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Drivers of the composition and diversity of carabid functional traits in UK coniferous plantations



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ABSTRACT

Functional diversity (FD) is increasingly used as a metric to evaluate the impact of forest management strategies on ecosystem functioning. Management interventions that aim to maximise FD require knowledge of multiple environmental drivers of FD, which have not been studied to date in temperate coniferous production forests. We quantified the relative importance of abiotic (forest management) and biotic (ground vegetation community) drivers of carabid FD and trait distribution in 44 coniferous plantation forest stands across the UK. Carabid FD declined with canopy cover and carabid body length correlated negatively with the percentage of open semi-natural area surrounding a plot. We conclude that forest management could enhance carabid FD through initiatives that emulate natural disturbance regimes through gap creation. We found that neither functional nor taxonomic metrics of vegetation diversity correlated with carabid FD, suggesting that restoration of plant communities, a major goal of forest restoration efforts, will not necessarily enhance carabid FD in coniferous plantations.

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1. Introduction

Research on the impacts of environmental change on invertebrate biodiversity has traditionally adopted a taxonomic approach by focusing on the composition and diversity of particular groups of species in a community (Fountain-Jones et al., 2015). This approach has limited scope for generalisations, especially when comparing different regions with different species pools (McGill et al., 2006). A recent shift towards consideration of functional traits has focused attention on the morphological, anatomical, biochemical, physiological or phenological traits of a species that influence its ability to acquire resources, disperse, reproduce and persist in the environment (Violle et al., 2007; Pavoine and Bonsall, 2011). Functional-trait analysis offers several advantages over taxonomic composition analysis for both conceptual and management purposes (McGill et al., 2006; Kleyer et al., 2012). It facilitates an understanding of the mechanisms that underlie both community responses to environmental change and ecosystem functioning (Díaz et al., 2007; Lavorel et al., 2008; Laliberte et al., 2010; Bachand et al., 2014).

Quantitative measures have been developed that use multivariate methods to integrate multiple traits into a single continuous trait diversity index. These measures capture the value, range or distribution of functional traits in a community (hereafter 'functional diversity'; FD; Hooper et al., 2005; Díaz et al., 2007). Unlike traditional taxonomic measures of species richness or diversity, FD presupposes a mechanistic link between diversity and the ecological phenomena in question (Cadotte et al., 2011), and it has become apparent that FD is more directly relevant to ecosystem functioning than taxonomic diversity (TD; Hooper et al., 2005; Díaz and Cabido, 2001; Vandewalle et al., 2010). It is thought that predator assemblages exhibiting high diversity in functional traits are likely to have high levels of complementarity in traits associated with natural enemy capture and consumption (Petchey and Gaston, 2002). Conversely, assemblages with low FD may be more likely to exhibit niche overlap, increasing interference competition and limited potential for biological control (Woodcock et al., 2010). A quantitative review by Gagic et al. (2015) revealed that functional trait-based indices of animal diversity consistently provided greater explanatory power than species richness or abundance in predicting various ecosystem functions including pollination and pest control. It follows that estimates of invertebrate FD may provide surrogate measures of such services (Woodcock et al., 2014).

Considering that species differ in their response to environmental factors and effects on ecosystem functioning, it is important to

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understand the impacts of environmental changes on biotic communities. In this study, we investigate the diversity and distribution of functional traits for carabid beetles and ground layer plants, in relation to environmental variation imposed by forest management in coniferous production forests in the UK. Carabid beetles are a diverse and abundant group of insects ubiquitous to most terrestrial ecosystems (Thiele, 1977), where they contribute to ecosystem functioning through predation of other invertebrates and granivory of plant seeds (Lang et al., 1999; Kotze et al., 2011). In forest ecosystems, carabid beetles are important natural enemies of insect pests (Alalouni et al., 2013) and contribute to nutrient cycling (Loreau, 1995; Prather et al., 2013). Carabids have experienced general declines in diversity and abundance across the UK, but have remained relatively stable in forest and hedgerow habitats (Brooks et al., 2012), presenting opportunities for forest management to increase their value as carabid biodiversity refuges at the landscape level (Brooks et al., 2012).

Management of plantation forests requires an understanding of the environmental drivers affecting FD across taxonomic groups in order to sustain the multifunctional roles of these forests. It has been suggested this appreciation will require unravelling complex biotic interactions (Gilman et al., 2010; Brooks et al., 2012). Trait-based extensions to multi-taxa assessments are consequently being advocated as a means to further our understanding of community assembly following disturbance (Moretti and Legg, 2009; Aubin et al., 2013; Bachand et al., 2014). In temperate forests, most vascular plant species occupy the ground layer, where they form the trophic and structural template for a diversity of invertebrate communities (Sabatini et al., 2014). Plant functional traits mediate interactions with the physical environment, which suggests that data on plant and invertebrate traits may reveal more than species compositional data about the relationships between these taxa and their interactions with the environment (Moretti and Legg, 2009). Trait-based multi-taxa approaches therefore permit analyses of the relative influences of abiotic drivers (e.g. forest management) and biotic drivers (e.g. the plant community) on responses by animal communities to disturbance events (Pakeman and Stockan, 2014).

In this study, we investigate the diversity and distribution of carabid and ground layer plant functional traits, in relation to environmental variation imposed by forest management. We use data from the Biodiversity Assessment Project, which has previously been analysed only from a taxonomic perspective (Jukes et al., 2001; Humphrey et al., 2003). The BAP found that carabid species diversity declined with increasing canopy cover and soil organic matter content, and that the abundance of forest specialist carabid species increased with stand age whilst non-woodland species declined (Jukes et al., 2001). The influence of forest management on carabid FD has received less attention. Aubin et al. (2013) studied the FD of several taxa, including carabids, in boreal plantation forests, in relation to the single environmental variable of stand age. Pakeman and Stockan (2014) considered multiple abiotic and biotic drivers of carabid in arable fields, pasture and moorland. Our study is the first to analyse responses of carabid functional trait composition and diversity in relation to environmental drivers in planted coniferous production forests. This type of forest comprises around a half (52%) of total UK forest area (Forestry Commission, 2012). Our objective is to determine the processes driving carabid community dynamics in coniferous forest plantations. We use chronosequence data from 44 conifer plantations distributed widely across the UK (Humphrey et al., 2003). Specifically, we set out to: (i) compare the relative importance of a number of abiotic and biotic drivers of carabid FD in plantation forests; (ii) test whether meaningful correlations exist between carabid FD and taxonomic and functional metrics of ground vegetation diversity (species richness, Shannon-Wiener, Simpson diversity and Rao's quadratic entropy); and (iii) identify a combination of

functional traits in ground layer plant and carabid species that are most sensitive to forest management and which could potentially be used to characterise priority groups for conservation action.

2. Materials and methods

2.1. The Biodiversity Assessment Project

All analyses used the dataset of the UK Forestry Commission's Biodiversity Assessment Project (BAP) which ran from 1995 to 1999. Here we summarise relevant features of sampling design (Humphrey et al., 2003).

2.1.1. Study location and design

Conifer plantation stands at 12 sites across the UK were selected for study (Fig. 1; Table 1). These comprised four prominent commercial crop types grown in the UK: Sitka spruce (*Picea sitchensis* L. Bong. Carr.), Scots pine (*Pinus sylvestris* L.), Corsican pine (*Pinus nigra* var. *maritime* L.), and Norway spruce (*Picea abies* L. Karst.).

At the 12 sites, 1-ha permanent sample plots were established in four forest stands, reflecting four growth stages of a typical commercial timber crop rotation. Humphrey et al. (2003) provide a full description of these structure classes. Each site comprised of plots dominated by a single crop type. The chronosequence stages used included (i) a pre-thicket restock stage, crop height 2–4 m, age 8–10 years, incomplete canopy closure; (ii) a mid-rotation stage – crop height 10–20 m, age 20–30 years, canopy closure, no understorey; (iii) a mature stage – crop height 20–25 m, age 50–80 years, canopy closure, some development of understorey layers; and (iv) an over-mature stage (beyond economic maturity and acquiring some of the ecological characteristics of natural old-growth forests *sensu* Oliver, 1981) – crop height > 25 m, age 60–250 years, canopy break-up, well-developed understorey layers, accumulation of deadwood. A randomised-block design was used to assign the four growth stages to each site. In practice, the overmature age class was not present at four of the sites, resulting in a working total of 44 plots. Furthermore, sites were not equally distributed across climatic zones in the BAP project, meaning that not all combinations of tree species and bioclimatic zones were represented, leading to these factors being confounded.

2.1.2. Ground vegetation sampling

Two 10 × 10-m quadrats were arranged diagonally across the centre of each 50 × 50-m quarter of the 1-ha plot, giving eight quadrats in total per plot. The composition of ground vegetation (vascular plants) was assessed visually using the DOMIN cover-abundance scale *sensu* Dahl and Hadač (1941), within eight 2 × 2-m quadrats nested within the 10 × 10-m quadrats. To aggregate quadrat values to the plot level, each quadrat DOMIN score was converted to an average percentage, the percentages were summed and divided by eight. This value was then assigned the appropriate score on the DOMIN scale.

2.1.3. Ground beetle sampling

Ground beetles were sampled by pitfall trapping. Five traps were positioned 10 m apart on a north–south transect through the centre of each 1-ha plot and trapping was carried out over a 20-week period from May to September for two consecutive years (Table 1) and emptied at fortnightly intervals. Pitfall trap catches were pooled to the plot level for analysis. Carabid identification was based on Forsythe (1987) and Lindroth (1974). Due to difficulties with taxonomy, *Pterostichus rhaeticus* Heer (Luff, 1990) was recorded as *Pterostichus nigrita* (Paykull). Similarly, *Asaphidion curtum* Heyden and *Asaphidion stierlini* Heyden (Speight et al., 1986) were not separated from *Asaphidion flavipes* (L.).

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