribute to better understanding of this mosaic landscape and give implications for optimal future management for the conservation of heathland species.

Methods

Thetford Forest is the largest lowland conifer forest in UK. It now covers 20,000ha or approximately one third of the Breckland region, which was historically dominated by heathland. Planting of Thetford Forest started in 1922 after periods of agricultural depression and it is now in the second rotation. Plantations are managed by clear-felling and replanting with nursery-grown trees.

Stands of pine trees are separated by a network of trackways of different width (Hemami *et al.* 2007). The middle part of trackways (this section is hereafter referred to as the 'track') is used by vehicles and is therefore physically disturbed by wheel ruts and can be clearly distinguished from surrounding verges. All trackways (with exception of those in the west half of Elveden block) are accessible to walkers and cyclists. Some of the trackways are a part of marked walking or cycling routes. Within the forest there are also permanent open patches of different area and shape, which were left unplanted after felling and harvest of the initial crop, to comply with guidelines of the UK forestry standard of allowing 10-20 percent of open space within the forested area.

Permanent open areas within the forest landscape are managed in several different ways. All trackways surrounded by stands older than 25 years are affected by heavy machinery approximately every five years when adjacent stands are thinned or felled. Both of the verges of trackways that form a part of walking or cycling routes, are swiped (vegetation is cut and left) approximately every two months. Trackways and open patches designated as conservation areas (mostly for their botanical interest) are forage harvested, with vegetation cut and removed at the end of growing season (August or September), once every year. Some trackways are mowed to increase visibility, to facilitate deer control, or for access reasons, but few records of this are kept. The largest open patches within the forest landscape are designated as heathland reversions and are extensively grazed by sheep. Because of this lack of consistency in management techniques I investigated the effects of management on ground beetle diversity (conservation trackways versus non-systematically managed trackways) only within the class of young trackways (Table 3. 1).

In 2005 and 2006 12 open patches of which two were never planted, seven have been left unplanted for 10-20 years and three have been left unplanted for fewer than 10 years were sampled (for details see Appendix 3. A). Sampled patches were located in Croxton, Lynford, High Lodge and Elveden forest management blocks. In each of the sampled open patches three transects of five pitfall traps each were set up on four occasions during spring/summer months (mid May, mid June, end of July and end of August). Traps in transect were approximately 30m apart. Sampled patches varied in area from 1.2 to 35.0ha with average area 7.7ha ± 10.2 SD (for details see Appendix 3. A).

As a network of linear permanently open elements, 39 trackways located in Lynford, High Lodge and Elveden management blocks were sampled on four occasions in spring/summer period in 2005. Trackway sites were classified into three groups (prefell, pole and young - Table 3. 1) according to the age of the youngest of the two adjacent plantations. Samples were collected using pitfall traps set in two parallel transects of five traps each, with traps within each transect set approximately 22m apart. One transect was set in the middle of the trackway (hereafter referred to as the “track”) and one in the verge (hereafter referred to as “verge”) of the trackway (1.5-2.5m away from the edge of the track wheel ruts, depending on the width of the verge) (Figure 3. 1). There were three trackways (one in each age class of surrounding plantation) where it was not possible to sample the track due to extremely hard surface, so only the verge was sampled. Sampled trackways were between 6.2m and 42.6m wide (width from tree crop to tree crop, including both verges and the central track), with an average width of 13.7m ± 8.0 SD. Width of tracks did not differ greatly among trackways from minimum of 1.4m to maximum of 3.9m. Variability in width of verges was much greater with minimum 2.2m to maximum of 30.8m, with average 6.8m ± 6.3 SD. There were no differences among the three trackway classes in width of tracks (Kruskal-Wallis x^2=1.42; P=0.492), in width of sampled verges (Kruskal-Wallis x^2=2.10; P=0.350), nor in width of the whole trackway (both verges and track) (Kruskal-Wallis x^2=2.55; P=0.280).

Of the 39 trackways, 21 were roughly north-south oriented and 18 were roughly east-west oriented. In trackways oriented north-south the widest of both verges was sampled (seven west verges and 14 east verges were sampled) and on trackways oriented east-west the northern verge was sampled. Location of the sampled verge was included in the analysis as variable orientation (north, east, west). The youngest of the two adjacent plantations was located in the north in four sites, in the south in six sites, in the east in seven sites and in the west in five sites. In 17 trackways both plantations were of equal age.

Pitfall traps were open for five consecutive days on each of the four sampling occasions. Pitfall traps were transparent plastic cups, 7.5cm deep and 6.5 cm in diameter filled with approximately 50ml of ethylene glycol as killing and preserving chemical. On each sampling occasion captures from each of the five pitfalls in each transect were pooled prior to identification.

Carabids collected were identified to species level according to Lindroth (1974), while nomenclature followed Luff (2007). Habitat preference classification followed Luff (2007) according to which species were divided into six groups: eurytopic, woodland, open woodland, moorland, arable and grassland + heathland + sandy habitat (GHS) associated species. Details of this classification have been described in Chapter two. Biodiversity conservation status of nationally scarce species was given to all notable A or notable B species (Hyman & Parsons 1992).

Table 3. 1; Classification of sampled trackways according to the age of adjacent plantations, width, management and orientation characteristics of each of the classes.

Type	N	Definition	Age of adjacent plantation (years)		Width(m) Min-max; Mean±SD	Number of conservation trackways	Orientation	
			Youngest	Oldest			North South	East West
PREFELL	9	Plantations on both sides of trackway >30 years old	31-82	31-82	6.4-14.6; 10.0±2.5	0	3	6
POLE	9	Plantation on one side of trackway 21-28 years old, opposite side > 20 years old	21-28	21-77	8.4-29.7; 15.2±7.1	3	4	5
YOUNG	21	At least one side 10-20 years old (thicket), second side variable age	10-20	11-78	6.2-42.6; 14.6±9.6	10	11	10

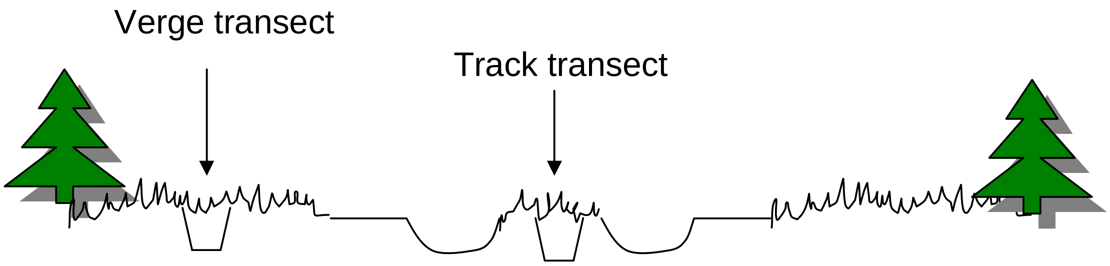


Figure 3. 1; Location of track and verge transects in the sampled trackways.

The composition and structure of ground vegetation in trackways was recorded in June 2005 and that of open patches was recorded in both June 2005 and June 2006. Percentage cover of 16 vegetation parameters were visually estimated in a 3x3m quadrate centred on each pitfall trap. Of these 16 parameters some were later pooled; thus data were analysed as eight parameters: bare ground (exposed sand or soil), litter, moss + lichen, bracken

(*Pteridium aquilinum* - pooling both growing fronds and dried previous year's growth), grass, herbs, heather (*Calluna vulgaris*) and other bushes (mainly gorse (*Ulex europaeus*), broom (*Cytisus europaeus*), birch (*Betula pendula*), bramble (*Rubus fruticosus*) and raspberry (*Rubus idaeus*)). Vegetation cover was constrained to 100 percent. The mean cover of each vegetation parameter in five quadrates was calculated to represent each transect. Presence or absence of 11 easily recognisable indicator plants (*Teucrium scordonia, Rumex acetosella, Urtica dioica, Pilosella officinarum* (sny. *Hieracium Pilosella*), *Gallium saxatile, Deschampsia flexuosa, Holcus* spp. *(H.lanatus + H.mollis), Carex arenaria*, *Polytrichum* spp. (*P.juniperum* + *P.piliferum*), *Dicranum* spp. (*D.bonjeani* + *D.scoparium*), *Campylopus introflexus*) was recorded in each 3x3m quadrate. Occurrence per transect was an ordinal value of frequency, between zero (not present) and five (present at each pitfall trap in a transect). Information on characteristics of preferred habitat of these 11 indicator species were gathered from the literature (Rose 1981, Fitter *et al.* 1984, Jahns 1987) and supplied by Paul Dolman (personal communication).

Sward height of ground vegetation was measured using a sward stick (disc diameter 90mm, weight 250g, rod diameter 17mm following Dolman & Sutherland (1992), at four points one meter away from each trap in both trackways (July 2005) and in open patches (July 2005 and 2006). Mean sward height was calculated for each trap and for each transect. The area of sampled open patches and the age of plantations surrounding sampled trackways were determined from the GIS shape file provided by the Forestry Commission. This shape file was also used to determine the orientation of trackways.

To test the effect of soil pH and organic matter content on carabid species composition four cylindrical soil cores (4.75 cm in diameter, 5.00 cm in depth, not including undecomposed organic litter) were collected from each open patch, each trackway verge and track, in July 2007. For each soil core the thickness of undecomposed organic litter layer (hereafter "litter layer thickness") was measured using a ruler and the mean for each transect was calculated. Four soil cores from each open patch, trackway track and verge were combined and mixed thoroughly. The pH of a 100 cm^3 soil subsample mixed with 100 cm^3 of distilled water was measured at the end of the day the sample was taken, using a Corning portable electronic pH meter. Remaining soil was air dried and passed through a 2mm sieve to remove stones and root fragments. Organic matter content (organic matter(g)/ 100g of soil) of three approximately 5g subsamples for each open patch, track and verge was calculated after the subsamples were dried overnight in a 60°C oven and the organic matter was combusted at 450°C overnight in a muffle furnace.

To explore differences in weather conditions in 2005 and 2006 I used meteorological data collected by the UK Meteorological Office, at the Santon-Downham weather station located in the central area of Thetford Forest. I compared mean rainfall and air temperature values for May, June, July and August 2005 and 2006 to mean values for these months over the last 18 year period (1990-2007).

DATA ANALYSIS

To be able to describe the characteristics of the sampling sites in detail I explored the percentage cover of vegetation, presence of indicator plant species, sward height and soil characteristics for tracks and verges of trackways separately (totalling six categories: three growth stages *x* track/verge). When also including open patches the number of habitat types totalled seven. On the contrary for carabids I could not prove that individuals living in tracks were different from those living in verges due to their high mobility rates, and the possibility that verges represent resting or refugia habitat and tracks foraging habitat within the daily movement of an individual. Therefore data on carabids for tracks and verges were combined and with open areas included, only four habitat types (open patches, trackways of prefell, pole and young class) were compared.

Due to differences in sampling effort between trackways (two transects per site) and open patches (three transects per site) data per transect rather than per site were used when comparing these habitat types.

Average percentage cover of eight vegetation parameters and sward height per transect was compared among seven habitat types using nonparametric Kruskal-Wallis tests for percentage cover of vegetation, and nested General Linear Model (hereafter GLM) for sward height (site nested within habitat type; pairwise comparisons with Sidak correction factor for multiple comparisons) using SPSS 16. Values per transect rather than per site were used to allow comparison of tracks and verges with open patches. For multiple comparisons of percentage cover of eight vegetation parameters in tracks and verges of different classes and open patches I used nonparametric Steel-Dwass pair-wise comparisons (as an equivalent of Tukey post-hoc test) in Kyplot 5.0 software.

For soil characteristics (soil pH, organic matter content and litter layer thickness) I collected data for track and verge transects in trackways and one value per site for open patches. These were compared among seven habitats using GLM with Tukey post hoc multiple comparison test ($P<0.05$) using non-transformed data for soil pH and square-root transformed data for organic matter content and litter layer thickness.

To explore whether sward height, percentage cover of eight vegetation parameters and soil characteristics, differed between young conservation trackways and young non-systematically managed trackways, groups were compared using student t-test for sward height and non-parametric Mann-Whitney U test for all other variables.

I used Spearman rank correlations to investigate relationships between the area (m^2) and longevity (time since left unplanted) of open patches and the percentage cover of eight vegetation parameters, sward height and soil characteristics of these sites.

Frequency (between zero and five) of 11 indicator plant species in each transect was analysed by Detrended correspondence analysis (DCA) of non-transformed data using CANOCO for Windows 4.5. Axis 1 and axis 2 sample scores were compared among seven habitat types using nested GLMs (with site nested within habitat type).

To compare the average temperature and rainfall of each of the sampling months in 2005 and 2006 to the 1990-2007 average values for these moths, I calculated one sample t-tests.

Composition of carabid community in permanent open areas in Thetford Forest was analysed using Principal component analysis (PCA) of transect data (sqrt transformation was applied before the analysis). PCA was selected because the largest value of the length of the gradient was less than four (Leps & Smilauer 2003) and the percentage variance explained by the first two axes of PCA was much larger than that of CA or DCA. An average sample score for each site was calculated using scores of all transects in each site (with exception of open patch with six sampled transects in 2006, where only first three transects were used to calculate average score for this site). Three trackways where only verges were sampled were excluded from further analysis. Species scores of six habitat preference groups and sample scores of four habitat types (open patches, prefell, pole and young trackways) were compared using GLMs. Tukey post-hoc test was used for pair-wise comparisons. To compare sample scores of open patches in 2005 and in 2006 I used Wilcoxon signed ranks test.

To explore relationships between PCA sample scores of open areas and the environmental variables (percentage cover of eight vegetation parameters, sward height, soil characteristics, area and longevity of open patches and width and age of surrounding plantations for trackways) I calculated Spearman rank correlations. To determine the most important environmental predictors affecting carabid community in open patches and trackways I selected environmental variables that correlated significantly with PCA axis 1 sample scores and had negligible colinearity. These were included in GLMs (as covariates) and the minimal model was obtained by backward elimination, at each stage deleting the variable with the highest *P* value in the GLM. The significance of remaining variables was decided by their *P* values, with variables remaining in the minimal model all having *P* values below 0.05. Models were built using SPSS 16.

Species richness (number) and pooled abundance of carabids within each of six habitat preference groups were compared among three classes of trackways (prefell, pole and young) and open patches using nested GLMs (site nested within habitat type). Data per transect rather than per site was used to overcome differences in sampling effort among trackways (two transects per site) and open patches (three transects per site). Analysis was performed on non transformed data of number of species and on Ln(n+1) transformed data of abundance. Pair-wise comparisons with Sidak correction factor for multiple comparisons were used.

I focused more closely on presence of open area specialist carabid species within the class of young trackways and used Spearman rank correlations to investigate the relationship between trackway orientation, width, sward height, soil characteristics and cover of eight vegetation parameters and the number and abundance of overall GHS, non-dominant GHS (i.e. all other GHS species while excluding two very abundant and widespread species) and just the nationally scarce GHS species. Three sites where only the verge was sampled were excluded from analysis, providing a sample of n=36 sites. I also explored the effect of current management for conservation on carabid community by comparing PCA axis scores on both axes between young conservation trackways (n=10) and non-systematically managed trackways (n=11) using Student t-test.

Results

VEGETATION AND SOIL CHARACTERISTICS

Mean percentage cover of bare ground, grass, moss+lichen, bracken, herbs and litter differed significantly among the seven habitat types (tracks and verges of three trackway age classes and open patches) (Figure 3. 2). In all habitats grass had the greatest cover but the Steel-Dwass pair-wise comparisons did not detect any difference among habitat types. There was very little bare ground in open patches or trackway verges, but it had significantly greater cover in tracks in all three classes of trackways. Moss + lichen cover was greater in young and pole verges than in young and prefell tracks, with other habitat types intermediate. Similarly the cover of bracken was greater in young verges than in young and pole tracks, with other habitat types intermediate. There was greater cover of herbs in young tracks than in open patches, and less cover of litter in young tracks than in either open patches, pole tracks or verges of all three trackway classes.

Vegetation height was shortest in tracks of young trackways, while open patches and verges of young trackways had the tallest sward height, with tracks and verges of pole and prefell trackways having intermediate values (Table 3. 2). Comparison of soil characteristics among seven habitat types showed that the depth of the soil litter layer was significantly shallower in tracks of all three trackway classes, compared to verges and open patches (Table 3. 2). Soil pH and organic matter content did not differ among the seven habitat types, but paired comparison of tracks and verges showed that tracks had significantly higher pH (Wilcoxon signed ranks test Z= -4.19; P<0.001) and significantly lower organic matter content (Wilcoxon signed ranks test Z= -3.08; P=0.002) than adjacent verges (Table 3. 2).

Thus, overall, structure of open patches was broadly similar to that of verges in terms of bracken cover, litter and reduced extent of bare ground. Tracks provided considerably greater extent of bare ground, little bracken, and had shallower soil litter layer than verges and open patches, though tracks adjacent to pole aged plantations were intermediate.

Current management for conservation does not affect sward height measured in June, as I could not find any difference between conservation rides managed by forage harvesting, and other rides (non-systematically managed), for either the tracks (t_{18}=0.48; P=0.639) or verges (t_{19}= -0.03; P=0.980). However trackways that were not systematically managed had significantly greater cover of grass in both tracks (Mann-Whitney $U_{10,11}$=19; P=0.019) and verges (Mann-Whitney $U_{10,11}$=24; P=0.029) than found in conservation trackways. Cover of other vegetation parameters did not differ between management classes, but there was less organic matter in the soil of tracks in young conservation trackways than in non-systematically managed trackways (Mann-Whitney $U_{10,11}$=20.5; P=0.016). These differences in soil and grass cover may relate to pre-existing differences influencing selection of trackways for conservation management, rather than to effects of management.

Open patches with varying area and longevity differed in some vegetation and soil characteristics. Sites that have been left unplanted for longer had less percentage cover of both litter (Rs= -0.558; P=0.005, n=12) and grass (Rs= -0.489; P=0.015) and a shallower soil litter layer (Rs= -0.655; P=0.001). Larger open patches had greater percentage cover of litter (Rs=0.471; P=0.020, n=12) and of moss + lichen (Rs=0.485; P=0.016), but lesser cover of bush (Rs= -0.459; P=0.024) and lower soil organic matter content (Rs= -0.469; P=0.021). These relationships with area are unlikely to be causal.

The first two axes of the DCA of plant indicator species successfully explained a large proportion (37 %) of the variance in indicator species composition (Figure 3. 3). The ordination showed a primary gradient on the first axis, from drought-tolerant species characteristic of bare dry disturbed soil (*Rumex acetosella, Dicranum* spp., *Polytrichum* spp., *Carex arenaria, Campylopus introflexus*) through species of more closed swards on relatively infertile acidic soil (*Gallium saxatile*, *Deschampsia flexuosa*) to species associated with higher fertility (*Urtica dioica*) or more mesic conditions (*Holcus lanatus, Teucrium scordonia)* (Figure 3. 3 A). Controlling for habitat type, samples with taller swards and a deeper soil litter layer had higher axis one and lower axis two scores (Table 3. 3). Sample ordination scores show that young and pole trackways (both verge and track) occur in the part of the ordination characterised by xeric disturbance-tolerant indicator plant species, while prefell trackway samples tend to have higher axis one scores, associated with the part of the ordination characterised by more mesic species

(Table 3. 3; Figure 3. 3 B,C). Samples from permanent open sites had a wide range of indicator plant species composition (Figure 3. 3 D).

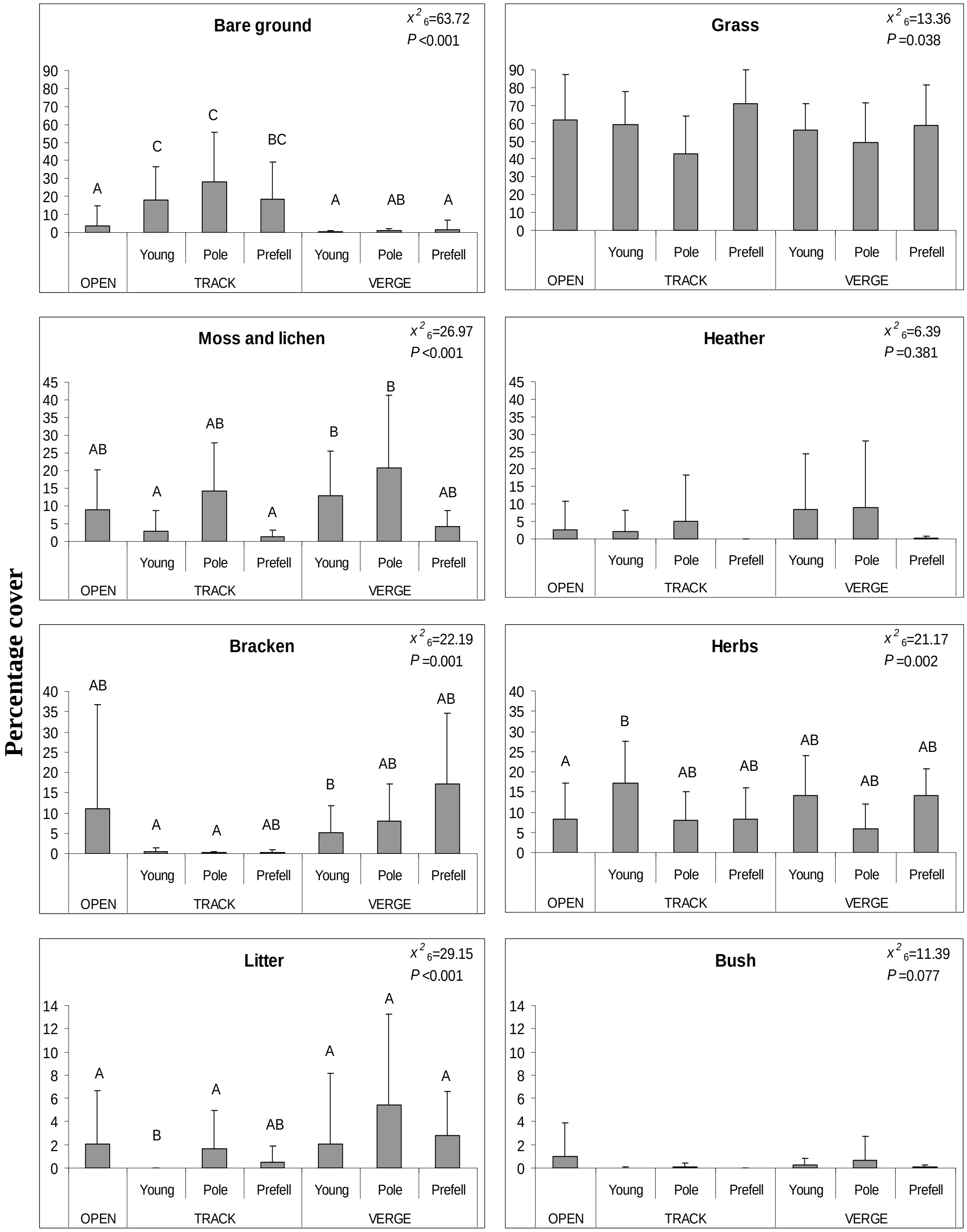


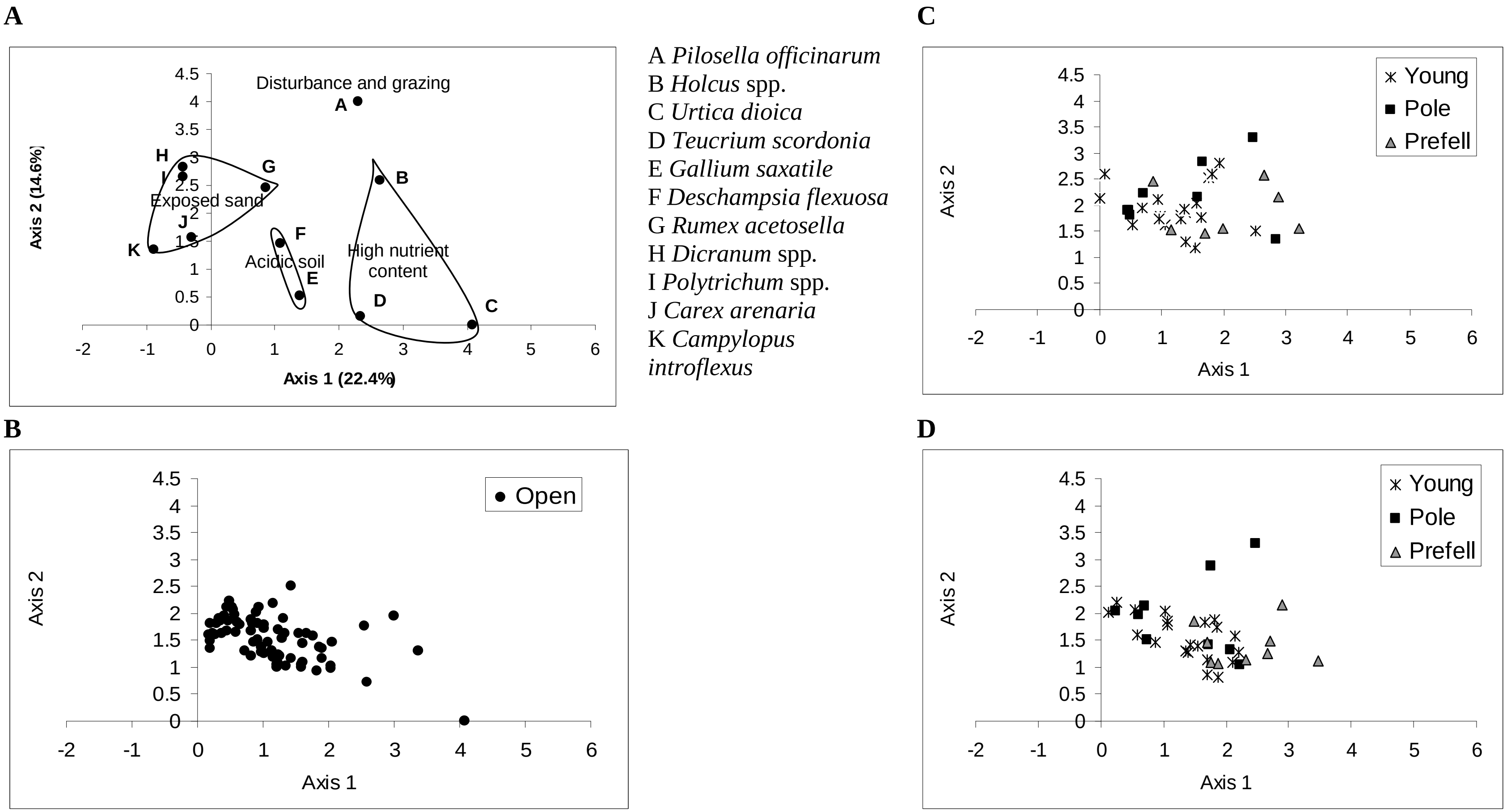
Figure 3. 2; Mean ± SD of percentage cover (per transect) of each of eight vegetation parameters, compared among open patches, and tracks and verges of three trackway classes (prefell, pole and young). Results of nonparametric Kruskal-Wallis test comparing the seven habitat types for each vegetation parameter are shown. Columns marked with the same letter do not differ significantly according to Steel-Dwass multiple comparisons test.

Table 3. 2; Mean ± SD of sward height (cm), litter layer thickness (cm), soil organic matter content (g organic matter/100g of oven-dry soil) and soil pH in seven habitat types in Thetford Forest. Results of nested GLM (site nested within habitat type) for sward height and of parametric GLMs for soil organic matter content, litter layer thickness and soil pH are shown; means sharing the same superscript do not differ according to Sidak pairwise comparisons.

	OPEN	TRACK			VERGE				df	*F*	*P*
		Young	Pole	Prefell	Young	Pole	Prefell				
Sward height	3.9±3.0 ^{a}	0.8±0.4 ^{c}	0.8±0.7 ^{bc}	1.0±0.7 ^{bc}	3.1±1.0 ^{a}	2.7±1.1 ^{abc}	2.9±1.2 ^{ab}	HabType	6	15.8	<0.001
								site(HabType)	80	2.9	<0.001
Litter layer thickness	4.3±1.5 ^{b}	1.3±0.8 ^{a}	1.2±0.8 ^{a}	1.4±0.9 ^{a}	3.2±1.0 ^{b}	2.8±1.2 ^{b}	3.2±1.0 ^{b}	HabType	6	16.24	<0.001
Soil organic matter	3.6±2.9 ^{a}	3.0±1.0 ^{a}	2.8±1.0 ^{a}	3.5±1.1 ^{a}	3.8±1.8 ^{a}	3.5±1.2 ^{a}	4.0±1.2 ^{a}	HabType	6	0.92	0.486
Soil pH	4.5±0.5 ^{a}	5.5±0.9 ^{a}	5.3±0.9 ^{a}	5.4±0.6 ^{a}	5.1±0.8 ^{a}	4.9±0.9 ^{a}	4.8±0.9 ^{a}	HabType	6	2.15	0.057

Table 3. 3; Mean ± SD sample scores of seven types of permanent open habitat on the first two DCA ordination axes performed on presence and absence data for 11 indicator plant species. Results of nested GLMs are shown; groups sharing superscripts do not differ significantly according to Sidak pair-wise comparisons.

	OPEN	TRACK			VERGE				df	*F*	*P*
		Young	Pole	Prefell	Young	Pole	Prefell				
Ax 1	1.16±0.75 ^{a}	1.24±0.61 ^{a}	1.34±0.96 ^{a}	2.14±0.85 ^{b}	1.35±0.61 ^{a}	1.39±0.82 ^{a}	2.32±0.66 ^{b}	HabType	6	22.99	<0.001
								site(HabType)	80	7.83	<0.001
Ax 2	1.52±0.41 ^{b}	1.93±0.44 ^{b}	2.19±0.62 ^{b}	1.98±0.51 ^{b}	1.55±0.40 ^{a}	1.96±0.74 ^{b}	1.40±0.39 ^{a}	HabType	6	11.50	<0.001
								site(HabType)	80	2.46	<0.001



A *Pilosella officinarum*
B *Holcus* spp.
C *Urtica dioica*
D *Teucrium scordonia*
E *Gallium saxatile*
F *Deschampsia flexuosa*
G *Rumex acetosella*
H *Dicranum* spp.
I *Polytrichum* spp.
J *Carex arenaria*
K *Campylopus introflexus*

Figure 3. 3; DCA axis 1 and axis 2 scores of presence of 11 indicator plant species in each transect; A) indicator plant species scores; B) open patches sample scores; C) trackways tracks samples scores for three trackway classes; D) trackway verges sample scores for three trackway classes.

The weather conditions in 2005 were very close to the long term means for 1990-2007, with only June and August temperatures below the long-term average (Table 3. 4). In 2006 there was much more fluctuation in air temperature and rainfall during spring/summer months with May, June and July temperatures above and August temperatures below the long-term average. May and August 2006 were very wet with August values being the highest of the entire 1990-2007 period. July 2006 on the contrary was very dry with rainfall below the long-term average (Table 3. 4).

Table 3. 4; A) Mean ± SD monthly air temperature (°C) and B) cumulative monthly rainfall ± SD (mm) in May, June, July and August for the period 1990 - 2007 inclusive and in sampling years 2005 and 2006. Results of one sample t-test comparisons of 2005 and 2006 monthly means, to each corresponding 1990-2007 monthly mean, are shown.

A

month	**1990-2007**	**2005**		**2006**	
May	11.6±1.2	11.3	Ns	12.7	t_{17}= -3.70; P=0.002
June	14.5±0.9	15.0	t_{17}= -2.32; P=0.033	15.5	t_{17}= -4.70; P<0.001
July	16.8±1.3	16.7	Ns	19.8	t_{17}= -9.52; P<0.001
August	16.7±1.3	15.4	t_{17}= 4.27; P=0.001	15.4	t_{17}= 4.2; P=0.001

B

month	**1990-2007**	**2005**		**2006**	
May	47.0±29.4	42.7	Ns	103.2	t_{17}= -8.12; P<0.001
June	58.7±49.3	50.9	Ns	38.2	Ns
July	54.0±26.6	63.5	Ns	25.7	t_{17}= 4.5; P<0.001
August	62.0±40.6	45.9	Ns	163.7	t_{17}= -10.63; P<0.001

The differences in weather conditions between 2005 and 2006 sampling year may have affected vegetation structure. In the 12 open patches that were all sampled in both years, cover of moss + lichen (Wilcoxon signed ranks test Z= -2.93; P=0.003) was on average 3.5 percent and the cover of bush (Wilcoxon signed ranks test Z= -2.25; P=0.024) on average 0.4 percent less in 2006 than in 2005. The cover of grass (Wilcoxon signed ranks test Z= -2.90; P=0.004) was on average 6.2 percent greater in 2006.

CARABIDS IN PERMANENT OPEN AREAS WITHIN THETFORD FOREST

A total of 70 species were recorded from permanent open habitats within the forest landscape with seven eurytopic species, ten woodland (two of which are nationally scarce), four open woodland, six moorland, 19 GHS (seven of which are nationally scarce) and 24 arable associated species (two of which are nationally scarce).

Of the 19 GHS species, four were only recorded in one of the habitats (Figure 3. 4). *Harpalus pumilus* (nationally scarce A; two individuals found in different sites) and *Masoreus weterhalii* (nationally scarce A; two individuals found in different sites) were only found in trackways, while *Calathus ambiguous* (nationally scarce B; three individuals all from the same site) and *Badister bullatus* (no status; two individuals found in different sites) were only found in open patches. In view of the very low numbers of individuals of these species captured, apparent restrictions to one or other landscape element are likely to be due to chance sampling.

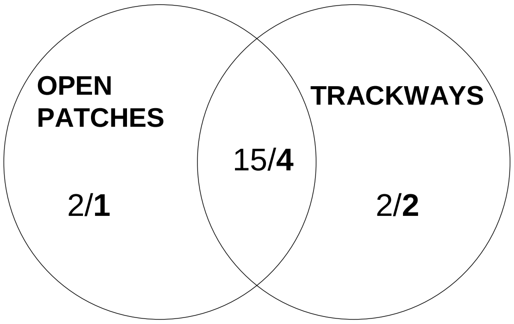


Figure 3. 4; Number of GHS species / nationally scarce GHS species of ground beetles found in open patches and trackways within Thetford Forest.

The composition of the carabid community analysed by principal component analysis explained 41.4 percent of the total variance, and showed strong non-random structure (Figure 3. 5; Figure 3. 6). The group of species associated with grassland, heathland or sandy habitats (GHS species) had significantly higher mean axis one scores than eurytopic and woodland species, with other habitat association groups (arable, moorland, open woodland) were intermediate (Figure 3. 5, Table 3. 5 A). Species scores of different habitat association groups did not differ significantly on the second PCA axis (Table 3. 5 A).

There were significant differences in sample scores of open areas, young, pole and prefell trackways on both PCA axes (Table 3. 5 B). Considering the first PCA axis, samples from open areas and young rides had the highest scores (corresponding to high scores of GHS, moorland and arable species), pole trackways had intermediate and prefell trackways had the lowest scores (corresponding to the lower scores of eurytopic and woodland species) (Table 3. 5 B). Surprisingly, open areas had very low scores on the second PCA axis and differed significantly from trackways of all classes, indicating a difference in species composition that does not directly relate to a difference in relative abundance of carabid species habitat association groups. There were no differences among scores of trackways belonging to different classes on the second axis (Table 3. 5 B). Carabids with low scores on the second axis, that were also notably abundant in open habitat samples include species such as *Pterostichus madidus* (eurytopic), *Carabus nemoralis* (eurytopic), *Carabus problematicus* (woodland), *Amara lunicollis* (open woodland) and *Harpalus rufipes* (arable) (Figure 3. 5). Of these, the first three are among the largest species found in this study (average body size of *Pterostichus madidu*s is 16.0mm, of *Carabus nemoralis* 23.0mm and of *Carabus problematicus* is 24.0mm) and all three are wingless.

Despite the differences in weather and in some vegetation parameters the carabid community composition of open patches did not differ between 2005 and 2006 in PCA sample scores either on the first axis (Wilcoxon signed ranks test Z= -0.94; P=0.347) or on the second axis (Wilcoxon signed ranks test Z= -1.96; P=0.050). Following these results I combined data collected in both years for further analysis.

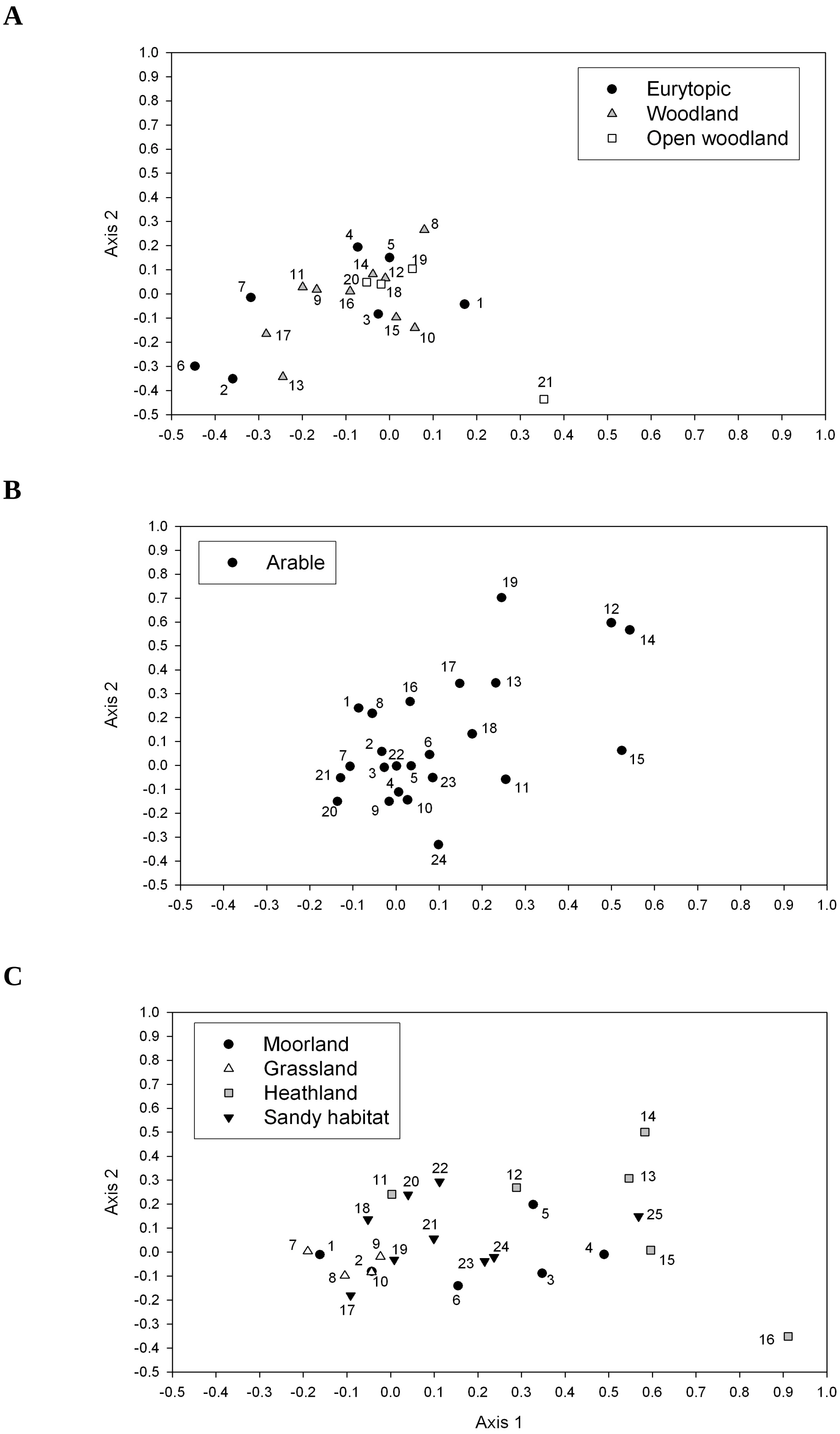


Figure 3. 5; PCA axis 1 and axis 2 species scores carabid community in permanent open habitats in Thetford Forest. A) eurytopic, woodland and open woodland; B) arable; C) moorland, grassland, heathland, sandy habitat associated species.

Species names of Figure 3.5 A

EURYTOPIC	**WOODLAND**	**OPEN WOODLAND**
1 *Bradycellus harpalinus*	8 *Badister sodalist* – W	18 *Synuchus vivalis* – OW,A,G
2 *Carabud nemoralis*	9 *Calathus rotundicollis* – W,A,S	19 *Agonum muelleri* – OW,A,G
3 *Loricera pilicornis*	10 *Leistus spinibarbis* – W,A,S	20 *Syntomus truncatellus* – OW,A,S
4 *Nebria brevicollis*	11 *Stomis pumicatus* – W,G	21 *Amara lunicollis* – OW,M,G
5 *Notiophilus biguttatus*	12 *Notiphilus palustris* – W,G	
6 *Pterostichus madidus*	13 *Carabus problematicus* – W,G,M	
7 *Pterostichus strenuus*	14 *Licinus depressus* – W,G,S	
	15 *Pterostichus quadrifoveolatus* – W,H	
	16 *Cychrus caraboides* – W,M	
	17 *Pterostichus niger* – W,M,G	

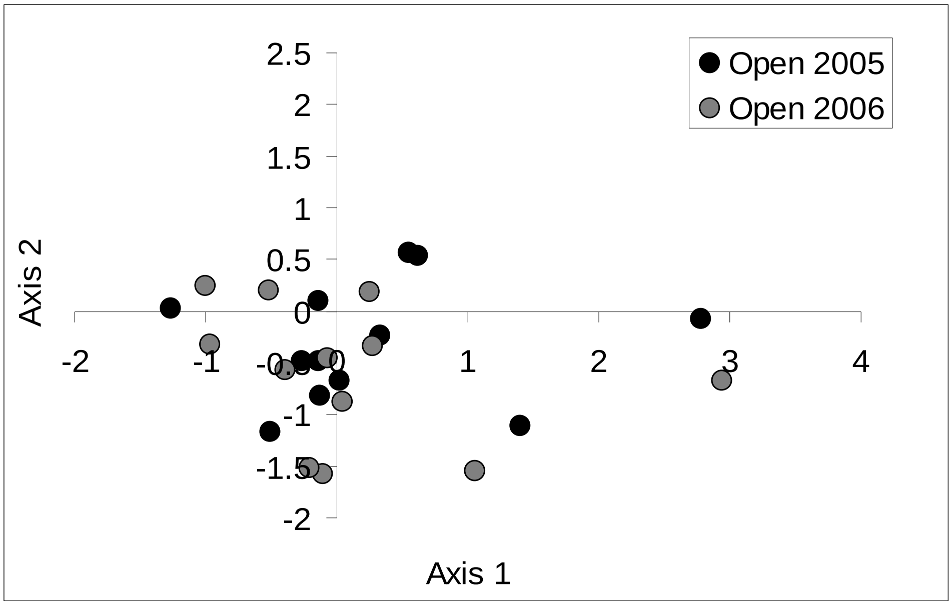
Species names of Figure 3.5 B

ARABLE		
1 *Bembidion lampros* –A	9 *Pterostichus melanarius* –A,G	17 *Harpalus affinis* – A,G,S
2 *Leistus ferrugineus* –A	10 *Poecilus cupreus* –A,G	18 *Harpalus rubripes* – A,G,S
3 *Ophonus rufibarbis* –A	11 *Anisodactylus binotatus* –A,G	19 *Amara aenea* – A,G,S
4 *Amara apricaria* –A	12 *Calathus fuscipes* –A,G	20 *Poecilus versicolor* – A,M,G
5 *Platyderus depressus* –A	13 *Calathus fuscipes* –A,G	21 *Trechus obtusus* – A,M,H
6 *Bembidion quadrimaculatum* –A	14 *Syntomus foveatus* –A,G,H	22 *Asaphidion sterlini* – A,S
7 *Curtonotus aulicus* –A,G	15 *Harpalus smaragdinus* –A,G,H	23 *Amara eurynota* – A,S
8 *Amara plebeja* –A,G	16 *Harpalus tardus* – A,G,S	24 *Harpalus rufipes* – A,S

Species names of Figure 3.5 C

MOORLAND	**HEATHLAND**	**SANDY HABITATS**
1 *Harpalus latus* – M,G	11 *Masoreus wetterhalli* – H,S	17 *Amara convexior* – S
2 *Amara communis* – M,G	12 *Nebria salina* – H,S	18 *Harpalus pumilus* – S
3 *Cicindela campestris* – M,G,H	13 *Harpalus anxius* – H,S	19 *Notiophilus substriatus* – S
4 *Notiophilus germinyi* – M,G,H	14 *Amara tibialis* – H,S	20 *Amara fulva* – S
5 *Notiophilus aquaticus* – M,G,S	15 *Calathus erratus* – H,S	21 *Amara montivaga* – S
6 *Olisthopus rotundatus* – M,H,S	16 *Harpalus rufipalpis* – H,S	22 *Harpalus attenuatus* – S
GRASSLAND		23 *Amara bifrons* – S
7 *Amara familiaris* – G,H,S		24 *Calathus ambiguous* – S
8 *Badister bullatus* – G,H,S		25 *Amara equestris* - S
9 *Amara lucida* – G,H,S		
10 *Panageus bipustulatus* – G,S		

A



B

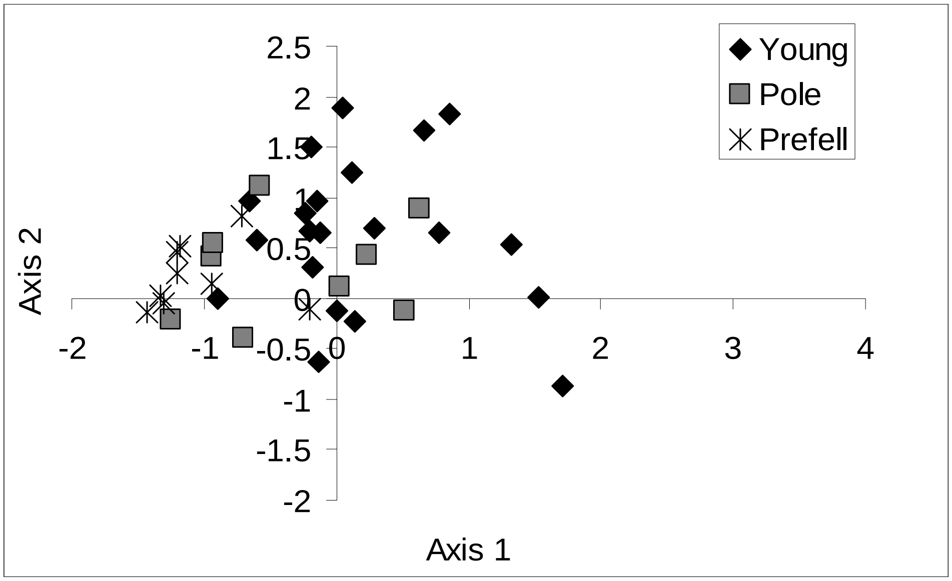


Figure 3. 6; PCA axis 1 and axis 2 scores of Carabid community in each sampled site of permanent open habitats in Thetford Forest. A) open patches in 2005 and 2006; B) sample scores of sites in each of the trackway classes.

Table 3. 5; Mean ± SD scores on the first two axes of a PCA of carabids in Thetford forest and results of GLMs. A) Species scores, considering six habitat preference groups of carabids and B) sample scores for four main habitat types of permanent open space. Means sharing superscript do not differ significantly according to Tukey post-hoc test.

A

	Eurytopic	Woodland	Open woodland	Arable	Moorland	GHS		*F*	*P*
Axis 1	-0.15±0.23^{a}	-0.08±0.25^{a}	0.08±0.19^{ab}	0.10±0.20^{ab}	0.19±0.25^{ab}	0.20±0.31^{b}	HabType	3.61	0.006
Axis 2	-0.06±0.21^{a}	-0.03±0.17^{a}	-0.06±0.25^{a}	0.10±0.26^{a}	-0.02±0.12^{a}	0.07±0.20^{a}	HabType	1.28	0.284

B

	Open	Trackways				*F*	*P*
		Young	Pole	Prefell			
Axis 1	0.19±1.02^{a}	0.20±0.71^{a}	-0.33±0.70^{ab}	-1.05±0.34^{b}	HabType	5.64	0.002
Axis 2	-0.46±0.63^{a}	0.63±0.76^{b}	0.31±0.51^{b}	0.21±0.33^{b}	HabType	12.00	<0.001

To confirm if PCA sample scores were mostly determined by the abundance of just the two most abundant GHS species within Thetford Forest (*Harpalus rufipalpis* and *Nebria salina*) I checked for correlations between sample scores on PCA axis 1 and number and abundance of overall, non-dominant and nationally scarce GHS species. In both trackways and open patches PCA axis 1 scores are very highly correlated not only with overall GHS species richness and abundance but also with non-dominant and nationally scarce GHS species richness and abundance (Table 3. 6).

Table 3. 6; Spearman rank correlation coefficients of axis 1 PCA sample scores in trackways and open patches and the number and abundance of overall, non-dominant and nationally scarce GHS species. ** indicate that correlation is significant below 0.01 level.

	Overall GHS		Non-dominant GHS		Nationally scarce GHS	
	Number of species	Abundance	Number of species	Abundance	Number of species	Abundance
Trackways	0.638**	0.928**	0.594**	0.785**	0.432**	0.580**
Open patches	0.688**	0.946**	0.693**	0.702**	0.354ns	0.634**

As the habitat preference groups of species represent a clear ecological gradient on the first PCA axis, I focused on exploring which environmental variables affect the scores of samples on this axis. Open patches samples with higher PCA axis 1 scores had significantly greater cover of bare sand (*Rs*=0.574; *P*=0.003, *n*=24) and of moss + lichen (*Rs* =0.603; *P*=0.002) and significantly lower sward height (*Rs*= -0.743; *P*<0.001) and shallower thickness of soil litter layer (*Rs*= -0.413; *P*=0.045). There was no effect of patch area or longevity on scores of open patch samples on the first PCA axis.

In trackways, the sample scores on the first PCA axis increase significantly with increasing trackway width (*Rs*=0.462; *P*=0.005, *n*=36), cover of heather in the tracks (*Rs*=0.334; *P*=0.047) and cover of moss + lichen in verges (*Rs*=0.486; *P*=0.003). Trackways sample scores decrease with greater age of the youngest surrounding plantation (*Rs*= -0.596; *P*<0.001), greater cover of grass in tracks (*Rs*= -0.520; *P*=0.001) and cover of litter in verges (*Rs*= -0.358; *P*=0.032).

Minimal models of the effect of environmental variables on carabid assemblage composition in trackways, showed that the age of the adjacent plantations, trackway width, cover of moss + lichen and of litter in verges explained 56 percent of variability in sample scores of PCA on the first axis (Table 3. 7 A). In open patches sward height, depth of soil litter layer and cover of grass explained 61 percent of variability in sample scores of PCA on the first axis (Table 3. 7 B).

Table 3. 7; Minimal models of effects of environmental variables on sample scores of individual sites on the first axis of PCA for A) trackways (*n*=36) and B) open patches (*n*=24). Mean ± SD values of environmental variables are given. All variable considered in the tests are given in the table; environmental variables had minimal collinearity.

A

		PCA axis 1 sample scores
		F (df) *P* (B SE)
Model	Mean ± SD	15.73 (32,36) <0.001
Age of youngest adjacent trees (years)	25.3±18.0	12.050 (32,36) 0.001 (-0.02±0.01)
Trackway width (m)	13.8±8.3	14.54 (32,36) 0.001 (0.04±0.01)
Cover of moss and lichen in verges (%)	13.4±14.8	8.66 (32,36) 0.006 (0.02±0.01)
Adjusted R^2		0.558

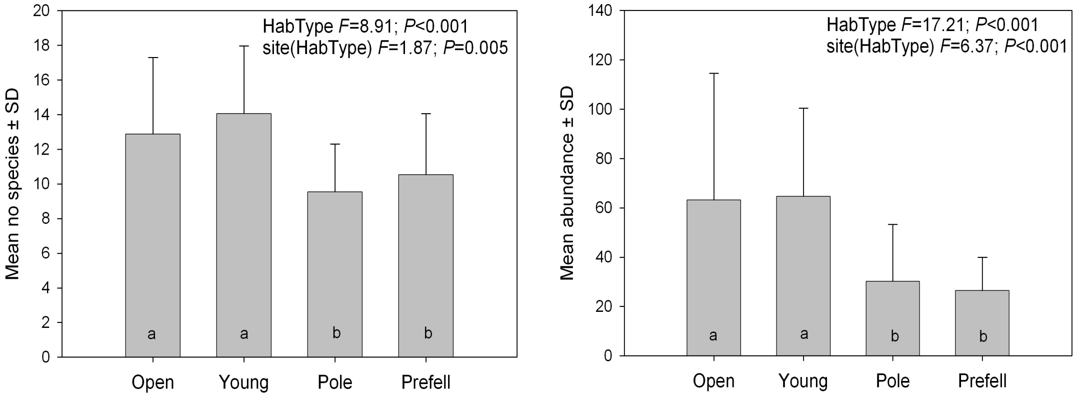
B

		PCA axis 1 sample scores
		F (df) *P* (B ± SE)
Model	Mean ± SD	18.76 (21,24) <0.001
Sward height (cm)	3.9±3.0	11.95 (21,24) 0.002 (-0.16±0.05)
Depth of soil litter layer (cm)	4.4±1.6	19.02 (21,24) <0.001 (-0.38±0.09)
Adjusted R^2		0.607

When exploring community structure further I found that for all habitat association groups except woodland species the species richness and abundance of individuals differed markedly among four open space habitat types (open patches, and trackways adjacent to prefell, pole and young stands) (Figure 3. 7). Open patches had similar species number and abundance of woodland, open woodland, moorland and non-dominant and overall GHS species as the young trackways (Figure 3. 7). However there was a greater number of eurytopic and lower abundance of arable species compared to young trackways. Compared to trackways adjacent to pole aged stands, open patches had higher abundance of eurytopic species, higher species richness and abundance of open woodland species and higher abundance of overall GHS species. Compared to prefell trackways open patches had lower species richness and abundance of eurytopic species and higher species richness and abundance of overall and non-dominant GHS species and abundance of open woodland species (Figure 3. 7).

Focusing on three classes of trackways, trackways adjacent to young plantations had the highest species richness and abundance of arable and overall GHS species and the highest abundance of non-dominant GHS and open woodland species (Figure 3. 7). Prefell trackways on the other extreme had the highest number and abundance of eurytopic species and the lowest species richness and abundance of both overall, and non-dominant, GHS species. Pole trackways had for most of the habitat association groups intermediate values: similar number and abundance of eurytopic species and species richness of non-dominant GHS species as young trackways and similar abundance of open woodland species, species richness and abundance of overall GHS and arable species as prefell trackways (Figure 3. 7).

All species



Eurytopic species

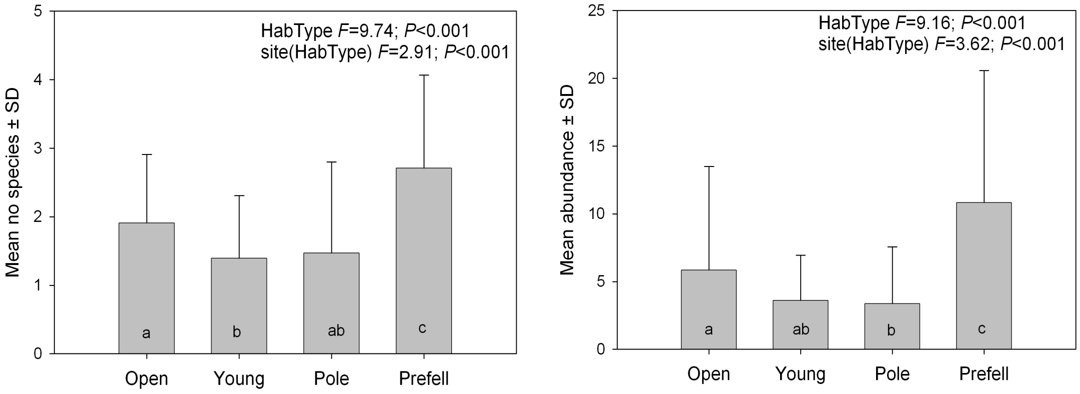
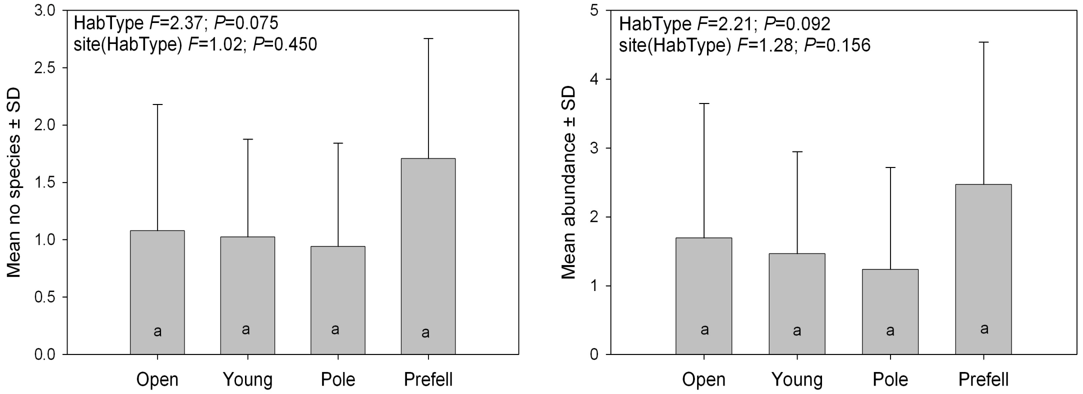
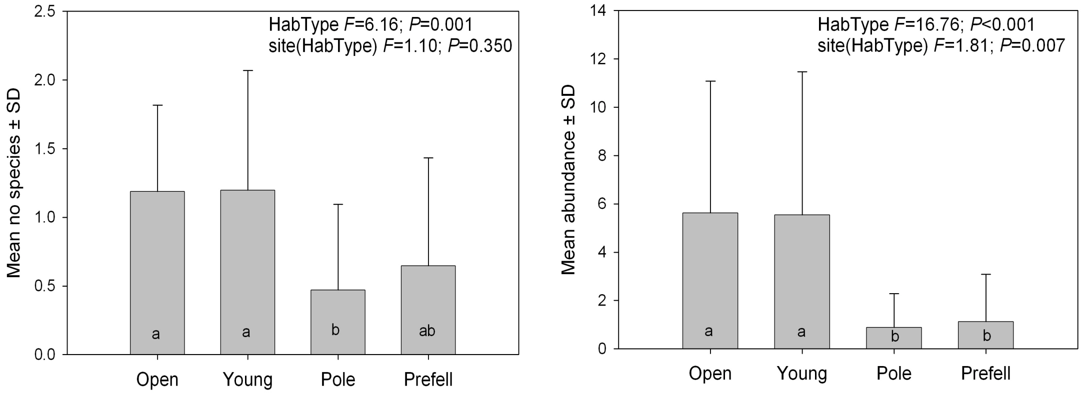


Figure 3. 7; Mean ± SD number and abundance of all, eurytopic, woodland, open woodland, moorland, GHS, non-dominant GHS and arable associated carabid species per transect in open patches and three classes of trackways (young, pole and prefell). Results of nested GLM (site nested within habitat type) are given. Columns marked with the same letter do not differ significantly according to Sidak pair-wise comparisons.

Woodland species



Open woodland species



Moorland species

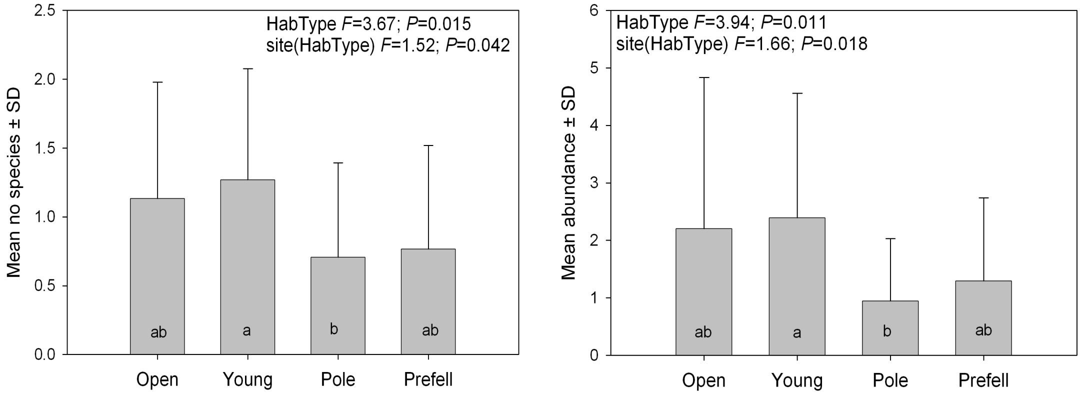
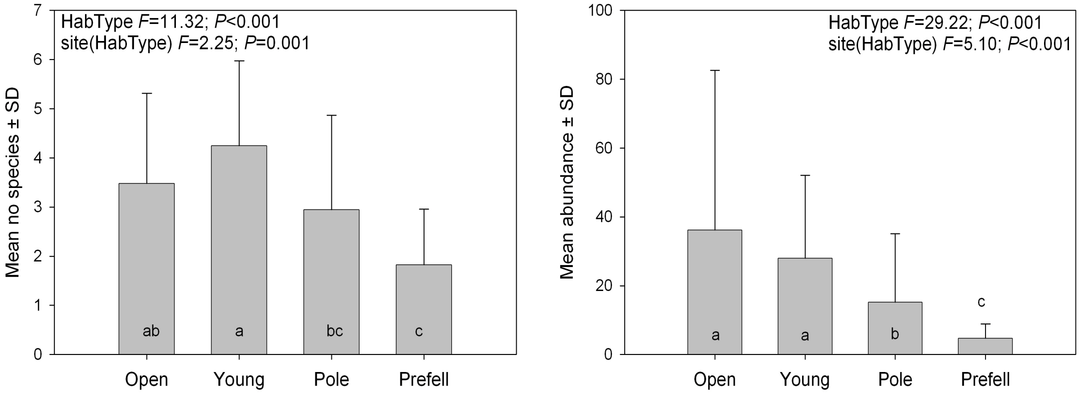
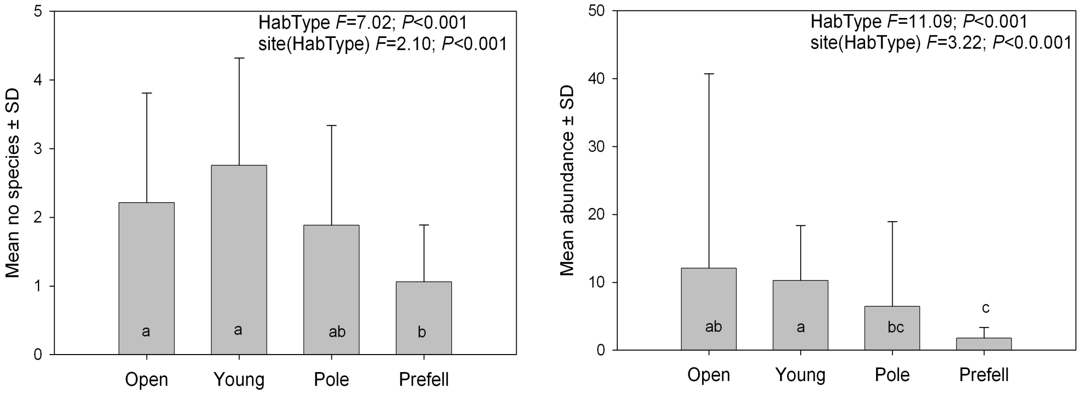


Figure 3. 7 continued

GHS species



GHS non-dominant species



Arable species

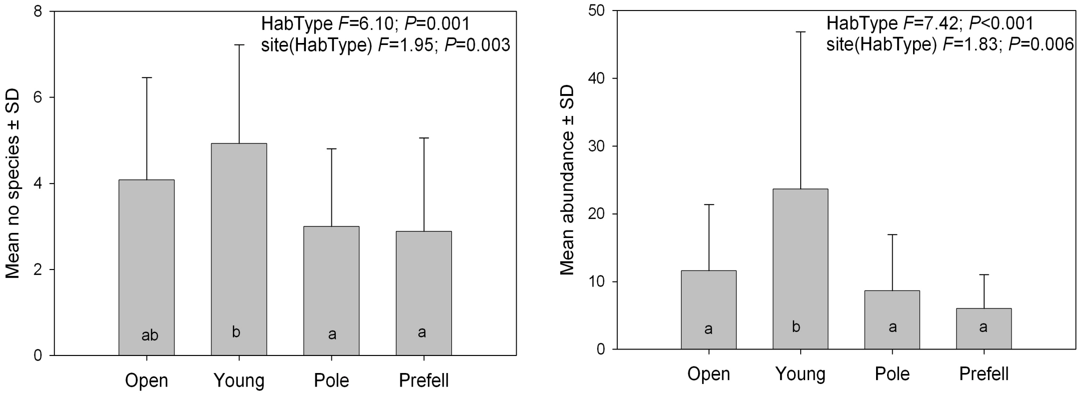


Figure 3. 7 continued

As the class of young trackways was the most suitable for open habitat specialists and as there was considerable variation in number and abundance of GHS species within this class I checked the effect of environmental variables on the number and abundance of species associated with grassland, heathland and sandy habitats within this class. Abundance of overall GHS species increased with greater cover of bare ground in verges (*Rs*=0.454; *P*=0.044, *n*=21) and decreased with increasing sward height (*Rs*= -0.603; *P*=0.005) and cover of bush (*Rs*= -0.472; *P*=0.035) in verges and greater cover of grass (*Rs*= -0.535; *P*=0.015) in tracks. For species richness of overall, non-dominant (i.e. excluding *H.rufipalpis* and *N.salina*) and nationally scarce GHS species and for the abundance of non-dominant and nationally scarce GHS species I could not find any significant correlations with the measured environmental variables (trackway orientation and width, sward height, soil characteristics and percentage cover of eight vegetation parameters). The correlation between abundance of overall and non-dominant GHS species is very strong (*Rs*= -0.736; *P*<0.001) but the variability in abundance of non-dominant GHS species was lower than for overall GHS species (Figure 3. 7) which might have reduced statistical power in tests of effect of environmental variables.

Forage harvesting as the current management for conservation within Thetford Forest does not seem to have any effect on carabid community. Within the class of young trackways there was no difference in PCA sample scores between conservation managed and non-systematically managed trackways on the first axis (*t*=0.80; *P*=0.096) nor on the second axis (*t*=0.041; *P*=0.967).

Discussion

Even though permanent open areas within the forest represent only 10 percent of the area they support important ground beetle diversity including 19 species restricted to dry grassland, heathland or open sandy habitats (GHS) of which seven are nationally scarce. Fifteen GHS species were found in both open patches and trackways and four species were only recorded from just one of the two permanently open habitat types. All four of these more restricted species were very rare, with only two or three individuals captured. It is possible that these four species are present in both types of permanent open habitats, but were not recorded due to their low abundance, low frequency, and consequent low probability of detection.

For trackways I found that the surrounding matrix greatly affects the conditions within these linear strips of open habitat. Older and taller trees will affect the amount of sunlight and the moisture conditions in trackways, thus affecting vegetation structure. The resulting direct and indirect effects on microclimate and microhabitat will affect carabid community composition, favouring species that prefer mesic conditions. Trackways adjacent to young plantations on at least one side, had the highest number and abundance of species associated with open habitats (GHS, arable, moorland and open woodland species) which were less abundant in trackways adjacent to pole stage plantation and practically disappeared from trackways located within prefell aged stands. The opposite was true for eurytopic and woodland associated species which were less abundant in young trackways but increased in trackways adjacent to pole and prefell aged stands. These results show that trackways do not represent a continuous network of habitats suitable for GHS species, but that trackways surrounded by younger plantations may have potential to function as stepping stones, distinct habitat patches, or as corridors, for these species. Pole and prefell trackways do not support resident populations of the open habitat species. These linear elements could potentially represent corridors for dispersal of carabids associated with open habitats, but only if individuals of these species will enter into trackways passing through these unfavourable and less preferred habitats, which seems unlikely given their virtual absence in pitfall trap material collected from these trackways.

Of the habitat quality characteristics measured in trackways the combined cover of mosses and lichen in verges was an important predictor of carabid community composition, with greater cover of moss and lichen favouring open area specialists. Within the class of young trackways, lower sward height in verges and less cover of grass in tracks were the strongest predictors of high abundance of overall GHS species, but not of non-dominant GHS species. From this I can conclude that these vegetation structure parameters affected mostly the two most abundant species *Harpalus rufipalpis* and *Nebria salina*. However, it may be that the low frequency (species richness) and low abundance of other GHS species reduced statistical power and thus the ability to detect such effects for the group once these two abundant species had been excluded. Nevertheless, the strong positive correlation between the abundance of these two species, and the abundance of other open ground GHS species suggests that good quality habitat for *H. rufipalpis* and *N. salina* also serves as an indicator of good quality habitat for other specialists carabids of disturbed dry grassland, heathland and sandy conditions.

For open patches I also found a strong effect of habitat quality on the presence of open habitat specialist species. Lower sward height, shallower soil litter layer thickness and greater cover of bare sand and of combined mosses and lichen, make patches more suitable for open area specialists.

As the habitat characteristics of open spaces within Thetford Forest depend mostly on the management techniques used, I investigated the effects of forage harvesting as current management for conservation within Thetford Forest, on vegetation and carabid community structure in trackways. Managed sites had lower cover of grass in tracks but I did not find any effect on the combined cover of mosses and lichen, on the cover of bare sand or on sward height, which were strong predictors of good quality habitat for open specialist species in trackways and open patches. There was also on differences in carabid community composition between managed and non-managed sites. Previous studies in Breckland demonstrated the importance of rabbit grazing for persistence of short swards containing a large component of lichens, cushion forming mosses and winter annuals which are features characteristic of historic Breckland grass heaths (Dolman & Sutherland 1992). Dolman & Sutherland (1992, 1994) suggest rotovation as a suitable management technique which creates disturbance and provides areas of bare soil.

Sampling the same open patches in both 2005 and 2006 enabled me to test the effect of year on the carabid assemblage structure. There was no difference in assemble structure between the two sampling years, even though the weather during the sampling months in 2006 differed from the longer term mean, with a very wet May, June and August and on the other extreme a very hot and dry July. This implies that the weather does not have pronounced effects on carabid community over periods of just one or two generations, even though it may have some effect on vegetation structure.

Surprisingly and to the contrary of predictions of island biogeography theory (Preston 1962, McArthur & Wilson 1967) I could not find any effect of patch size on number and abundance of GHS species present. Absence of effect of patch size is also not in accordance with findings of empirical studies of effects of fragmentation on heathland invertebrates where fewer heathland species of ground beetles were found in smaller (deVries *et al.* 1996) and more isolated patches (Webb 1989). A possible explanation for this is that the limited range in area of the open habitat patches sampled in the current study did not provide the magnitude of variation required to detect such effects. The area of open patches in current study was between 1.2ha and 35ha compared to 0.5ha to 1500ha in study by deVries and colleagues (1996) and 0.1ha to 500ha in study by Webb (1989). Alternatively, the edge effects in small heathland sites in these two published studies affected habitat quality and consequently suitability for heathland invertebrates. Furthermore, in the present study there were important differences in habitat structure for both patch area and longevity that may confound results.

However, despite the relatively low range of variation in open patch area, the results of this study did not provide any evidence that these large patches supported either a greater species richness or greater abundance of open habitat specialists, or nationally scarce GHS species, than open habitat arranged as narrow linear elements. In trackways, wider sites had a higher proportion of open specialists, which was most likely not due to increased area but because the negative effect of older surrounding trees was reduced with increasing width of trackway. The fact that I did not find any effect of width on presence and abundance of open specialists within the class of young trackways, where increase in width would mean increase in area, supports this interpretation. Thus wider trackways are more likely to support GHS species when trees in the surrounding plantation reach unfavourable age. For a given area or quantity of open space, arranging this as a linear strip not a discrete area provides much greater potential for connectivity between isolated locations. Thus the results of this study support arranging the finite amount of open space permitted by forest design constraints as linear networks, rather than as discrete stepping stones or as large patches of ‘heathland’.

Finally, these results show that habitat quality plays the most important role in determining the suitability of remnants of semi-natural habitat such as heathland for carabids specialised for this habitat. When planning conservation of semi-natural habitats we must consider not only connectivity but also the great importance of the structure and quality of these habitats, which mostly depends on the type of management used. There is no evidence to suggest that creating large areas of poor quality reverted heathland will offer any substantive benefit.

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Appendix 3. A; Location and characteristics of 12 permanent open patches in Thetford Forest sampled in 2005 and 2006 including forest management block, area of patches, number of years since the trees were removed (longevity) and mean ± SD soil pH.

	Block	**Area (ha)**	**Longevity (years)**	**Grazed by sheep (Y/N)**	**Mean ± SD soil pH**
Open 1	Croxton	4.1	10	N	3.8±0.1
Open 2	Lynford	3.5	13	N	4.1±0.1
Open 3	Lynford	5.7	2	Y	4.2±0.1
Open 4	Lynford	4.2	Never planted	N	4.5±0.1
Open 5	Lynford	1.2	Never planted	N	4.7±0.1
Open 6	Lynford	1.9	11	N	4.2±0.1
Open 7	Lynford	22.0	10	N	4.3±0.1
Open 8	High Lodge	3.4	7	N	5.6±0.3
Open 9	High Lodge	1.3	19	N	4.1±0.1
Open 10	Elveden	5.6	19	N	5.2±0.6
Open 11	Elveden	4.8	19	N	5.1±0.2
Open 12	Elveden	35.0	4	Y	4.6±0.1

Chapter 4: Colonisation of newly created open space within Thetford Forest plantation

Abstract

Within the lowland conifer plantations of Thetford Forest in Breckland, conservation interests focus on open spaces and their potential for conservation of heathland species. In addition to the network of trackways and occasional open patches representing permanent open spaces, ephemeral open areas are created by clear-felling management of plantations. Treatment by herbicides and ploughing of clear-fells before replanting reduced variability in vegetation structure thus providing a controlled opportunity to study effects of isolation and patch size on early colonisation of these areas by ground beetles. Colonisation by open-habitat associated species was very fast, with 35 species not recorded in mature forest stands colonising newly created open areas within three years after removal of trees. I did not find any effects of patch size and isolation from permanent open patches and young restocks ("stepping stones") nor from trackways ("corridors") on number and abundance of colonisers. These results indicate that on the current scale of management of Thetford Forest, connectivity among open areas is sufficient for persistence of open-habitat associated species.

Introduction

Land-use changes over the past 200 years have greatly reduced the area of heathland in the UK (Moore 1962, Farrell 1993, Rose *et al.* 2000) with approximately 58,000ha of heathland remaining. The re-establishment of lowland heathland is a priority within the UK Biodiversity Action Plan, with a target of 6,000ha to be created by 2005 (Biodiversity Steering Group 1995).

The goal of most restoration projects is to return ecosystems to a pre-defined reference conditions by manipulating physical environment and/or vegetation structure (Block *et al.* 2001). However, relying on the so called “field of dreams” assumption: build it and they will come (Palmer *et al.* 1997), does not take into account findings of island biogeography studies that show important effects of isolation and patch size on colonisation (McArthur & Wilson 1967). Similarly, numerous studies of invertebrate metapopulations, or patchily distributed sub-populations, have also found important effects of isolation on probability of occupancy or colonisation (Thomas & Harrison 1992, Hanski & Thomas 1994, Hill *et al.* 1996, Hanski 1999). Differences in species diversity between recreated areas and natural areas confirm this (Grimbacher & Catterall 2007, Nakamura *et al.* 2008).

However the conclusions of island biogeography theory may not hold for all types of habitats. Brose (2003) showed the size of habitat and its isolation did not influence species richness of carabid beetles in temporary wetlands in Germany. Small and colleagues (2006) found similar results for carabid beetles of derelict sites in England with assemblages being principally related to habitat quality such as substrate type and vegetation community. Therefore investigation of colonisation of early successional habitats such as heathland is needed to assess potential for restoration of such areas (Littlewood *et al.* 2009).

Effects of isolation on the number and abundance of species present in habitat patches can be obscured by confounding effects of differences in habitat quality (Sutcliffe *et al.* 1997, Baguette *et al.* 2000, Hill *et al.* 2001, Hill *et al.* 2002). The results of Chapter three indicate that for GHS carabid species, the most important predictor of species richness and abundance is habitat quality which could obscure less pronounced effects of isolation and patch size. Therefore a study of early colonisation of patches by ground beetles, where habitat has been homogenised by spraying of vegetation and ploughing, may provide a controlled opportunity to examine effects of isolation and patch size on colonisation. The Thetford Forest plantation in Breckland provides a useful opportunity for such an experiment, as replicate patches of similar soil, age and treatment are available simultaneously.

Methods

Within Thetford Forest, lowland conifer plantation in Eastern England, approximately 10 percent of the land is left unplanted to comply with forestry commission guidelines (UKWAS 2006) and an additional 10 percent of the forest landscape comprises ephemeral open space created by clear-felling. As shown in Chapter two these open areas support important carabid species associated with heathland and other open habitats which are the focus of conservation interests in Thetford Forest. Open habitats are of two types: 1) open patches and early successional stands of different shape and size located throughout the forest landscape and 2) a network of trackways of different width that separate polygonal compartments in which the forest was originally planted.

Management by clear-felling creates ephemeral open areas (clear-felled and young replanted stands) in which open conditions persist for 5-7 years after felling (Eycott *et al.* 2006), with the species richness and abundance of open habitat carabids peaking in two to three year old plantations and declining to extirpation in five to seven years old plantations (Lin 2005). Following the current forestry standard guidelines (UKWAS 2006) the minimum interval between felling of adjacent areas is 7-15 years. Thus adjacent stands cannot act as a source of open habitat colonists for the newly felled and cleared stands.

Most clear-felled stands are treated with herbicides (atrazine, glyphosate, asulam and asulox) at the end of the last growing season before replanting, to control competitor plant species, mostly bramble *Rubus fruticosus* and bracken *Pteridium aquilinum* (Eycott *et al.* 2006). Herbicides can reduce the abundance of carabid larvae (Holland 2002). On more alkaline soils tree stumps are removed before replanting but such stands were not included in my experiment. In all stands planting lines are ploughed, before stands are replanted with approximately 50cm tall nursery grown trees. Plough lines consist of single furrows, c. 30cm deep and c. 50cm wide, separated by 2-2.5 metres (Forest Enterprise 2001). The overlying vegetation (e.g. tussocks of *Deschampsia flexuousa* or rhizomes of bracken) as well as the litter and organic humus layers are turned back from furrow margins, exposing mineral soil and creating alternating bands of undisturbed vegetated inter-furrows, overturned turfs and litter, and linear furrows of exposed mineral sand or soil. Tree seedlings are planted approximately 1.6 metres apart and are initially too short, and so thin, that they do not affect the environmental conditions within furrows. Thus recently clear-felled stands provide open unshaded conditions, but with little or no exposed bare ground and a deep litter layer, while newly planted stands provide complex heterogeneity with exposed soil and remnant vegetation. Hereafter, I refer to clear-felled but unplanted stands as “felled-unplanted”, and recently replanted stands as “restocks”. Replanted stands in the first growth season after planting are referred to as “zero year stands”.

To explore early stages of colonisation by ground beetles after clear-felling and replanting of pine trees in Thetford Forest I sampled 12 felled-unplanted stands and four zero year restocks in 2005 and eight zero year restocks in 2006 (all of which were also sampled in 2005 as felled-unplanted). Sampled stands were deliberately selected to be more or less isolated (closer or further away) from sources of colonisers, using an *a priori* assumption that permanent patches of open habitat, wide open trackways and 1-5 years old plantations all represent sources of colonisers (following results described in Chapter two and in (Lin 2005)). Selected felled-unplanted stands were felled during the autumn/winter season in 2003/2004 and were in the second growth season after felling when they were sampled in spring/summer 2005. All zero year stands were sampled in the first spring/summer season following ploughing and replanting. Sampled stands varied in size from 3.1 to 14.5ha with average size 8.7ha ± 4.0 SD.

For collecting ground beetles I used pitfall traps (transparent plastic cups, 7.5cm deep and 6.5 cm in diameter) which were filled with ethylene glycol as killing and preserving solution. In each of the sampled stands three transects, each of five pitfall traps, were set up on four occasions during spring/summer months (mid May, mid June, end of July and end of August 2005 and 2006). Traps within each transect were approximately 30 metres apart to ensure their independence. In restocks transects were placed across the direction of planting rows therefore traps were placed randomly with some traps within and some between the ploughing furrows. Pitfall traps were opened for five consequent days on each of the four sampling occasions. The relatively short trapping period was used to ensure consistent and standardised catching effort between replicate stands, as long trapping periods become less consistent as an unpredictable proportion of traps within any transect may become non-functional due to filling with sand, filling with rainwater, or damage by mammals. Niemela and colleagues (1990) showed that, in boreal forest in Finland, two sampling periods of ten days each, totalling 20 days, provided good representation of the carabid fauna compared to continuous trapping throughout the season. On each sampling occasion captures from each of the five pitfalls in transect were pooled prior to identification; thus the individual transect is the unit of sample replication.

Carabids collected were identified to species level according to Lindroth (1974), while nomenclature followed Luff (2007). The information on species habitat preference, average body size, wing morphology and distribution within UK (number of $10km^2$ squares within UK occupied by the species) were obtained as described in Chapter two. This chapter focuses on new arrivals / colonisers of newly created open areas which were classified into two groups:

1) "all colonisers" – defined as all species (regardless of their habitat preference) that were not found in mature (prefell growth stage) but that were found in felled-unplanted and zero year stands.
2) "open colonisers" - those species associated with open habitats (arable, moorland, grassland, heathland and sandy habitats) that were not found in prefell aged stands, but that were found in felled-unplanted and zero year stands.

The percentage cover of eight vegetation parameters, the presence and absence of 11 indicator plant species and sward height were measured as described in Chapter three. In felled-unplanted and zero year stands only nine indicator species were observed (*Teucrium scordonia, Rumex acetosella, Urtica dioica, Deschampsia flexuosa, Holcus* spp. (*H. lanatus* + *H. mollis*), *Carex arenaria*, *Polytrichum* spp. *(P. juniperum + P. piliferum), Dicranum* spp. (*D. bonjeani + D. scoparium*) but *Pilosella officinarum (*syn.*Hieracium pilosella), Gallium saxatile* and *Campylopus introflexus* were not present.

Isolation of stands was measured in several different ways, to test alternative hypotheses concerning the spatial dynamics of carabid populations that give differing emphasis to stepping stone patches, refugia or dispersal corridors. Landscape structure data were obtained from the Thetford Forest shape-file provided by Forestry commission using ArcGIS 9.2. I calculated the amount of four types of sources within 600m buffers centred on perimeter of each stand, resulting in four types of isolation measures:

1) the area of permanent open patches and one to five year old restocks,

2) the area of one to five year old restocks (permanent open patches were excluded as carabid assemblage has been shown to vary greatly with habitat quality of which information is only available for 12 sampled patches as described in Chapter three)
3) the area of all trackways, and
4) the area of trackways passing through young plantations (less than 20 years) or through permanent open patches (in Chapter three trackways surrounded by plantation younger than 20 years have been shown to support high species richness and abundance of GHS species).

The area of trackways was calculated using the length measured in shape-file multiplied by 14 metres, which is the average width of trackways within Thetford Forest (see Chapter two). A buffer of 600m was selected as the distance beyond which individuals are very unlikely to be able to reach the newly created open area within a lifetime (Baars 1979).

As buffers were centred on perimeters of stands differing in size, larger stands had larger buffer areas. To overcome these differences in buffer areas I calculated the percent of source habitat within the buffer by dividing the amount of sources within the buffer by the area of the buffer and multiplying this with 100. The percent cover of source habitat within 600m buffers ranged between 0.3 and 25.3% with average 10.5% ± 7.2 SD for the first isolation measure, between 0 and 19.7% with average 4.7% ± 5.1 SD for the second isolation measure, between 7.0 and 13.0% with average 9.2% ± 1.4 SD for the third isolation measure and between 2.0 and 7.0% with average 4.6 % ± 1.5 SD for the fourth isolation measure.

DATA ANALYSIS

All data for vegetation structure, vegetation composition, sward height and caught ground beetles was pooled on the level of stand prior to analysis.

To determine which of the eight vegetation parameters measured have similar percentage cover within each of the habitat types I used non-parametric Kruskall-Wallis test (using

SPSS 16 software) and nonparametric Steel-Dwass pair-wise comparisons (using Kyplot 5.0 software) for multiple comparisons.

Change in percentage cover of eight vegetation parameters due to ploughing and replanting was tested using paired t-test of eight stands sampled as felled-unplanted in 2005 and resampled as zero year restocks in 2006.

Principal component analysis (PCA) was used to analyse composition (presence of 11 indicator plant species) and structure (percentage cover of eight vegetation parameters) of ground vegetation in sampled sites (using CANOCO for Windows 4.5 software). Indicator plant species were grouped according to associated habitat characteristic into three groups and PCA species scores of the three groups were compared using general linear model (GLM) with Tukey post-hoc test for pair-wise comparisons. To compare PCA sample scores of vegetation composition among eight stands sampled as felled-unplanted in 2005 and as zero year stands in 2006, paired t-test was used. A t-test of PCA sample scores of all sampled stands was used to estimate the difference in vegetation structure (percentage cover of eight vegetation parameters) between felled-unplanted and zero year stands.

T-tests were used to compare body size of carabid species and their distribution in UK (number of $10km^2$ within UK occupied by the species) between the open associated species found in prefell and those only found in newly created open areas. Information about carabid species and their abundance in prefell forest stands was obtained from data collected by (Lin 2005) in two stands in 2001 and in five stands in 2002 using the same protocol as was used in the present study. Presence of wings (mactopterous and dimorphic winged species *versus* brachipterous species) in open-habitat species recorded from prefell and those only found in open areas was compared using Fisher exact probability test.

I used Spearman rank correlations to test weather abundance of open coloniser species in clear-fells and restocks was associated with their body size and Mann-Whitney test to decide whether abundance of winged open coloniser species was higher than that of brachipterous open coloniser species.

The difference in species richness and abundance of GHS, all coloniser and open coloniser species in eight stands sampled as felled-unplanted in 2005 and resampled as zero year stands in 2006 was examined using paired t-tests.
Paired t-tests were also used to compare the difference in number of individuals caught in felled-unplanted and in zero year stands for each of the species within the groups of all colonisers, open colonisers and GHS species.

To test the effects of four isolation measures on species richness and abundance of all colonisers, open colonisers and GHS species in both felled-unplanted and zero year stands I used separate GLMs for each of the isolation measure with habitat type (felled-unplanted / zero year) as fixed factor and isolation measure as covariate.

To explore the effect of vegetation structure (as summarised by PCA of vegetation cover of eight selected parameters), the sward height and the size of the patch on species richness and their abundance of all coloniser, open coloniser and GHS species, univariate Spearman rank correlations were used. Any confounding intercorrelation between the habitat measures were checked using Spearman rank correlations and habitat measures with minimal colinearity were used.

Results

SOIL AND VEGETATION CHARACTERISTICS OF CLEAR-FELLS AND YOUNG RESTOCKS

In felled-unplanted stands grass, herbs and litter had on average the largest cover and bare ground and moss the lowest, with bracken and bush having intermediate values (Figure 4. 1). In ploughed and restocked stands bare ground had the largest cover followed by litter, grass and herbs cover. Bush had the lowest cover in restocked areas with bracken and moss having intermediate values (Figure 4. 1). Heather was not found in any of the sampled felled-unplanted or in the sampled restocked stands. Ploughing and replanting of felled stands greatly increased the percentage cover of bare ground and reduced the cover of moss, bracken and grass but it had no effect on the cover of litter, herbs and bush (Table 4. 1). The large difference in amount of bare ground is also evident in scores of samples on the first axis of vegetation cover PCA, which differ significantly between felled-unplanted and zero year stands (*t*=10.0, *P*<0.001) (Figure 4. 2). On the second PCA axis of vegetation cover the differences among samples are mostly driven by the amount of grass and bush (high scores) and bracken (low scores). The variability in the scores of samples on the second PCA axis is much higher in felled-unplanted sites (mean is 0.2 ± 1.3 SD) than in zero year restocks (mean is -0.2 ± 0.7 SD) indicating homogenisation of vegetation structure by herbicide treatments and ploughing.

Average sward height in felled-unplanted sites was 3.3cm ± 2.0 SD and 1.5cm ± 0.9 SD in restocked sites.

Table 4. 1; Change in percentage cover of eight vegetation parameters from felled-unplanted to zero year old in eight stands, tested by paired t-tests (*n* = 8 pairs).

	Bare ground	Litter	Moss	Bracken	Grass	Herbs	Bush
t	-10.0	0.8	3.20	3.5	2.7	1.0	1.4
P	**<0.001**	0.444	**0.015**	**0.010**	**0.030**	0.367	0.209

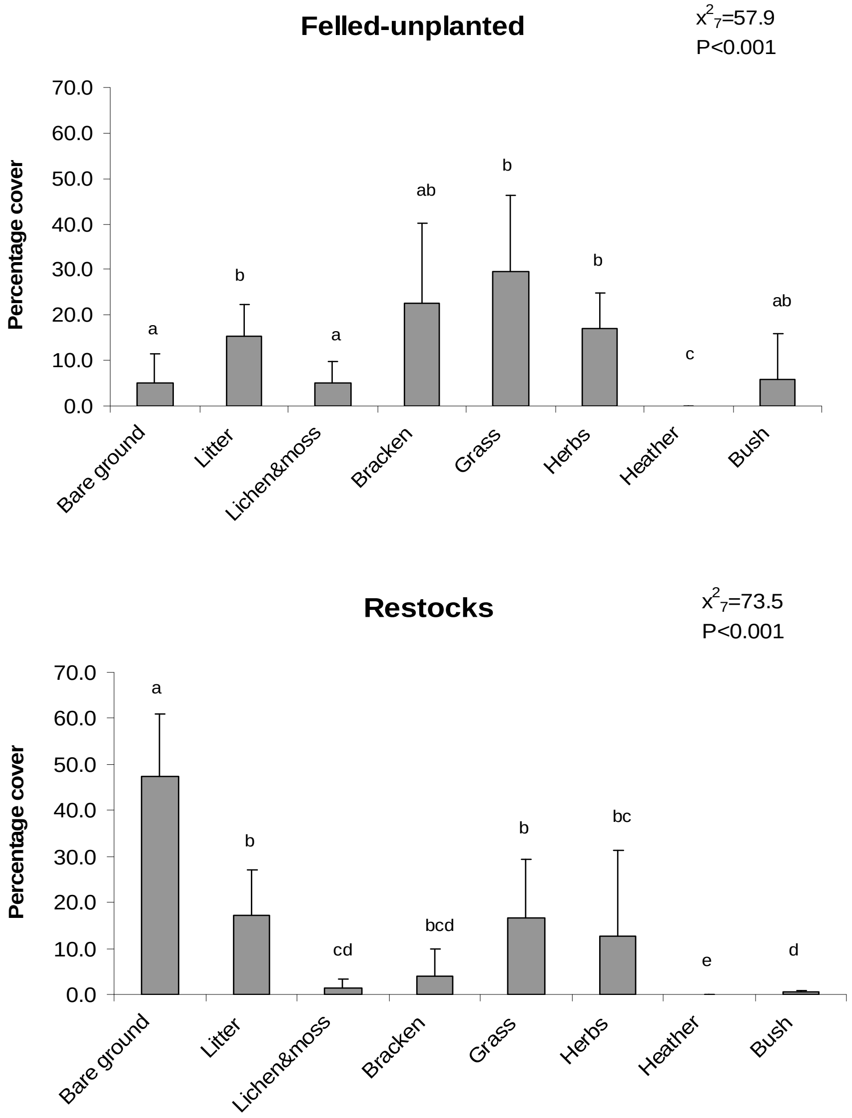

Figure 4. 1; Average + SD percentage cover of eight vegetation parameters in felled-unplanted and restocked stands. Results of Kruskall-Wallis test are shown. Vegetation parameters with the same letters do not differ significantly according to Steel-Dwass pair-wise comparisons.

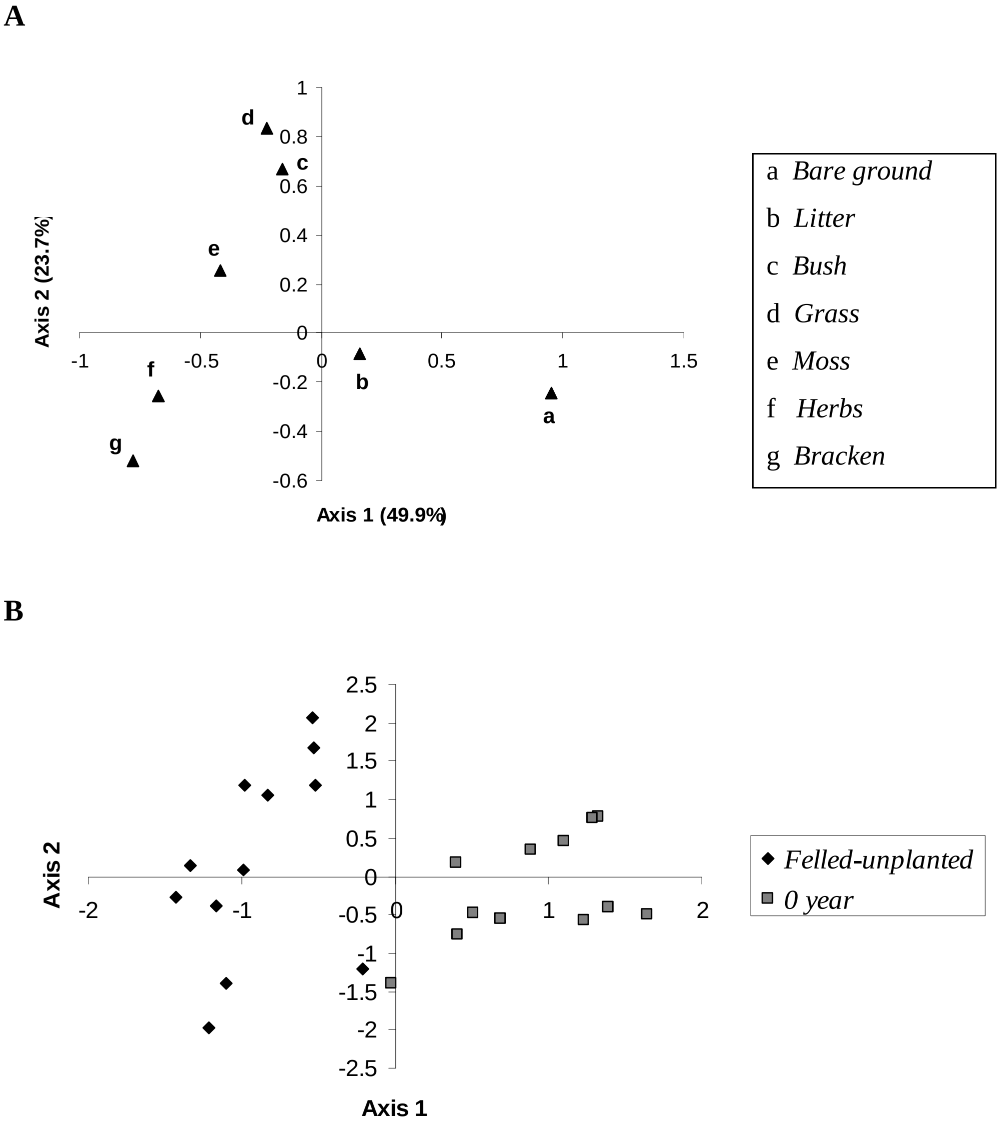

Figure 4. 2; First and second axis scores of PCA of percentage cover of seven vegetation parameters. A) species scores; B) sample scores of felled-unplanted and zero year restocks.

PCA species scores for the presence and absence of indicator species in clear-felled and zero year stands, form three clearly separated groups on the first axis ($F_{2,6}$=8.3; P=0.019) with species associated with high soil nutrient content having the highest values, species associated with exposed sand having intermediate values and species growing on acidic soils the lowest values (Figure 4. 3 A). There are no differences among these three groups of plant indicator species on the second PCA axis ($F_{2,6}$=3.1; *P*=0.119; Figure 4.3 A).

Ploughing and replanting of clear-felled stands does not affect presence of indicator species, as there were no differences in PCA sample scores of the indicator species on the first axis (paired t-test; *t*= -0.47; *P*=0.651) or on the second axis (paired t-test; *t*=2.12; *P*=0.072) among clear-felled stands that were resampled as zero year plantations (Figure 4. 3 B,C).

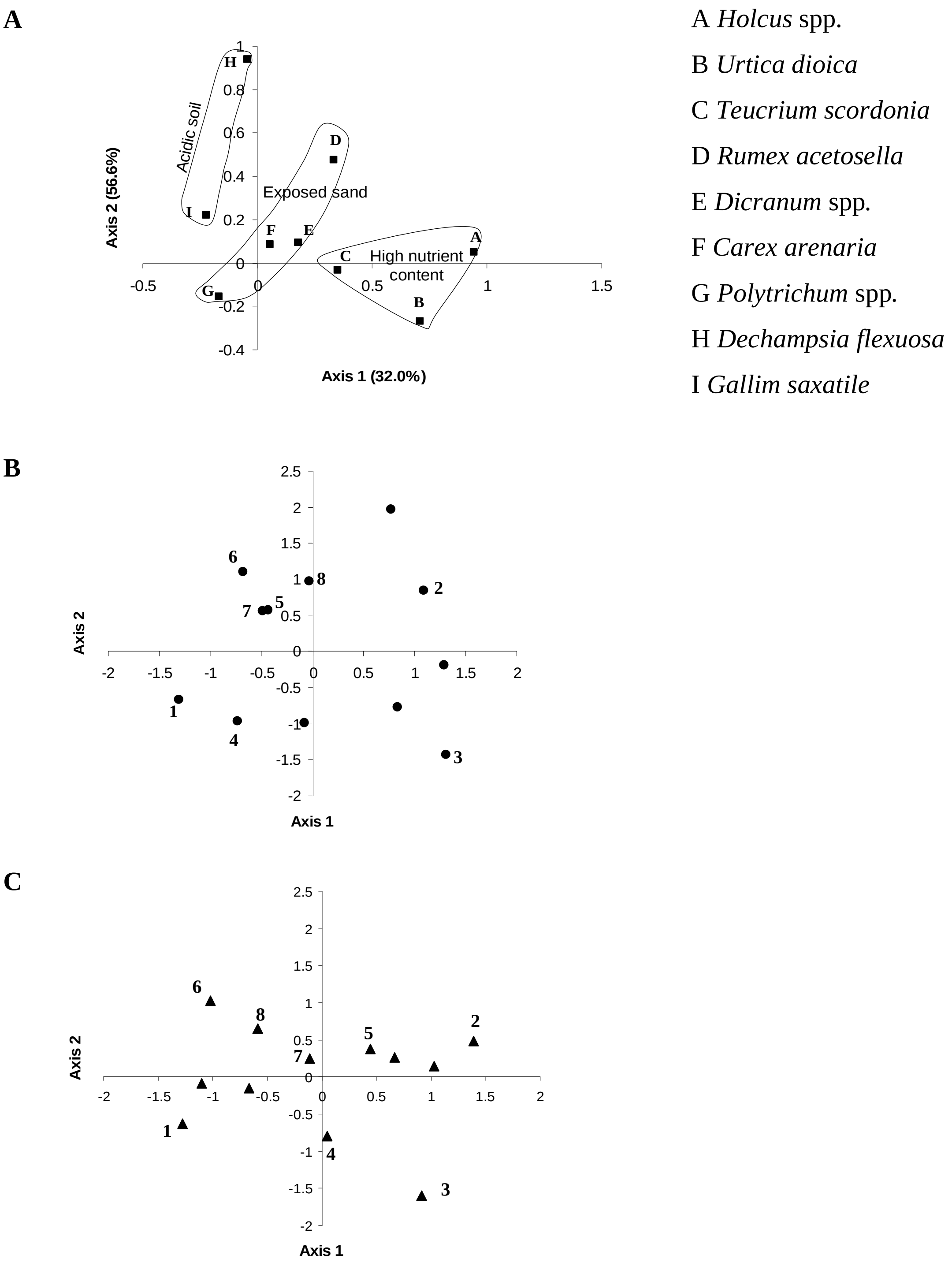

Figure 4. 3; Scores of the first two axes of PCA of presence and absence of nine indicator plant species for A) species B) felled-unplanted stands and C) zero year restocked stands. Sample scores of eight stands that were sampled as clear-fells and resampled as restocks share the same numbers.

COLONISATION OF EPHEMERAL OPEN AREAS BY CARABID BEETLES

During sampling of felled-unplanted and zero year stands in 2005 and 2006 I caught 5,038 carabids belonging to 64 species; of these 4,403 individuals belong to 23 species that are also present in mature forest before it is cut (prefell stage). Forty one species (635 individuals) colonise stands after felling and replanting and 35 of these species (553 individuals) are associated with open habitats (arable, moorland, grassland, heathland and sandy habitats), of which 15 are exclusive to grassland, heathland and sandy habitats (Figure 4. 4).

Three species (*Harpalus rufipalpis, Nebria salina* and *Amara convexior*) associated with grassland, heathland and sandy habitats (GHS) are also found in prefell stands. These are three of the most abundant GHS species found within the forest landscape together representing 86% of all individuals belonging to GHS species (ie. 8870 individuals - see Chapter two) but only nine individuals were collected in prefell stands.

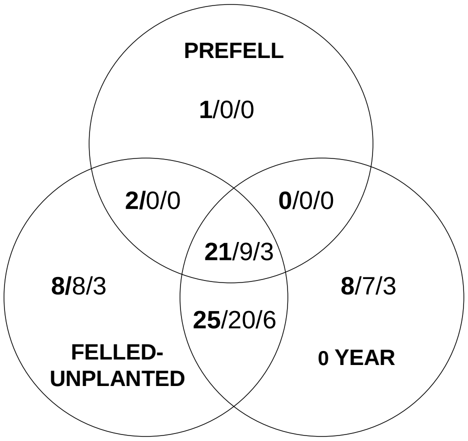

Figure 4. 4; Total number of species / number of species associated with open habitats (arable, moorland, grassland, heathland and sandy habitats)/ number of GHS species of ground beetles in prefell, felled-unplanted and zero year restocks and the number of species that overlap between habitat types.

Species associated with open habitats (arable, moorland, grassland, heathland and sandy habitats) that were also found in prefell are on average larger in size (average size: 10.3mm ± 1.9 SD, *n* =9) than species only found in clearfells and restocks (average size: 7.6mm ± 3.0 SD; *n*=35; *t*=2.7; *P*=0.011;). There are no differences among open associated species also found in prefell and those only found in newly created open areas in wing morphology (ratio winged : brachipterous for species also found in prefell is 8:1; for open colonisers not found in prefell is 30:5; x^2=0.644) nor in distribution within the UK (average number of 10km^2 within UK occupied by the species also found in prefell is 291.0 ± 207.9 SD; for open colonisers not found in prefell is 415.8 ± 274.9 SD; *t*=-1.27; *P*=0.212).

The abundance of open colonisers in newly created open areas was not determined by the species characteristics as there was no difference in abundance of winged (mean abundance of individuals per stand is 15.5 ± 34.0 SD) and brachipterous species (mean abundance of individuals per stand is 17.6 ± 21.4 SD; *U*=54.5; *P*=0.328). The abundance of open coloniser species in newly created open areas was not correlated with species size (*Rs*=0.231; *P*=0.182).

Of the 41 species which colonised newly created areas eight species were only found in clear-felled stands, eight only in zero year stands and 25 species in both clear-felled and zero year stands (Figure 4. 4). Twenty one of these coloniser species were very rare represented by three or fewer individuals, which altogether represented 6.0 percent of individuals of all colonisers. Out of 15 GHS species caught in newly created open spaces nine were represented by fewer than three individuals and represented 0.9 percent of GHS individuals caught. Two most abundant GHS species in sampled clear-fells and restocks were *Harpalus rufipalpis* (1733 individuals: 83.1%) and *Nebria salina* (211 individuals: 10.1%).

The increase in time since felling by one year and the change from felled-unplanted to restocks did not affect the species richness of GHS, all colonisers and open associated coloniser species (Table 4. 2). However, the abundance of each of these three groups increased substantially in zero year compared to felled-unplanted areas (Table 4. 2; see also **Error! Reference source not found.**). This increase is driven mostly by great increase in the abundance of few species: abundance of *Cicindela campestris* increased from two individuals in felled-unplanted to 173 in zero year restocks; abundance of *Harpalus rufipalpis* increased from 606 in felled-unplanted to 1127 in restocks; abundance of *Nebria salina* increased from 19 in felled-unplanted to 192 in restocks.

Table 4. 2; Change in species richness and abundance from felled unplanted to zero year restocks, of GHS species, all colonisers not found in prefell and open associated colonisers not found in prefell. Eight felled-unplanted stands sampled in 2005 and resampled in 2006 after planting, are compared by paired t-tests.

	Felled-unplanted	**0 yr**	*t*	*P*
All colonisers abundance	16.8 ± 6.3	40.8 ± 15.5	-4.7	**0.002**
All colonisers No. spp.	9.8 ± 2.1	10.0 ± 3.2	-0.2	0.840
Open colonisers abundance	13.3 ± 4.1	37.9 ± 15.8	-4.6	**0.003**
Open colonisers No. spp.	8.0 ± 2.2	8.0 ± 2.4	<0.1	1.0
GHS abundance	61.0 ± 45.8	144.3 ± 85.3	-4.9	**0.002**
GHS No. spp.	5.1 ± 1.5	4.8 ± 1.8	0.5	0.612

When the change in number of individuals caught in felled-unplanted compared to zero year restocks was examined for each of the species there were no differences for the species in the group of all colonizers (Wilcoxon signed ranks test *Z*= -0.79; *P*=0.429), for the species in the group of open colonizers (Wilcoxon signed ranks test *Z*= -1.34; *P*=0.181) and for GHS species (Wilcoxon signed ranks test *Z* = -1.01; *P*=0.313).

None of the tests of effects of the four isolation measures on number and abundance of each of the three groups of species (all colonizers, open colonizers and GHS species) in newly created open spaces were statistically significant. As these tests also included habitat type as an independent variable they also confirmed previously described differences in abundance of all three groups of species between felled-unplanted and 0 year restocks (results of tests of effect of isolation measures and habitat type on number of species and abundance are in the appendix A and B, respectively).

When exploring effects of vegetation structure and sward height on number and abundance of colonisers and GHS species in felled-unplanted stands I found stands with greater cover of grass and less cover of bracken (higher PCA axis 2 scores of vegetation structure) had higher abundance of GHS species (Table 4. 3 A). The size of stands was excluded from this analysis as it was correlated with vegetation structure with larger stands having lower PCA axis 1 (*Rs*= -0.671; *P*=0.017) and axis 2 scores (*Rs*= -0.685; *P*=0.014).

Restocked stands with less bare ground (lower scores on PCA axis 1 of vegetation structure) had higher number of species of colonisers and stands with higher vegetation sward height had higher abundance of colonisers and GHS species (Table 4. 3 B). In restocked stands with higher average sward height there was greater cover of grass and bushes (higher scores on PCA axis 2) therefore the vegetation cover PCA scores on the second axis were excluded from analysis.

Table 4. 3; Spearman rank correlation coefficients of environmental variables (vegetation structure, sward height and stand size) with minimal collinearity and the number and abundance of all colonisers, open colonisers and GHS species in A) felled-unplanted and B) zero year stands.

A

	PCA axis 1 of vegetation structure	PCA axis 2 vegetation structure	Sward height (cm^2)
All colonisers abundance	-0.021	-0.204	0.176
All colonisers number of species	-0.126	-0.410	0.018
Open colonisers abundance	0.049	-0.331	-0.035
Open colonisers number of species	-0.039	-0.429	-0.105
GHS abundance	0.231	**0.594***	0.210
GHS number of species	0.330	-0.019	-0.304

(* = P<0.005)

B

	PCA axis 1 of vegetation structure	Sward height (cm^2)	Size of the stand (m^2)
All colonisers abundance	-0.245	**0.623***	-0.343
All colonisers number of species	**-0.573***	0.258	0.315
Open colonisers abundance	-0.168	**0.727****	-0.441
All colonisers number of species	**-0.624***	0.254	0.370
GHS abundance	0.214	**0.604***	-0.351
GHS number of species	-0.375	0.182	0.244

(* = P<0.005 and ** = P<0.001)

Discussion

Sampling of clear-fells and zero year restocks showed that colonisation of these early succession stages by ground beetles is very fast with 41 species colonising newly created areas within three years after removal of trees. Most of these new arrivals (35 species) are associated with open habitats and approximately half of these are associated with grassland, heathland and sandy habitats. Colonisation of newly created open habitats by open habitat associated carabid species has also been observed in studies of clear-felled managed plantation in Northeast England (Butterfield 1997), within boreal forest in Finland (Heliola *et al.* 2001, Koivula 2002, Koivula & Niemela 2003), in conifer plantation in Berkshire, UK (Fuller *et al.* 2008) and in low-lying conifer plantation in Southern Ireland (Mullen *et al.* 2008). In Finland, open-habitat species increased in abundance in the openings one year after logging (Koivula & Niemela 2003).

The abundance of all colonisers, open colonisers and GHS carabid species increased in zero year patches (following ploughing) compared to felled-unplanted patches, but I did not detect any change in the number of species. Pihlaja and colleagues (2006) found similar results, with higher abundance of open habitat carabids in harrowed than in undisturbed clear-fells in Finland. However, this change in abundance of individuals was not consistent for all the species and the significant increase is mostly due to a very large increase in abundance of *Cicindela campestris*, *Harpalus rufipalis* and *Nebria salina*. *Cicindela campestris* (‘Green Tiger Beetle’) has preference for sandy and heathy ground (Lindroth 1974) whose adults are active already early in the spring and take to flight extremely readily (Luff 1998). This species appears to be highly mobile and highly dispersive. An increase in the amount of bare sand and movement by flight early in the spring enabled large numbers of individuals of this species to colonise within a short time after ploughing. *Harpalus rufipalpis* and *Nebria salina* are both macropterous species associated with heathland and sandy habitats, that may have increased in abundance due to rapid reproduction after colonisation of clear-fells. As most of the British ground beetles (except some larger species such as *Carabus*) have an annual life cycle (Luff 2007), an increase in larval survival due to favourable conditions in ploughed stands would result in a high number of adults in the following season. However, it is not clear whether these species have benefitted from the exposure of mineral sand in ploughed stands, or the creation of inverted decomposing organic turves of bracken and grass litter. An alternative explanation is that the abundance increased because more individuals managed to colonise these areas within the additional time (year). More than half of the coloniser species were represented by very few individuals. Such low catchability of a large part of the coloniser fauna could have prevented detection of change in species number in zero year restocks.

Early successional habitat rather than permanent open areas were selected to test the effects of isolation on early colonisation, because treatments of vegetation by herbicides and ploughing was expected to homogenise the habitat quality conditions of these patches and therefore exclude its effect on colonisation. According to lower variability in scores of zero year samples compared to felled-unplanted samples on the second axis of PCA of vegetation structure (Figure 4. 2) homogenisation does take place. However, there are still some differences in environmental conditions among sampled patches as the ploughing and herbicide treatment did not affect changes in presence of indicator plant species.

Even though clear-felled sites were sampled in the second growth season after felling, differences among sites in vegetation structure were already mirrored in abundance of GHS species, with more individuals found in sites with greater cover of grass and less cover of bracken (and thus less cover of deep bracken litter also). This indicates that at least some of the GHS species can respond to favourable conditions by very fast reproduction. Ploughing had interesting consequences for carabid assemblage, as sites with greater percentage cover of bare sand had fewer species of colonisers. The opposite was found for permanent open areas where greater cover of bare ground was favoured by GHS species (see Chapter three). There was however considerable difference in the average cover of bare ground in permanent open spaces (patches and trackways) being 7.1 percent and in zero year restocks 48.7 percent. Considering that single ploughing of stands in Thetford Forest, that disturbed strips of soil with intervening vegetation left undisturbed, had negative effects on GHS ground beetles, such mechanically very disruptive management used on entire sites every year could therefore have detrimental effects in the long term which has also been suggested by Collier (1995).

Among species associated with grassland, heathland and sandy habitats, very few individuals of only three species were recorded from the mature prefell growth stage;

therefore it is very unlikely that GHS species persist in stands throughout the forestry cycle. Colonisers of newly created clear-fells and restocks must originate from other areas.

Assuming source of colonisers are permanent open patches, 1-5 year old restocks and trackways I selected four different isolation measures. However, variation in values of these isolation measures among sampled sites was not large with coefficient of variation for the first isolation measure 0.7, of the second 1.1, of the third 0.2 and of the fourth isolation measure 0.3. In this experiment I did not find any effects of isolation or size of stands on number of species or number of individuals that colonise newly created open areas. As discussed in Chapter three this is contrary to the predictions of island biogeography theory (McArthur & Wilson 1967). One potential explanation for not finding any effect of isolation is the low variability in isolation values among sampled sites, as described above. There was also no indication that species with better dispersal abilities colonised newly created areas faster or in greater numbers. The current scale of management with average stand size being 8.7ha, with all newly created stands readily connected by the extensive network of trackways, of which those surrounded by plantations younger than 20 years represent suitable habitat for GHS species, with the additional presence of occasional permanent open patches, seems to present sufficient connectivity to enable persistence of open habitat associated species within Thetford Forest.

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Appendix 4. A; General linear models of effect of habitat type (felled-unplanted vs zero year restocks) and each of the four isolation measures on number of species of all colonizers, open colonizers and GHS species.

	All colonizers **No.species**	**Open colonizers** **No.species**	**GHS species** **No.Species**
	F (df) P (B ± SE)	F (df) P (B ± SE)	F (df) P (B ± SE)
Model	0.58 (2,21) 0.569	0.54 (2,21) 0.591	0.10 (2,21) 0.909
Habitat type: **Felled-unplanted** **0 year**	0.19 (1,21) 0.664 (-0.6±1.2) 0	0.26 (1,21) 0.616 (-0.6±1.3) 0	0.12 (1,21) 0.730 (-0.2±0.7) 0
Isolation measure 1	1.16 (1,21) 0.249 (8.7±8.6)	1.03 (1,21) 0.321 (9.7±12.7)	0.13 (1,21) 0.725 (1.7±4.9)
R^2 (adjusted)	-0.038	-0.042	-0.085

	F (df) P (B ± SE)	F (df) P (B ± SE)	F (df) P (B ± SE)
Model	0.58 (2,21) 0.569	0.32 (2,21) 0.732	0.27 (2,21) 0.799
Hab.type(Fu/0)year **Fu** **0yr**	0.19 (1,21) 0.664 (-0.7±1.5) 0	0.23 (1,21) 0.640 (-0.6±1.3) 0	0.21 (1,21) 0.648 (-0.3±0.7) 0
Isolation measure 2	1.16 (1,21) 0.249 (-0.1±0.1)	0.59 (1,21) 0.452 (9.7±12.7)	0.39 (1,21) 0.540 (4.4±7.0)
R^2 (adjusted)	-0.038	-0.063	-0.072

Model	0.186 (2,21) 0.831	0.027 (2,21) 0.974	0.552 (2,21) 0.584
Hab.type(Fu/0)year **Fu** **0yr**	0.02 (1,21) 0.900 (-0.2±1.5) 0	0.05 (1,21) 0.828 (-0.3±1.2) 0	0.02 (1,21) 0.890 (-0.1±0.7) 0
Isolation measure 3	0.37 (1,21) 0.550 (-31.2±51.3)	0.01 (1,21) 0.923 (-4.1±42.3)	1.04 (1,21) 0.320 (23.2±22.8)
R^2 (adjusted)	-0.076	-0.092	-0.040

Model	0.13 (2,21) 0.880	0.219 (2,21) 0.805	0.933 (2,21) 0.409
Hab.type(Fu/0)year **Fu** **0yr**	0.02 (1,21) 0.897 (-0.2±1.5) 0	0.09 (1,21) 0.766 (-0.4±1.2) 0	0.21 (1,21) 0.652 (-0.3±0.6) 0
Isolation measure 4	0.25 (1,21) 0.620 (-24.4±48.5)	0.39 (1,21) 0.537 (-24.8±39.5)	1.80 (1,21) 0.19 (-28.3±21.1)
R^2 (adjusted)	-0.082	-0.073	-0.006

Appendix 4. B; General linear models of effect of habitat type (felled-unplanted vs zero year restocks) and each of the four isolation measures on abundance of all colonizers, open colonizers and GHS species.

	All colonizers Abundance	**Open colonizers Abundance**	**GHS species Abundance**
	F (df) P (B ± SE)	F (df) P (B ± SE)	F (df) P (B ± SE)
Model	**4.60 (2,21) 0.017**	**7.70 (2,21) 0.003**	2.40 (2,21) 0.115
Hab.type(Fu/0)year	**8.07 (1,21) 0.010**	**11.93 (1,21) 0.002**	**4.78 (1,21) 0.040**
Fu	(-16.7±6.0)	(-18.4±5.3)	**(-61.4±28.1)**
0yr	0	0	**0**
Isolation measure 1	0.20 (1,21) 0.658	0.553 (1,21) 0.465	0.25 (1,21) 0.623
	(-19.0±42.2)	(-28.0±37.6)	(99.0±198.2)
R^2 (adjusted)	0.256	0.368	0.109

	F (df) P (B ± SE)	F (df) P (B ± SE)	F (df) P (B ± SE)
Model	**5.01 (2,21) 0.017**	**7.23 (2,21) 0.004**	2.69 (2,21) 0.091
Hab.type(Fu/0)year	**9.61 (1,21) 0.005**	**12.46 (1,21) 0.002**	2.93 (1,21) 0.102
Fu	(-18.9±6.1)	(-19.5±5.5)	(-48.6±28.4)
0yr	0	0	0
Isolation measure 2	0.27 (1,21) 0.609	0.01 (1,21) 0.956	0.72 (1,21) 0.407
	(31.9±61.4)	(-3.1±55.6)	(-241.9±286.1)
R^2 (adjusted)	0.258	0.351	0.128

Model	**5.42 (2,21) 0.013**	**7.53 (2,21) 0.003**	2.950 (2,21) 0.074
Hab.type(Fu/0)year	**10.55 (1,21) 0.004**	**15.04 (1,21) 0.001**	4.17 (1,21) 0.054
Fu	(-18.4±5.7)	(-20.0±5.1)	(-53.9±26.4)
0yr	0	0	0
Isolation measure 3	0.84 (1,21) 0.370	0.36 (1,21) 0.557	1.15 (1,21) 0.296
	(-182.79±199.42)	(-108.31±181.51)	(998.76±932.02)
R^2 (adjusted)	0.278	0.362	0.145

Model	**5.76 (2,21) 0.010**	**8.21 (2,21) 0.002**	2.260 (2,21) 0.129
Hab.type(Fu/0)year	**11.08 (1,21) 0.003**	**16.17 (1,21) 0.001**	**4.48 (1,21) 0.046**
Fu	(-18.7±5.6)	(-20.4±5.1)	(-57.6±27.2)
0yr	0	0	0
Isolation measure 4	1.30 (1,21) 0.266	1.16 (1,21) 0.293	0.01 (1,21) 0.914
	(-212.4±186.0)	(-181.0±167.9)	(-98.2±301.9)
R^2 (adjusted)	0.293	0.385	0.099

Chapter 5: Matrix affects conduit suitability of trackway corridors for an arenicolous specialist beetle

Abstract

Effects of contrasting matrix structure on the suitability and function of trackways as corridors for dispersal of an arenicolous carabid species, *Harpalus rufipalpis*, was studied within managed pine plantation using mark-release-recapture. A total of 1120 marked *Harpalus rufipalpus* were released over three dates, into four trackways (two within thicket stage stands, aged 13-16 years and two within mature plantations aged 26-37 years) and dispersal was monitored by pitfall transects placed across trackways at intervals of four meters, extending 44 m north and south of the release point. The surrounding matrix affected trackway suitability with greater abundance of resident *H.rufipalpis* found in trackways surrounded by younger forest. Daily movement rates in both types of trackways were relatively high (average 3.5m/day and maximum 22m/day) but there was no strong evidence of differences in rates of dispersal between trackway types. Edge permeability (leakage) differed between matrix types, with more individuals leaving the conduit to enter the matrix in the less suitable habitat (trackway surrounded by mature trees).

Introduction

Humans have been altering the landscape for their needs for thousands of years and one of the consequences is habitat fragmentation. As well as edge effects, that for core species effectively further reduce the area of available habitat or reduce habitat quality (Saunders *et al.* 1991, Didham *et al.* 1998, Laurance *et al.* 1998, Dupont & Nielsen 2006), fragmentation can have effects on population viability via increased local extinction, decreased colonisation and disruption of dispersal (Harrison & Bruna 1999, Fahrig 2003, Ewers & Didham 2006) .

Corridors have been suggested as a possible solution to increase the effective size of local populations and to increase population persistence by allowing continued exchange of individuals among a previously connected population.

The literature on corridors is contradictory because of the ambiguous use of the term “corridor”, which is often used to describe landscape components with divergent functions (Simberloff *et al.* 1992, Rosenberg *et al.* 1999, Hess & Fischer 2001) such as facilitating movement within an individual’s home range, maintenance of connectivity among seasonal habitats, facilitating movement across barriers such as highways, or dispersal of individuals to new areas either in the context of local populations (rescue effect, recolonisation of vacant habitat) or facilitating range expansion. I will focus on corridors as linear landscape elements, embedded in a dissimilar matrix, that provide for movement between habitat patches, but not necessarily reproduction (Rosenberg *et al.* 1999).

Studies of the use of corridors by different groups of insects have shown varying and sometimes contradictory results. Corridors increased movement rates between patches for two butterfly species (Tewksbury *et al.* 2002), house flies (Fried *et al.* 2005) and maintained species richness of microarthropods in the fragmented landscape of moss patches (Gilbert *et al.* 1998). Behavioural studies showed that two specialist open-habitat butterfly species were more likely to leave patches through corridors than expected by random movement and moved straight ahead at higher frequencies in corridors than in habitat patches (Haddad 1999). Berggren and colleagues (2002) found that approximately

30 percent more individuals of Roesel's bush-cricket used the corridor than would be expected if dispersal direction was random but that individuals that moved through the corridor moved slower but straighter than individuals that moved through the more exposed short grass matrix. Other studies show no influence on rate of colonisation or reduction of insect species loss (Collinge 2000) but suggested that the relative effect of corridors may depend significantly on fragment size, on resource availability and movement ability of animals.

Corridors may inherently provide low-quality habitat for many animals and plants, because they are typically narrow strips with high edge-to-area ratios. But high-quality corridors are not necessary to be effective at promoting movement or gene flow because establishment and reproduction are not required within a corridor for plants or animals to traverse it (Haddad & Tewksbury 2005). They showed that for two mobile butterfly species that can traverse corridors within a generation, corridor habitat may be of lower quality than larger patches and still increase dispersal and gene flow.

Corridors like habitat patches can be bound by either hard or soft edges, where a hard edge is an impenetrable boundary that dispersing individuals virtually never cross in order to enter surrounding habitats (Stamps *et al.* 1987). A soft edge is reasonably permeable to emigrating individuals. Hard edges are able to direct movements of individuals in the landscape better because very few individuals will cross them (Mader 1984). House flies were more likely to follow forest edges with dense understory without passing through them into the forest than open forest edges with little understory (Fried *et al.* 2005). Ries & Debinski (2001) found that butterflies may respond strongly to even subtle habitat boundaries, but those responses may be modified by the edge structure, species habitat preference (specialists versus generalists), time of the year, wind direction and density of conspecifics. I can assume that corridors with hard edges will be able to direct species along the corridor better than soft edges where many individuals could get lost in matrix. Both corridor quality, edge permeability and suitability of surrounding habitat should be considered when planning corridor networks to act as conduits for specific organisms.

In my study system, arenicolous, xerophytic species survive in a system of permanent open habitats and ephemeral patches of suitable habitat that are colonised and occupied, embedded in a matrix of unsuitable forest habitat but linked by a network of linear trackway elements. I examined effects of surrounding matrix on quality, suitability and the use of trackway corridors by *Harpalus rufipalpis*, an arenicolous specialist ground beetle.

Methods

STUDY SITE

The study was conducted in the Elveden block of Thetford Forest (0°40'E, 52º27'N), the largest lowland coniferous plantation forest in the UK. Thetford Forest occupies approximately one third of Breckland, an area of East Anglia characterised by sandy soils and semi-continental climate, historically dominated by anthropogenic heath and extensive agricultural land (Dolman & Sutherland 1991, Dolman & Sutherland 1992). In an extensive afforestation program planting of the forest began in 1922 covering c. 20,000ha (Dolman & Sutherland 1991). The reduction in area of heathland is estimated at about 76 percent (Lambley 1990).

The forest is a Site of Special Scientific Interest (under the Countryside and Rights of Way Act 2000) of which designation requires maintenance of scarce vertebrate and invertebrate populations. Breckland has also been recognised as a stronghold for characteristic and declining carabid fauna (Telfer & Eversham 1996). Half of all nationally scarce terrestrial carabid species recorded from Breckland, were also found in ephemeral habitats (clearfelled and restocked plantations) and permanent open areas within Thetford Forest (Lin *et al.* 2007) which shows the importance of maintaining possibility of dispersal between these areas.

Thetford Forest is managed by clear-felling and replanting of large even-aged stands. Corsican pine (*Pinus nigra* var. *maritima*) and Scots pine (*Pinus sylvestis*) comprise more than 80 percent of the planted area. Stands are clearfelled 60-80 years after planting, and the stand is replanted usually within the next two years. Thinning begins at 23-25 years, continuing every five years until the stand is felled. Management compartments are subdivided by a trackway network (Eycott *et al.* 2006) that provides potential corridor connectivity among source and target patches.

STUDY SPECIES

The species used was *Harpalus rufipalpis*, a macropterus species which lives in open habitats on sandy soil, including heaths, dunes and sand pits (Luff 1998). It is common only in the south of England, but is found locally throughout the rest of England. Since 1970 it has been recorded in 86 10km^2 in UK with six of these in Breckland. It is a univoltine spring breeder and overwinters as an adult (Luff 1998). Its body size ranges from 8 to 11mm (Lindroth 1974). In the study area it is most abundant from May until the end of August (Lin 2005) in recently replanted stands (0-5 years) where mean density per trap per trapping day was 0.4 individuals in 2001 and 0.3 individuals in 2002. Using the same sampling protocol as Lin (2005) from May until the end of August 2006 I collected one individual in thicket stage forest (three sites) and none in pole stage forest (three sites) (Chapter two).

Several congeners were found in previous studies of the Breckland carabid fauna (Lin 2005, Lin *et al.* 2007) which could potentially be confused with *H.rufipalpis,* including *H.affinis*, *H.anxius*, *H.attenuatus*, *H.froelichii*, *H.latus*, *H.pumilis*, *H.rubripes*, *H.rufipes*, *H.serripes*, *H.servus*, *H.smaragdinus* and *H.tardus*. However, *H.rufipalpis* was the most abundant congener in restocks within Thetford Forest (Lin 2005) with 86 percent of all captured Harpalus belonging to this species. Identification of *Harpalus rufipalpis* by naked eye was tested in the lab on preserved specimens from 17 different samples prior to experiment in the field with identification checked using a microscope. Out of 107 specimens, 98 (92 %) were correctly identified by the naked eye.

Beetles were collected using dry pitfall traps and were brought to the laboratory where they were kept for up to one week in plastic containers with sand and vegetation and were fed with moistened cat food (Tesco premium cat crunchies). Beetles were marked by abrasion of a small part of elytra, marking was specific for each of the three release dates. It was not possible to individually mark beetles due to their small size and the short persistence time of different colour markings in experimental attempts to apply individual codes. As marks were therefore only cohort specific and not individual, any successive recaptures of individuals could not be distinguished. I was therefore only able to record cumulative distance moved since release and the number of days elapsed, but could not measure distance and relative direction moved between subsequent recaptures.

The effects of marking by abrasion on survival of *Harpalus rufipalpis* were tested in a laboratory setting. A total of 120 individuals captured using dry pitfall traps were kept in plastic boxes with sand and turf collected in Thetford Forest and fed with cat food. Sixty individuals were marked by abrasion of a small part of elytra and were kept in four boxes, with 15 individuals in each box. In each of the boxes 15 non-marked individuals were also added. Boxes were kept moist and the number of live and dead individuals was checked once per week. After four weeks numbers of live marked (mean per box 12.3 ± 3.6 SD) and non-marked (mean per box 12.5 ± 2.7 SD) *Harpalus rufipalpis* in each of the boxes were similar, showing no effect of marking by abrasion on subsequent survival (paired t test, t=0.40, P=0.718).

The mark-release-recapture experiment was carried out between 17 June and 21 July 2006. Four release sites were selected all being north-east to south-west oriented trackways of approximately the same width (12m). All trackways comprised lightly used vehicle tracks over the unmodified parent substrate (sandy soil), with grassy verge margins. Two trackways were surrounded by thicket stage pine plantations aged 13-16 years with average tree height 7.2m ± 1.7 SD (hereafter referred to as “young”), and two were surrounded by mature plantations aged 26-37 years with average tree height 13.6m ± 1.6 SD (hereafter referred to as “old”). A total of 1120 marked individuals were released over three dates. The first release took place on 25 June, second on 29 June and third on 5 July 2006 with 70, 110 and 100 marked individuals released at each site respectively (total 280 individuals per site).

In all release sites the setup of dry pitfall traps was the same. There were 23 parallel transects each of five traps placed across the trackway with one trap in the middle of the track, two traps in adjacent verges and two traps in adjacent forest, placed beyond the first tree planting row (Figure 5. 1). All traps were four meters apart from each other thus forming a 16 metres wide and 88 metres long grid along the trackway. The 23 traps forming transects along the trackway placed in west forest, west verge, middle, east verge and east forest will hereafter be referred to as trackway sections. Pitfall traps were white plastic cups (200ml volume) 8cm deep, 7cm diameter on the top and 4.5cm diameter on the bottom. In each trap two strips of soft plastic green netting were provided as refuge.

All traps were checked every second day starting on 27 June and finishing on 21 July 2006. On each occasion the number of marked and non marked *Harpalus rufipalpis* in each trap was recorded. Marked individuals were released 1.5 meters from the trap in one of six directions (60º, 120º, 180º, 240º, 300º, 360º from the line parallel to the track). Direction was selected according to the number of previously released animals on the same site and each animal was released in the direction clockwise following the release direction of the last caught animal. Non marked individuals of *H.rufipalpis* were collected, marked in the lab and released as a part of the mark-release-recapture experiment or used in the tests of abrasion on survival.

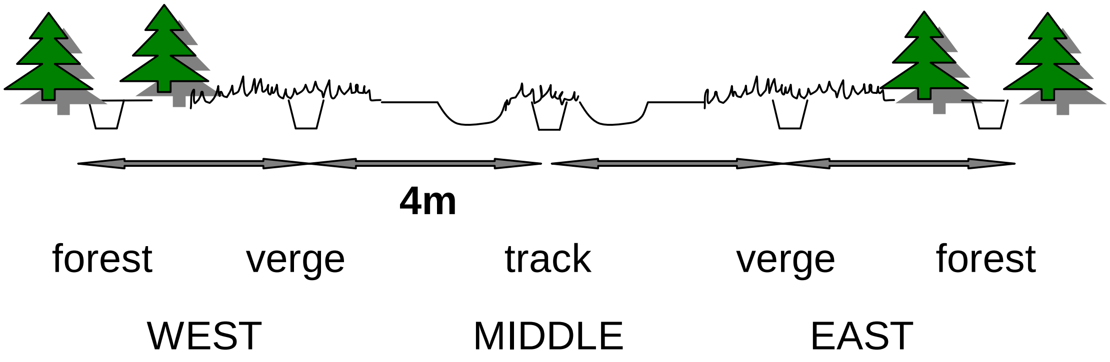

Figure 5. 1; Setup of pitfall traps in trackway sections at release sites.

VEGETATION SURVEY

The composition and sward height of vegetation was recorded between 7 and 15 July 2006. Percentage cover of each of eleven vegetation parameters: bare soil, litter, moss, growing bracken (*Pteridium aquilinum*), dry bracken (previous years growth), short grass (<5cm), long grass (>5cm), herbs, bramble (*Rubus fruticosus*) and raspberry (*Rubus idaeus*), heather (*Calluna vulgaris*) and broom (*Cytisus europaeus*) was estimated within a 3x3m quadrate centred on each trap and the mean cover of each parameter calculated for each trackway section. Sward height was measured using a sward stick (disc diameter 90mm, weight 250g, rod diameter 17mm following (Dolman & Sutherland 1992)), at one point approximately 1m away from each trap, in one of four directions (east, south, west, north), 90° clockwise from that of the previous trap in the transect. Mean sward height was calculated for each trackway section (forest west, verge west, middle, verge east, forest east).

DATA ANALYSIS

To summarise differences in vegetation composition between young and old trackways and between different trackway sections Detrended correspondence analysis (DCA) was conducted on percentage cover of the eleven vegetation parameters, using CANOCO for Windows 4.5 (ter Braak & Smilauer 1997). For each trackway section, mean DCA axis 1 and axis 2 sample scores were calculated.

During the mark-release-recapture experiment I collected data on recapture rates, recorded recapture site (location of the trap) and time elapsed from the release. I also recorded the number of resident (unmarked) *Harpalus rufipalpis* caught in each of five trackway sections at each site (Figure 5. 1). Number of unmarked individuals caught was compared between trackway types (young versus old trackways) and between trackway sections (*n* = five levels) using general linear models (GLMs) that included a term for site replicate, nested within habitat type. Data were Ln (n+1) transformed before the analysis.

Numbers of recaptures in different trackway sections were compared between young and old trackways using GLMs with site nested within habitat type, on Ln(n+1) transformed data.

To test whether number of recaptures changed with distance from the release point GLM was carried out on Ln(n) transformed data. Interaction terms of trackway type * distance and of north / south direction * distance were included to explore whether distance from the release point had a similar effect on number of recaptures in young and old tranckways and in the north and south direction.

I calculated the distance of movement as the direct-line distance from the release point to the point of recapture. Daily movement rate is direct-line distance divided by the number of days since the release, calculated for each recapture. Maximum daily rate is the highest value of daily movement rates obtained at each site. Daily rate of movement for recaptures made two days after release was also calculated to exclude effects of backwards movements toward the release point that might have occurred as time since the release increased. Ln(n) transformed data of daily movement rates (both for two days after release and for all recaptures) were compared between young and old trackways using GLMs with site nested within trackway type.

I compared the decline in frequency of recaptures over time between young and old trackways using GLMs with release cohort as a categorical variable and days since the release as a covariate. Because of different release dates I calculated the proportions of beetles recaptured on different days since the release. Data used in analysis were square-root transformed.

Results

VEGETATION STRUCTURE OF YOUNG AND OLD TRACKWAYS

The first two axes of a Detrended correspondence analysis explained 52.8 percent of the variation in vegetation cover. Vegetation composition was similar in verges and adjacent forest on both east and west track margins (Figure 5. 2), comprising mainly bracken, long grass, heather and broom. Vegetation height was also very similar in east and west verges in both young and old trackways (Figure 5. 3). The middle section of trackways differed from verges, comprising mostly bare ground in young (81.1% ± 1.32 SD) and short grass in old trackways (71.8% ± 8.4 SD short grass cover, only 5.5% ± 0.7 SD bare ground cover).

BACKGROUND DENSITY OF *H.rufipalpis* IN CORRIDORS WITHIN YOUNG AND OLD FOREST

More unmarked *Harpalus rufipalpis* were caught in young (total 991) than in old trackways (48) over the 25 day period. Within trackways, significantly greater numbers were caught in western than in eastern sections, with this effect differing between trackway types (significant interaction term, Table 5. 1), with the effect of aspect greater in younger trackways (ratio of captures from east : mid : west of 1: 1.8 : 4.2) than in old trackways (1 : 2.3 : 2.7).

Relative to numbers captured within trackways the numbers of unmarked *H.rufipalpis* caught in adjacent forest was proportionally greater in adjacent old forest (6:48; 12.5%) than in adjacent young forest (35:991; 3.5%) (χ^2 =7.69, P=0.006).

DIRECTION OF MOVEMENTS OF *H.rufipalpis* IN CORRIDORS WITHIN YOUNG AND OLD FOREST

In total 238 marked *Harpalus rufipalpis* were recaptured out of 1120 released. There were significantly fewer recaptures in young (total 95) than in old trackways (total 143) (χ^2=7.6, P=0.058).

The number of recaptures differed among trackway sections with most recaptures in the middle and west verge, fewer in east verge and fewest in east and west forest (Table 5. 2). However effects of aspect differed between young and old trackways (Table 5. 2, interaction), with significantly more recaptures in the west verge of young trackways, but similar numbers in west and east verge in old trackways. There were three recaptures in the surrounding forest out of a total of 95 recaptures in the young but 19 recaptures in the forest out of a total of 143 in the old trackways (Fisher exact test, P=0.010).

Number of recaptures decreased with distance from the release point (Figure 5. 4) and the rate of this decrease was similar between young and old trackways, and between the north and south direction, as shown by the non-significance of interaction terms in this model (Table 5. 3).

Considering only the most distant five traps in each direction, similar numbers were caught to north (7.0 ± 2.8 SD) and south (10.0 ± 0.8 SD). There were 12 recapture in the north and 19 in the south in young trackways and 21 in the north and 16 in the south in old trackways (χ^2 =0.02, P=0.888).

DAILY MOVEMENT RATES OF *H.rufipalpis*

The highest daily movement rate (22 metres) was observed in young site 2 (Table 5. 4). Although average daily movement rates within two days of release appeared somewhat greater in young than in old trackways, this difference was not significant (Table 5. 4). Looking at average daily movement rates for all recaptures however, these were marginally lower in trackways surrounded by young forest than those surrounded by mature forest (Table 5. 4).

DECLINE IN FREQUENCY OF RECAPTURES OVER TIME

The proportion of released beetles that were recaptured declined with time in both young and old trackways (Figure 5. 4) but this decline was faster in old than in young trackways, as shown by the significant interaction term in the model (Table 5. 5).

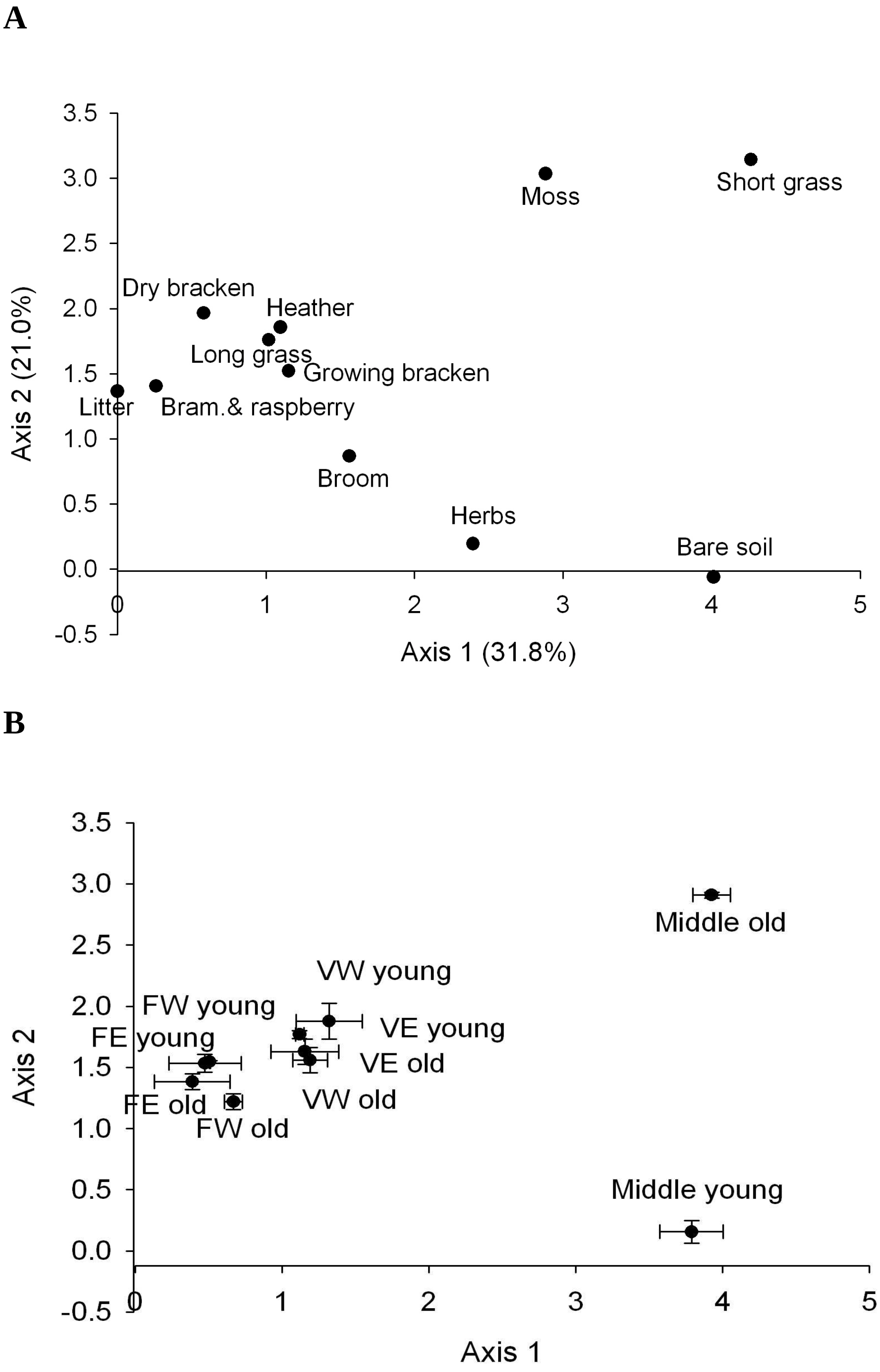

Figure 5. 2; Results of Detrended correspondence analysis of vegetation composition showing A) habitat scores and B) mean ± SD scores for trackway sections in young and old trackways.

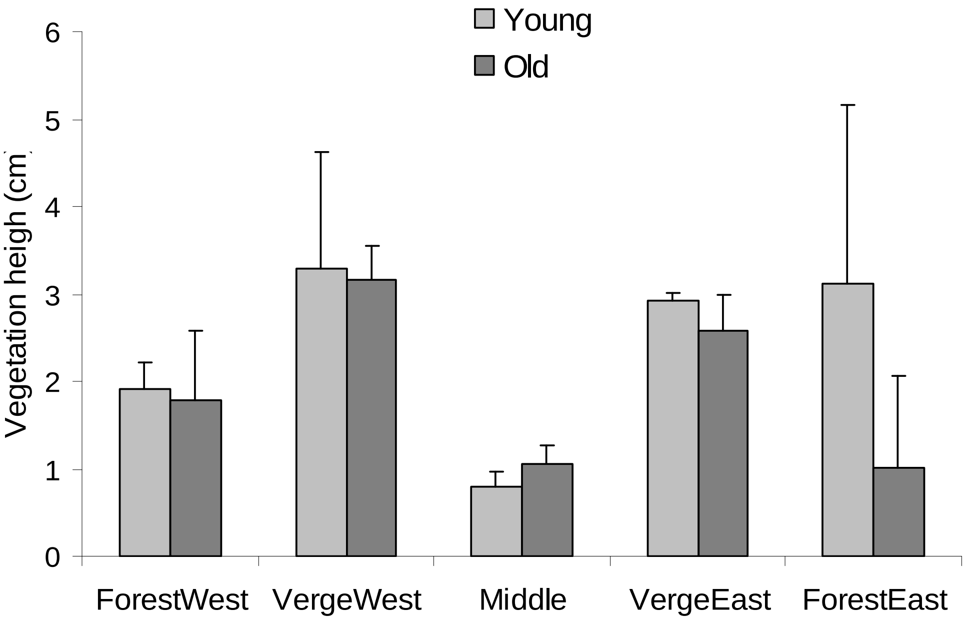

Figure 5. 3; Mean ± SD vegetation height of trackway sections in young (*n*=2) and old (*n*=2) trackways.

Table 5. 1; Mean ± SD number of unmarked individuals of *Harpalus rufipalpis* caught in dry pitfall traps in five trackway sections in young and old trackways. Results of a nested GLM performed on Ln(n+1) transformed data are shown.

	Forest west	Verge west	Middle	Verge east	Forest east		df	*F*	*P*
YOUNG	12.5 ± 0.7	288.0 ± 4.2	121.5 ± 26.2	68.5 ± 37.5	5.0 ± 1.4	(a) Young / Old	1	213.18	<0.001
						(b) Trackway section	4	43.33	<0.001
OLD	2.0 ± 1.4	9.5 ± 0.7	8.0 ± 2.8	3.5 ± 3.5	1.0 ± 1.4	a * b	4	6.21	0.014
						Site (Young / Old)	2	4.61	0.047

Table 5. 2; Mean ± SD number of recaptures in five trackway sections (forest west, verge west, middle, verge east, forest east) in young and old trackways. Results of nested GLM performed on Ln(n+1) transformed data are shown.

	Forest west	Verge west	Middle	Verge east	Forest east		df	*F*	*P*
YOUNG	0	27.0 ± 6.6	14.0 ± 1.4	4.5 ± 2.1	1.5 ± 0.7	(a) Young / Old	1	28.06	0.001
						(b) Trackway section	4	44.77	<0.001
OLD	5.0 ± 1.4	12.0 ± 4.2	39.0 ± 17.0	11.0 ± 2.8	4.5 ± 0.7	a * b	4	9.85	0.004
						Site (Young / Old)	2	0.13	0.882

Table 5. 3; Results of GLM of the effect of distance from the release point (covariate) on the number of recaptures. Interactions of trackway type*distance from the release point and orientation*distance from the release point were included in the model. Number of recaptures data were Ln(n) transformed.

	Number of recaptures
	F (df) *P* (B±SE)
Model	**7.61 (3,84) <0.001**
(Dist) Distance from the release point	**19.93 (1,84) < 0.001** (-0.02±0.01)
Interaction 1	1.54 (1,84) 0.219
Young*Dist	(-0.02±0.01)
Old*Dist	0
Interaction 2	1.36 (1,84) 0.246
North*Dist	(-0.02±0.01)
South*Dist	0
Adjuster R^2	0.186

Table 5. 4; Maximal and mean ± SD daily rates of movement in two young and two old sites and results of a nested GLMs comparing average daily movement rates among two trackway types (young / old) with site nested within trackway type. Daily rates of movement were Ln(n) transformed before the analysis. Number of recaptures is given in brackets.

	YOUNG		OLD					
	Site 1	Site 2	Site 3	Site 4				
Maximal daily rate (m)	18.1	22.0	16.0	16.0		*df*	*F*	*P*
Daily rate (m) for recaptures 2 days after release	10.1 ±6.8 (n=7)	9.2±7.4 (n=6)	8.6±4.6 (n=11)	5.6±4.4 (n=21)	Young / Old Site (Young/Old)	1 2	1.76 1.95	0.192 0.155
Daily rate (m) for all recaptures	3.0 ±4.0 (n=52)	3.7 ±4.2 (n=43)	3.8±3.4 (n=61)	3.3±3.2 (n=82)	Young / Old Site (Young/Old)	1 2	4.1 2.1	0.043 0.124

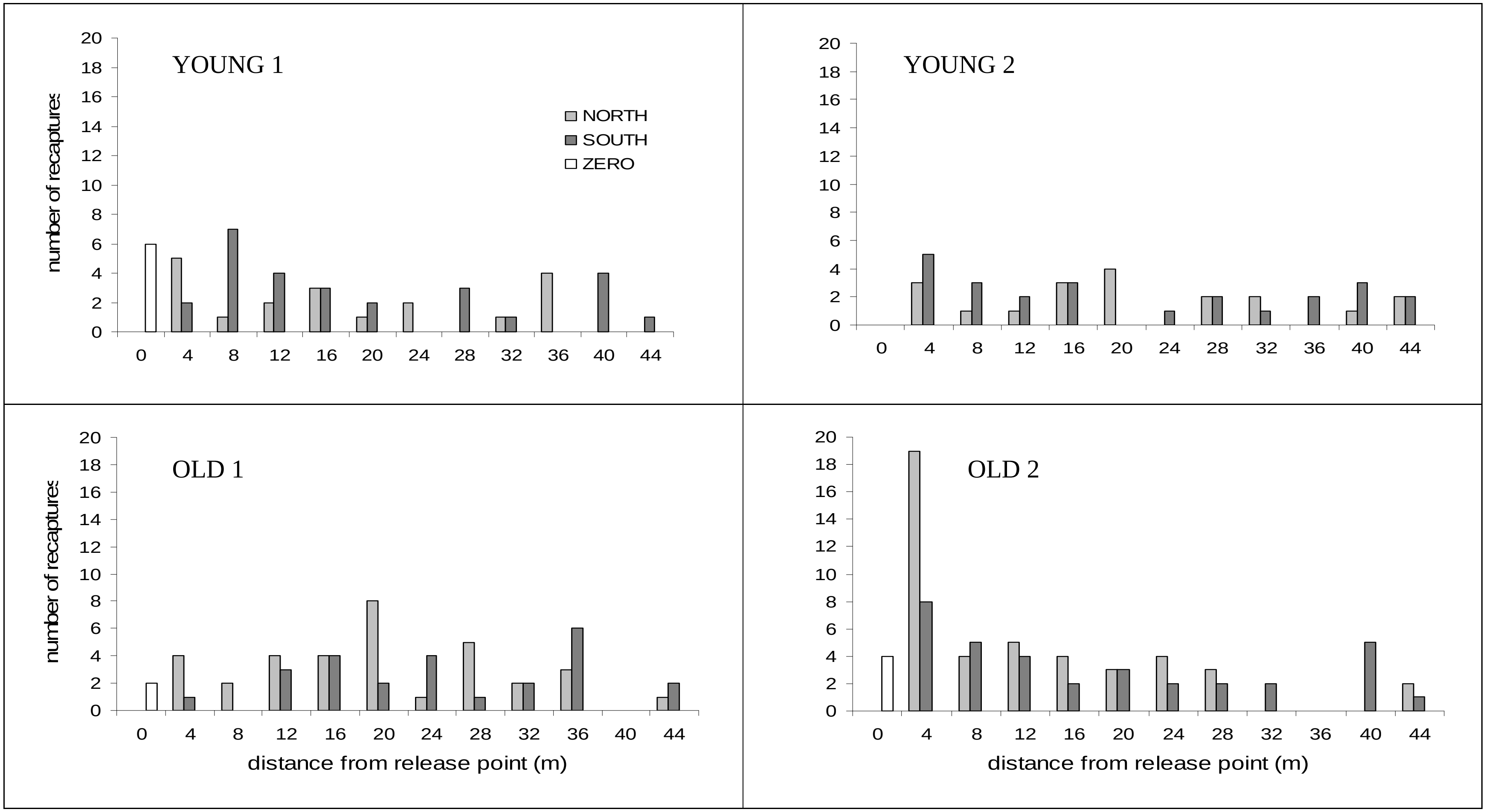

Figure 5. 4; Total number of recaptures in transects at different distances from the release point for each of four sampled sites.

Table 5. 5; Results of GLM of the effect of trackway type (young / old), release cohort and time since release on proportion of recaptured beetles on 2,4,6...26 days since release. Proportion of recaptured beetles data were square-root transformed before the analysis.

	Proportion of recaptured beetles
	F (df) *P* (B ± SE)
Model	**8.00 (5,122) <0.001**
Habitat Type	**12.11 (1,122) 0.001**
Young	(-0.01±0.03)
Old	0
Release cohort	**4.63 (2,122) 0.012**
1.release	(0.01±0.02)
2.release	(0.05±0.02)
3.release	0
(D) Days since release	**18.11 (1,122) <0.001** (-0.01±0.001)
Interaction	**10.00 (1,122) 0.002**
Young * D	(0.01±0.002)
Old * D	0
Adjusted R^2	0.216

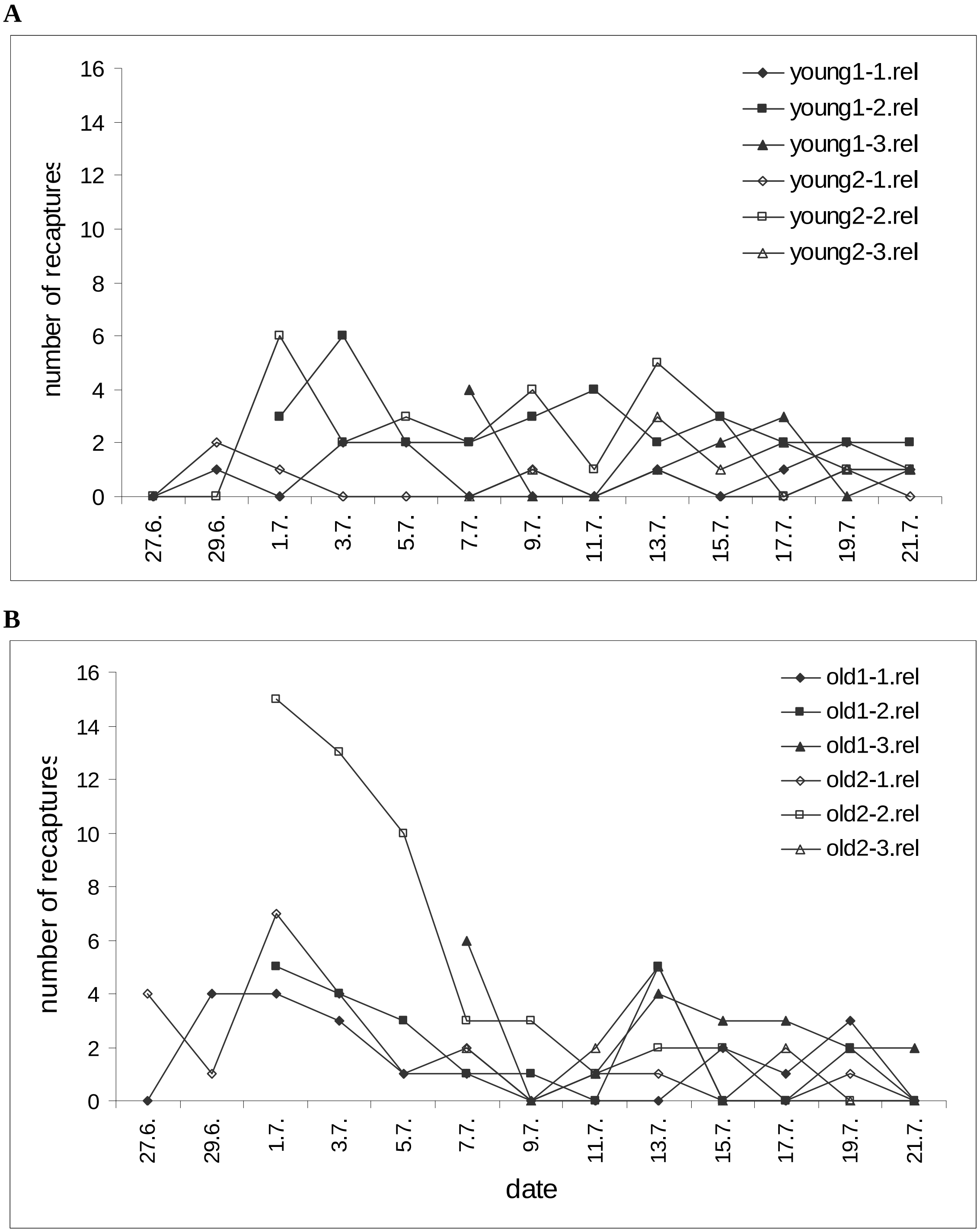

Figure 5. 5; Number of recaptures at each date from three release cohorts in replicate trackways surrounded by A) young and B) old forest.

Discussion

My results show that the surrounding matrix affects suitability of trackways for this arenicolous carabid, with trackways surrounded by younger forest supporting a higher density of *Harpalus rufipalpis* (captures of unmarked individuals). This effect of the age of trees surrounding potential corridors is probably due to shading of trees which makes old trackways colder and damper, with more grass and less bare ground in track centres and thus less suitable for open area specialist. These differences in density of resident population between the two habitats could potentially affect the behaviour of introduced marked individuals. To reduce this effect I removed non-marked individuals caught in pitfall traps during the experiment.

For *Harpalus rufipalpis* the forest edge is not an impenetrable barrier but very few individuals cross it. Leakage from the conduit into the matrix was greater in the older trackways, with a greater proportion of marked individuals recaptured within the forest matrix. The same was found for resident *H.rufipalpis* of which proportionately more unmarked individuals (relative to the number of captures within the trackway) were captured in old plantations adjacent to trackways than in young plantations, although the absolute number of captures was much less. Due to the lack of individual markings I do not know if individuals that entered the matrix also continued dispersing within the matrix, or whether they returned to the corridor after “sampling” the matrix. Differences in behaviour of invertebrates at different types of edges have been reported in literature (see introduction). It is therefore important to take the type of edge into account when planning dispersal corridors.

Results of this experiment suggest the matrix also affects the level of activity of *Harpalus rufipalpis* which were marginally more active in trackways surrounded by old forest (less suitable environment), as inferred from the greater number of recaptures. The number of recaptures declined faster with time in trackways surrounded by old forest but these differences were marginal so further experiments would be needed to confirm it. The latter could also be interpreted as higher mortality rate or as consequence of higher barrier leakage and dispersal into the matrix and beyond the experimental plot.

The maximal daily movement rates of *H.rufipalpis* in my experiment were unexpectedly high (max 22m per day, over two days). Although the experimental trapping grid extended 44 metres each direction from the central release point, this was limited relative to the high movement rates, so that these could be underestimated. This problem has been previously reported in the literature (Baker *et al.* 1995, Schneider 2003). Daily movement rates could have been underestimated also because I was not able to apply individual markings to animals and therefore could not detect movements of animals backwards toward the release point. This could also explain the marginally higher daily movement rates in trackways surrounded by old plantations than those surrounded by young plantations. Movement rates in the first two days after the release were higher than movement rates when all recapture were considered, which could also be consequence of very high density of individuals at the release point just after the release.

These results give some insight into dispersal potential of open area specialist ground beetle through corridors of different quality. Low quality corridors can function as movement conduits even though *H.rufipalpis* is less common in them, but the boundary with old forest is more permeable which could mean more individuals get lost in the surrounding matrix. The species studied is common in the study area and reaches high densities, which makes the use of mark-release-recapture possible. Smaller, less mobile and rarer species are likely to be more restricted in their movements and extension of these results should proceed with caution.

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Chapter 6: Summary and conclusions

Habitat quality determines the value of fragmented open areas within conifer plantation for conservation of heathland associated carabids

There have been 37 GHS species of ground beetles recorded from Breckland of which at least 22 are also present within the afforested landscape of Thetford Forest; of these 21 were recorded in the present study. Specialist GHS species recorded elsewhere in Breckland, but that were not recorded from the forest landscape, tend to be rarer regionally but there are no indications of them being dispersal limited. These species may be restricted to relict heathland and ‘brown field’ sites because they are highly specialised and open habitats within the forest do not provide suitable conditions. For example, *Broscus cephalotes*, *Calathus mollis* and *Harpalus servus* are associated with sand dunes (Telfer & Eversham 1996) and depend on windblown sand which is absent from within the forest. *Cymindis axillaris* and *Cymindis macularis* are also associated with areas of bare sandy soil (Welch & Hammond 1995); however numerous other species also dependent on dry sandy soil were recorded within the forest landscape so the particular requirements excluding these species are not clear. The importance of disturbance and presence of bare sand for specialised ground beetle species of Breckland has already been emphasised by Telfter & Eversham (1996) and the Breckland carabid fauna has similarities with faunas of coastal dunes. On the other hand *Amara infima* and *Anisodactylus nemorivagus*, that were absent from the forest, are associated with *Calluna* heathland (Telfer & Eversham 1996) and *Amara fusca* is associated with the rare and highly localised plant *Artemisia campestris* (Telfer & Eversham 1995), that is not found within the forest landscape. A systematic comparison of environmental conditions such as soil characteristics, cover of bare sand, and perhaps importantly insolation and aspect, between protected heaths and open areas within Thetford Forest would enable better understanding of the difference in ground beetle fauna. In addition, a transplant experiment that would introduce species now restricted to heaths into potentially suitable areas within the plantation would clarify whether these species can survive within the plantation, or alternatively whether carabid species only found on remaining protected heaths may be restricted to remaining small populations by low viability (producing very few dispersers) and relative isolation, rather than by low dispersal ability.

Some of the differences in species recorded in heaths and in Thetford Forest could be due to a failure to record all species that are present within the forest landscape, which may have arisen from the differences in sampling techniques used. The information for species found in protected heaths in Breckland is thought to be comprehensive due to the combination of selective records of rare species contributed by specialist recorders to the Invertebrate Site Register and systematic surveys (Lin *et al.* 2007). In survey of forest habitats pitfall traps were used, which are the most efficient trapping method for the time and effort used (Spence & Niemela 1994). Catches of pitfall traps have been shown to represent variations in relative carabid community composition among habitats (Lin *et al.* 2005) but are biased towards larger and more active species (Greenslade 1964, Spence & Niemela 1994, Andersen 1995). Therefore, the use of additional sampling techniques such as hand searching or extraction from the litter by Tullgren funnels might have produced some additional species. However, species accumulation curves approached an asymptote suggesting that few additional species remain unrecorded within the forest landscape.

Within the forest landscape permanent open spaces enable persistence of populations of GHS carabid species. Surprisingly, and contrary to the predictions of island biogeography theory, larger open patches did not support a carabid community with a greater number of GHS species. Instead habitat quality was the strongest predictor of the structure of carabid community in permanent open areas with heathland species favouring areas with greater cover of bare sand, moss and lichen and with lower swards.

The potential of narrow strips of open habitat along trackways to support carabid species associated with open habitats has been shown by Eversham & Telfer (1994) for a sandy roadside verge in Breckland, UK, by Vermeulen (1994) for a heathy road verge in the Netherlands and by Koivula (2005) for six forest roads surrounded by mature forest in Finland. Sampling of 39 trackways within Thetford Forest showed the suitability of trackways for GHS species differs greatly and is strongly affected by the surrounding matrix (the age of surrounding plantations). Older and taller trees provide more shading and consequently the conditions in such trackways are colder and moist, with very few GHS species found in these areas. Even if such trackways can be traversed by mature individuals (functioning as corridors, or conduit), resident populations are unlikely to establish. This is due to the high sensitivity of larval stages to specific environmental requirements, among which soil moisture is likely to be the most influential (Luff 1996, Holland 2002). If, on the other hand, at least one of the surrounding plantations is younger than 20 years, such linear strips of habitat supported similar number and abundance of GHS species as permanent open patches. Even though the presence of larval stages was not examined, GHS species almost undoubtedly reproduce in these good quality linear strips that represent sources of colonisers for newly created clear-fells and restocks.

These results indicate that habitat quality and therefore management of open spaces within Breckland is very important for the persistence of ground beetles associated with heathland and open ruderal habitats, even within heterogeneous fragmented mosaic of open spaces such as Thetford Forest.

Current management for conservation of heathland conditions in trackways within the forest landscape is by forage harvesting, where vegetation is cut and removed once per year. Comparison of trackways surrounded by younger plantations (<20 years) that are under the current management for conservation, *versus* non-managed sites, did show some differences in vegetation composition, but no differences in carabid community composition. Telfer and Eversham (1996) found that unbroken or nearly complete grass swards support few of the rare heathland dependant carabid species; therefore an important feature for such carabid assemblages is the disturbance regime. In his comparison of five management regimes on species richness of heathland indicator carabid species in a non-replicated experiment in Cranwich heath (a calcareous grass heath site recently recreated from closed canopy plantation), Collier (1995) found rotovation to be the most effective, as also suggested by Dolman & Sutherland (1992). According to Collier (1995) caution is advisable when using rotovation as this is a very disruptive process that might have detrimental effects on the life cycle and population persistence of beetles if used every year. Collier (1995) also suggests a combination of management techniques that would remove the top soil layer and thus reduce soil organic content. Results of Chapter three confirm the importance of this suggestion, as sampled open patches within Theford forest with shallow thickness of soil litter layer supported more GHS species. However, as suggested above for rotovation, the extent of areas subjected to this type of management and its frequency should be studied further. Therefore optimal approach to management for conservation of heathland associated invertebrates should be explored further using replicated experiment of several management techniques while examining their long term consequences for invertebrate communities.

Temporal dynamics of carabid assemblages within Thetford Forest pine plantation

Within the forest landscape component, closed canopy plantations have the lowest diversity of ground beetles, mostly due to the absence of species associated with open habitats. The same pattern was found in forests in northern England (Butterfield 1997), Ireland (Mullen *et al.* 2008) and in Finland (Heliola *et al.* 2001, Koivula *et al.* 2002). In Thetford Forest, GHS associated species are mostly restricted to both permanent open areas (open patches and trackways) and ephemeral open areas (clear-fells and young restocks).

Changes of environmental conditions in ephemeral open spaces depend on the clear-fell management cycle of plantations, with the development of the tree crop and subsequent shading having a strong influence on the ground flora of the stands (Eycott *et al.* 2006). In accordance with above mentioned dependence of ground beetles on environmental conditions and habitat quality, carabid community changes in clear-fells and restocks are closely connected with succession of vegetation. Lin (2005) showed that the number and abundance of GHS species peak in three year old restocks, start to decline in four and five year old plantations and practically disappear by the time plantation are 10 years old (present study, Chapter two). Despite the short period of suitability, the species richness and abundance of GHS species in ephemeral open areas reaches similar values to those of permanent open areas. However, from the point of view of long term persistence of populations within the landscape, ephemeral open areas can serve as sources of open associated colonisers only for approximately five years after replanting of stands.

Changes in environmental conditions within the network of trackways also depend on ageing of surrounding plantations, but according to changes in carabid community, open conditions in trackways persist until the surrounding plantations are 20 years old.

In permanent open patches environmental conditions are not associated with forest succession, therefore these areas can act as source of colonisers for an indefinite time as long as the habitat quality within them is maintained by appropriate management. Therefore under current management permanent open areas are important for maintaining populations of GHS species within the plantation landscape.

Importance of connectivity for persistence of open-habitat associated carabids within plantation

The network of trackways within Thetford Forest was expected to represent a continuous linking open habitat which could act as a source of colonisers or provide corridors for movement of these colonisers. However, the pattern of these linear elements does not necessarily equate to their function, as the environmental conditions within trackways and thus the carabid community within them, are determined by the age of surrounding plantations. Differences among trackways and permanent open patches in habitat quality and consequently suitability for GHS species create a mosaic of suitable patches of different size that can represent sources of colonisers, and of unsuitable matrix habitats (Figure 1). How exactly GHS associated species manage to get to newly created open areas remains unclear.

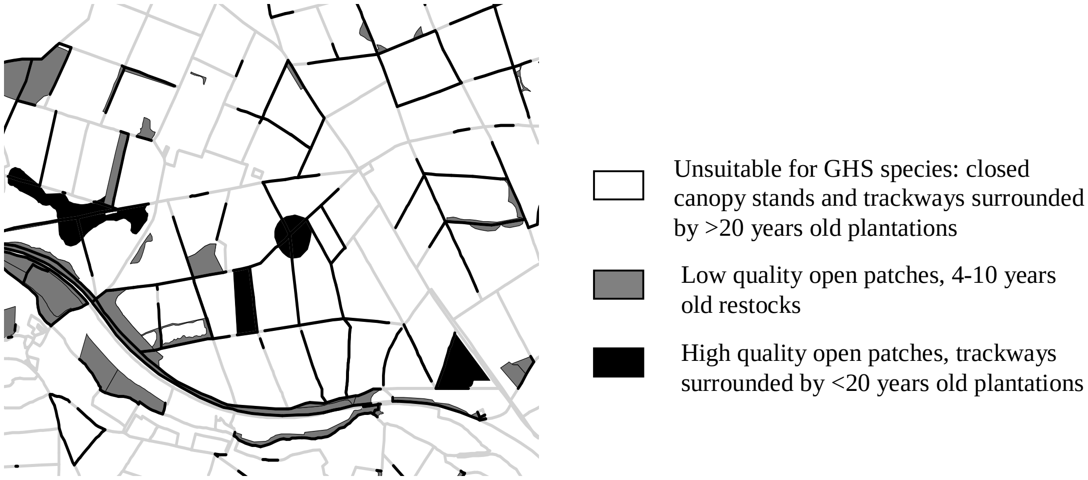

Figure 6. 1; Representation of patchy mosaic landscape of Thetford Forest according to suitability of stands and trackways for GHS species.

The potential of trackways surrounded by mature plantations to act as corridors could not be proven. Mark-release-recapture experiment showed that *Harpalus rufipalpis*, selected as a representative model stenotopic GHS species, has higher activity levels in low quality trackways surrounded by mature forest, but there were no clear differences in average daily movement rates between the trackways surrounded by mature or by young plantations. Habitat type is expected to influence dispersal rate which is expected to be greater in habitat of low quality (McPeek & Holt 1992). A possible reason for not finding any differences in daily movement rates is that in my experiment daily movement rates were probably underestimated, due to the limited range of the experimental grid which would not detect individuals travelling very long distances (i.e. > 40m), and due to the lack of individual markings, which would enable detection of movements backwards towards the release point. In trackways surrounded by mature forest there was a higher leakage of individuals through the corridor-matrix barrier, with a greater number of individuals dispersing into the matrix. This permeability of the edge could represent limitation to the use of low quality trackways as dispersal corridors as more individuals get lost in the matrix (Fried *et al.* 2005). The estimated mean rate of daily movement within suitable trackways (i.e. those located within young plantations <20 years old), combined with the relatively low rate of leakage from these trackways, together suggest that seasonal rates of linear dispersal up to 400 metres may be possible. Thus these trackways have potential to act as corridors or conduits for percolation.

In contrast, low quality corridors such as trackways surrounded by mature trees appear unlikely to support dispersal by stenotopic heathland species. The number of unmarked *Harpalus rufipalpis* caught in mark-release-recapture experiment indicates very few individuals do enter linear strips of open habitat surrounded by mature plantation. This is a good example of situation where the pattern of the landscape does not equate with presumed function. Narrow linear strips of open habitat surrounded by mature plantations may appear as corridors to human observers, but the evidence from this study suggests they might not function as such.

Colonisation of newly created open areas within the plantation (clear-fells and young restock) by specialist open-habitat species is very fast, with 41 species colonising newly created areas within three years after removal of trees. Current forestry guidelines do not permit clear-fells to be created next to plantations younger than seven years (pre-thicket). As shown in Chapter two the abundance of GHS species in pre-thicket (7-10 years) and older thicket, pole and prefell aged plantations is very low; therefore these areas are unlikely to provide sources of colonisers for new clear-fells. The most probable sources of open habitat specialist colonisers are permanent open patches and the trackways passing through young plantations (<20 years old). Very few of the GHS species are restricted to permanent open spaces within the plantation and almost all GHS species are able to colonise ephemeral open patches within five years after felling, when species richness in restocks reached its peak. I did not find any effects of patch size or its isolation on early colonisation by GHS species. There are several possible explanations for this. Within buffers of sampled ephemeral open stands trackways surrounded by young plantations represented 51 percent of all trackways therefore all newly created open spaces are close to a linear source of colonisers. The variability in the selected isolation measures among sampled sites was relatively low (with average coefficient of variation 0.6), reducing the power of statistical tests. The selected isolation measure was the amount of source habitats within 600m buffer around sampled patches; this could in itself present a problem as the source habitats were shown to vary greatly in habitat quality and consequently in number of GHS species and individuals present. To precisely determine the amount of good quality source habitat I would have to determine the characteristics of all open patches and trackways within the surrounding landscape.

The sampling design of the Thetford forest study focused on assemblages rather than dynamics of each species and I am therefore not able to draw conclusions about applicability of metapopulation theory for GHS species dynamics in this study system. Some of the GHS species of carabids in Thetford forest might function as metapopulations but as most of the these species were found in all types of open habitat they are more likely a patchy population with a high level of connectivity among local populations.

Conclusions

For persistence of carabid species associated with grassland, heathland and sandy habitats which are currently present in the forest landscape, within patch dynamics are essential as only areas of good quality habitat (whether these were permanent open patches, linear trackways, or ephemeral restocks) supported high species richness of these specialists. The fact that newly created areas were confirmed to be colonised by almost all the GHS species present in permanent open spaces, indicates that fragmentation on the scale of current management of Thetford Forest does not have a negative effect on these ground beetles species.

In their review of effects of fragmentation on natural populations Ewers & Didham (2006) show that species traits such as dispersal ability and habitat specialisation mediate species responses to fragmentation. The type of habitat surveyed in this thesis is early successional ephemeral habitat and Travis & Dytham (1999) showed habitat persistence is an important determinant of the rate of dispersal that evolved for asexual model species, with dispersal favoured in temporary short lived habitats. In their comparison of dispersal abilities of 35 wing dimorphic species of plant hoppers (Homoptera: Delphacidae) living in habitats of varying persistence, Denno and colleagues (1991) found that levels of migration (percent of macropterous individuals within species) in populations decreased significantly with increasing persistence of habitat. Ribera and colleagues (2001) found higher frequency of macropterous species of ground beetles in highly managed habitats (which are made effectively temporary by the high frequency of ploughing and cutting) compared to extensive occasionally burnt upland grasslands. A comparison of dispersal abilities of ground beetles in Breckland (as were described by Lin and colleagues (2007)) showed similar results, with only nine percent of brachipterous species within the arable associated group (which occupy habitat that is regularly and severely disturbed, so that dispersal is crucial to local persistence), 22 percent of brachipterous species within the moorland and GHS associated group and 32 percent brachipterous species within the woodland associated and eurytopic species (for which habitat is effectively continuous). In his study of origin of the carabid fauna associated with dry open anthropogenic habitat in Western Europe Andersen (2000) showed that the majority originated from naturally open habitats similar to steppe and invaded naturally open habitats such as heaths, dunes, “talus” (scree) and “alvar” (steppe) in Europe soon after deglaciation. In order to survive in these short-lived habitats these species would necessarily have to develop good dispersal power, which would make them less responsive to habitat isolation. Species living in permanent habitats are not adapted to colonisation of new areas therefore fragmentation and increase in isolation of remnant patches can have very negative effects on overall persistence of population. Consequently probability of recolonisation of patches, where local population is extinct is low. On the other hand, species adapted to life in temporary habitats, where persistence of population always depended on colonisation of newly created patches after conditions within existing patches were no longer suitable, good dispersal abilities had to evolve. Studies of effects of fragmentation on assemblages or communities connected with different types of habitat should therefore consider general characteristics and adaptations of species.

I can conclude that in a heterogeneous landscape on a similar scale as that of Thetford forest, where a semi-natural early successional habitat such as heathland is a conservation priority the habitat quality and habitat management should be a priority if specialist species are to persist. As explained above in such habitats connectivity among patches might be less important as species adapted to these types of habitat usually have good dispersal abilities.

However, the scale of the system should always be considered when making decisions about priorities in management strategies. When considering carabid communities on the scale of Breckland rather than Thetford forest, 40 percent of the GHS species were not found within the forest landscape and are probably restricted to protected heaths because of very specific habitat requirements. Management on a larger regional scale connecting isolated remnants of heaths would also require management of linkages on the regional scale as suggested by (Bennett 2003). As described in the first chapter the size and scale of corridors for movement of invertebrates tested in the literature has been very limited with corridor lengths between five and five hundred metres. Regional corridors would have to be designed on a larger scale connecting patches far from each other. Due to small size of most invertebrates, movement through such linkages would not happen within an individual's lifetime and connecting landscape elements would have to represent habitat with resources enabling reproduction and indirectly movement by percolation. Results of sampling of trackways within Thetford forest plantation confirmed that even narrow strips of habitat can support typical heathland assemblage of ground beetles, as long as habitat quality is high. Therefore, it would be relatively cheap and easy to create such regional linkages along which species could move by percolation.

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