

## Multi-taxa trait and functional responses to physical disturbance

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### Summary

**1.** Examining assemblage trait responses to environmental stressors extends our understanding beyond patterns of taxonomic diversity and composition, with results potentially transferable among bioregions. But the degree to which trait responses may be generalized across taxonomic groups remains incompletely understood.

**2.** We compared trait responses among carabids, spiders and plants to an experimentally manipulated gradient of physical disturbance, replicated in open habitats within a forested landscape. Recolonization of recently disturbed habitats is expected to favour species with traits that promote greater dispersal ability, independent of taxa. We specifically predicted that physical disturbance would increase the representation of carabids with smaller body size, wings or wing dimorphism, spiders able to disperse aerially, and plants with therophyte life-history and wind-dispersed seed.

**3.** We sampled 197 arthropod species (14 738 individuals) and 164 species of plant. The strength of association between each trait and the disturbance intensity was quantified by correlating matrices of species by traits, species abundance by sites and sites by environment, with significance assessed by comparison with a null model.

**4.** Responses of biological traits varied among taxa but could be consistently interpreted in terms of dispersal ability. Trait shifts for carabid and plant assemblages were as predicted and correspond to those observed in other disturbance regimes. Assemblages after disturbance comprised smaller and winged carabids, and smaller plants with wind-dispersed seed, consistent with selection for species with better dispersal ability. In contrast, aerial dispersal did not appear important in spider recolonization, instead terrestrial dispersal ability was suggested by the increased abundance of larger-bodied and cursorial species. However, larger spider body size was also associated with an active-hunting strategy, also favoured in the post-disturbance environment.

**5.** Trait–function linkage differed among taxa and was sometimes diffuse, with covariance among biological traits and the mapping of individual traits to multiple ecological functions. In particular, body size responses reflected correlations with life history, susceptibility to perturbation and dispersal ability that were inconsistent between the two arthropod groups. Selection of traits for assessment should therefore be taxa specific. Generalizations of trait responses across taxa should only be conducted where functional or ecological significance of assembly-level changes can be understood.

**Key-words:** assembly rules, body size, brachypterous, colonization, community-weighted mean trait, dispersal ability, environmental filters, functional response, macropterous

### Introduction

There is a need to better understand how biodiversity will respond to increasing anthropogenic environmental change and perturbation (Millennium Ecosystem

Assessment 2005; McGill *et al.* 2006). But examining responses of species composition only provides information that is context and bioregion specific, while measures such as richness or diversity do not inform ecological function (Vandewalle *et al.* 2010). There is, therefore, growing interest in trait- and function-based approaches that offer a mechanistic understanding across multiple species (McGill *et al.* 2006). Within ecosystems or habi-

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tats, biological and functional trait responses to ecological processes may be robust to geographic turnover in species composition, allowing generality across bioregions (Statzner *et al.* 2001; Pont *et al.* 2006; Vandewalle *et al.* 2010). For example, generalizing responses of aquatic assemblages across regions provided indices quantifying human modification of river channel states or pollution loads, allowing the development of continent-wide monitoring criteria (Vandewalle *et al.* 2010).

For trait studies to go beyond the description of patterns and be predictive or provide mechanistic understanding requires the testing of explicit *a priori* hypotheses in terms of assemblage trait responses to environmental drivers (McGill *et al.* 2006). Furthermore, biological traits (e.g. morphological, phenological or behavioural) selected for investigation should represent meaningful ecological or demographic functions (McGill *et al.* 2006; Gray *et al.* 2007; Vandewalle *et al.* 2010), such as dispersal, trophic role, fecundity or rates of population increase. However, the link between morphological or life-history traits and ecological function may be complex as commonly measured traits may be associated with multiple ecological and functional attributes. For example, body size may be associated with dispersal ability, feeding niche, fecundity and also competitive dominance (Kotze & O'Hara 2003; McGill *et al.* 2006; Williams *et al.* 2010). Therefore, to support mechanistic understanding in a particular ecosystem or landscape, it is important to identify the key environmental pressures or effects and from these, the expected ecological and functional responses (McGill *et al.* 2006). This allows directional tests of morphological or ecophysiological trait responses.

In fragmented and anthropogenically perturbed habitats, assemblages may be filtered by species dispersal ability (Heino & Hanski 2001; Ribera *et al.* 2001), with dispersal one of the most important traits for assemblage recovery after disturbance in both arthropods (Roff 1990; Mullen *et al.* 2008; Malmstrom 2012) and plants (Kyle & Leishman 2009; Moretti & Legg 2009). However, disturbed ecosystems have also been found to select for smaller and more fecund species, while larger slow-growing species are better suited to stable habitats (Statzner & Beche 2010; Chiu & Kuo 2012). Disturbance and subsequent successional recovery also affect vegetation structure, microclimates, environmental stressors such as aridity, and resource spectra such as soil fauna or plant seeds, with implications for other functional traits (Entling *et al.* 2007; Schirmel & Buchholz 2011). Therefore, trait responses to disturbance may be complex and mediated by multiple environmental effects in addition to filters of dispersal ability. To understand such complex trait responses and explore the degree to which they may be generalized, approaches that examine community assembly across environmental gradients have been recommended (McGill *et al.* 2006).

We created an experimental gradient of physical disturbance, embedded in an extensive network of open habitats

within a forested landscape that permits recolonization from regional source populations (Pedley *et al.* 2013b). We used this experiment to examine whether assemblage response of attributes associated with dispersal (e.g. body size or aerial flight) was consistent across taxonomic groups. We also examine responses of biological traits for diet, foraging strategy and environmental tolerance, and the intercorrelation between these and attributes associated with dispersal.

We contrast the trait responses of two arthropod groups (carabids and spiders) to those of vascular plants. Simultaneous examination of both arthropod groups and plants permits exploration of the extent that trait responses may be generalized across taxonomic groups (Moretti & Legg 2009), facilitating the search for general rules in community ecology (MacArthur 1972; McGill *et al.* 2006). Carabid life histories are known for European species and have been used to examine trait responses to disturbance and landscape change (Ribera *et al.* 2001; Desender *et al.* 2010); in comparison, trait analysis of spiders has been more limited (though see Lambeets *et al.* 2008; Langlands *et al.* 2011). Vascular plants provided an excellent comparative group as species traits are well known (Cornelissen *et al.* 2003), and trait–disturbance responses have been generalized (e.g. McIntyre & Lavorel 2001; Keith *et al.* 2007).

Physical disturbance treatments ranged along a gradient of intensity to enable us to address the following questions: (i) Does disturbance cause trait shifts? (ii) Are trait responses similar across contrasting taxonomic groups, particularly responses of size, dispersal ability and phenology? (iii) Do trait shifts in response to physical disturbance concur with responses to other disturbance types such as fire, flooding and management intensification? Based on trait response in other disturbance regimes, we hypothesized that assemblages that developed after high intensities of disturbance would have a reduced representation of arthropod species with large bodies and poorer powers of dispersal (Ribera *et al.* 2001; Cole *et al.* 2002; Langlands *et al.* 2011). We also test the hypothesis that disturbance would reduce the relative abundance of plant species with slow maturation, short-lived seed banks and lacking mechanisms for medium- or long-distance seed dispersal (McIntyre, Lavorel & Tremont 1995; Lavorel *et al.* 1998; Kyle & Leishman 2009).

## Materials and methods

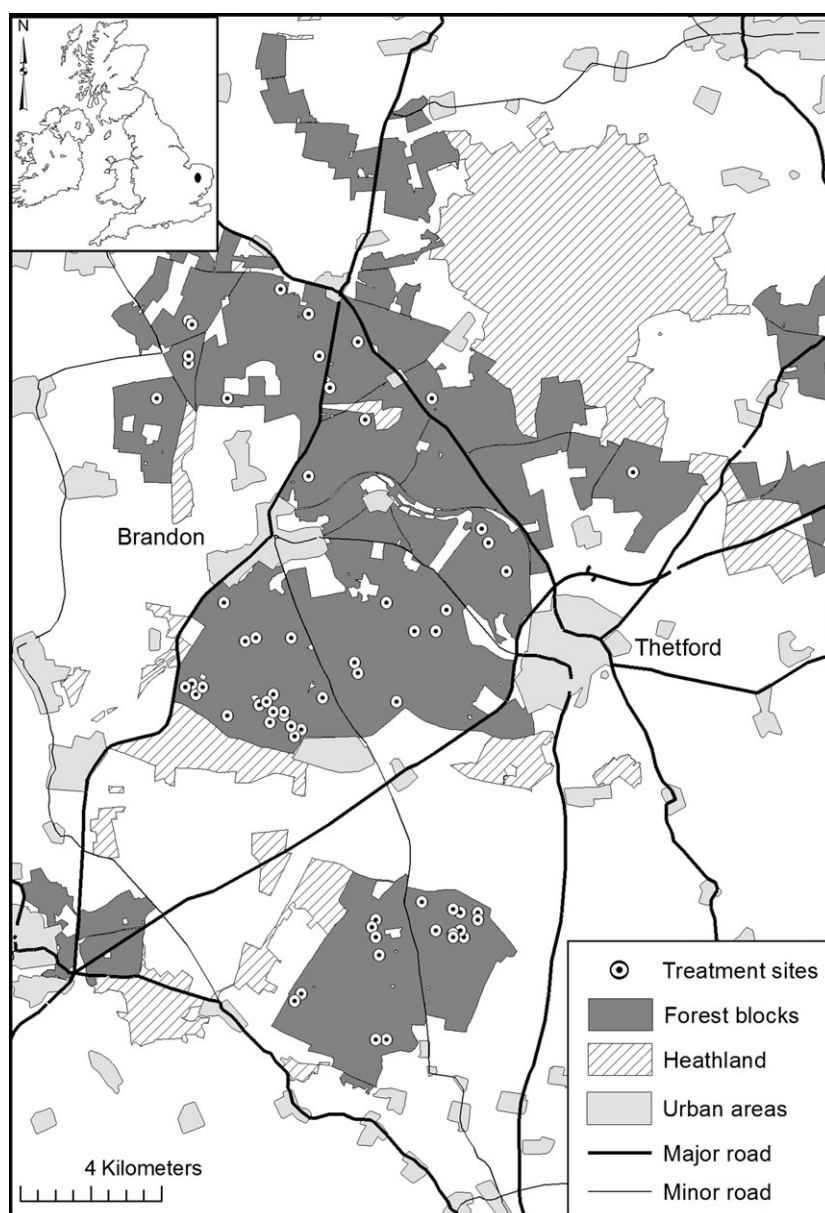
### STUDY DESIGN

Our study was conducted within Thetford Forest, a conifer-dominated plantation established in the early 20th century, occupying 185 km<sup>2</sup> of Breckland, eastern England (0°40'E, 52°27'N). This region is characterized by sandy soils and historically supported species associated with heathland and ruderal land uses (Dolman & Sutherland 1992). Present forest management consists of clear-felling (typically at 60–80 years) and replanting of even-aged

patches of tree crop (mean 9.0 ha  $\pm$  8.6 SD). These patches are subdivided by a network of forestry trackways (with a central part occasionally used by forestry vehicles, flanked on both sides by wide vegetated verges) that support diverse carabid and spider assemblages, comprising both open-habitat and forest species (Bertoncelj & Dolman 2013a; Pedley, Bertoncelj & Dolman 2013a; Pedley *et al.* 2013b).

Six mechanical disturbance treatments were applied together with a set of untreated controls, and each were replicated nine times in February 2009 (Fig. 1). Treatments represented a gradient of disturbance severity, ranked as: (1) sward cutting (cutting of standing vegetation without removal); (2) sward cutting with removal of clippings; (3) disc harrowing (that vertically cuts through vegetation, litter and roots, killing some plants, but without inverting litter or soil horizons); (4) parallel individual plough lines that inverted vegetation and litter, exposing mineral soil, separated by an undisturbed strip of vegetation approximately 0.5 m wide; (5) agricultural ploughing that chopped up

and inverted all vegetation exposing mineral soil across the entire plot; and (6) 'bulldozing' to remove all above-ground plant material and root mass, litter and organic soil horizons to expose mineral soil. Each treatment replicate comprised a single plot 150 m long with a mean width of 4 m, located within a forest trackway (minimum width 9 m, mean 13.5 m  $\pm$  3.7 SD, range 9–24 m) verge, adjacent to planted forest. We acknowledge that, although invertebrates can show marked behavioural responses to habitat boundaries (Bertoncelj & Dolman 2013b), the narrow plot dimension and associated edge effect may result in oversampling of more mobile eurytopic species; however, it was not practical to increase plot size sufficiently to exclude this. Trackways for treatment placement were located within tree crops aged 10–25 years to avoid confounding effects of shade and insolation, with treatments placed at least 100 m from plantation edges, recently felled areas or other open habitats. Treatments and untreated controls were allocated randomly across 63 suitable trackways; the resulting distribution of treatments was



**Fig. 1.** The distribution of treatment plots within Thetford Forest; urban and remnant heathland areas are shown, and the remaining matrix is predominantly agricultural.

spatially random within the forest as shown by analysis of variance of longitude ( $F_{6,56} = 1.396$ ,  $P = 0.232$ ) and latitude ( $F_{6,56} = 1.014$ ,  $P = 0.426$ ). Spatial autocorrelation in assemblage composition was examined separately for each taxa by Mantel tests (Legendre & Legendre 1998) performed on the first two axes of a non-metric multidimensional scaling (NMDS) ordination. NMDS was performed on species abundance data using the *VEGAN* package (Oksanen *et al.* 2010) in R (R Development Core Team 2012).

#### SAMPLING PROTOCOL

In each plot, abundance of each vascular plant species was quantified as its frequency of presence across 20 independent replicate  $1 \times 1$  m quadrats placed along the main axis of the plot, sampled once during May to August 2010. Ground-living carabids and epigeic (surface dwelling) spiders were sampled in each treatment plot with pitfall traps set in May, June and late July/early August 2010, 15–17 months after the application of disturbance treatments. Traps were set in a single transect along the centre of each treatment plot, 37.5 m in from each end, with six individual traps (each 7.5 cm deep, 6.5 cm in diameter, filled with 50 mL of 70% ethylene glycol) set 15 m apart and opened for seven consecutive days in each period. Traps in each transect were combined to give one composite sample of material for identification, and data from each trapping period were combined to give a composite sample for analysis, comprising 126 trap days per treatment plot. Pitfall trap catches, as with any trapping method, have inherent biases and can be influenced by factors including habitat structure, weather conditions and animal activity (Topping & Sunderland 1992). However, pitfall trapping successfully reflects ecological differences among areas, as long as it is remembered that interpretation is not based on population density but on the actual catch (Luff & Eyre 1988). In our study, standardized pitfall trapping is an appropriate collection method as we aimed to compare trait responses of ground-active invertebrates as affected by disturbance and not to provide complete site inventories.

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

#### SPECIES' TRAITS

Attributes of morphology, life history, phenology, trophic guild, ecophysiological tolerance and behaviours such as migration (e.g. Pont *et al.* 2006; Vandewalle *et al.* 2010) are phenotypic traits. Although considered in some trait studies, we excluded local abundance or range extent (e.g. Davies, Margules & Lawrence 2000; Henle *et al.* 2004; Gray *et al.* 2007; Barbaro & van Halder 2009) and habitat association (e.g. Davies *et al.* 2010; Vandewalle *et al.* 2010), as we did not consider these to be strict biological traits, but rather to be ecological attributes that may vary across a species range (Gaston, Blackburn & Lawton 1997) or with regional climate (Davies *et al.* 2006).

For carabids, spiders and vascular plants, we selected life-history traits that were considered likely to respond to disturbance, and for which species-specific information was available from published literature. It was not possible to develop identical sets

of traits for each of the contrasting taxonomic groups; rather we aimed to quantify consistent morphological (e.g. life-form, body size, winged), behavioural and life-history (e.g. phenology), feeding strategy and ecophysiological (e.g. tolerance of aridity or of shade) traits. Although scores for aridity tolerance were available for plants and spiders, equivalent information was not available for carabids; we did not wish to infer this trait from published information on carabid habitat associations. Traits used in the analysis are detailed in Table 1.

For carabids and plants, dispersal ability was inferred from traits for wings, or seed morphology. For spiders, although it is sometimes assumed that all species are capable of dispersal by ballooning, a comprehensive review by Bell *et al.* (2005) suggests this behaviour is not ubiquitous to all families. Among wolf spiders of the genus *Pardosa*, variation in 'tip-toe' (pre-flight) behaviour indicated variation in ballooning propensity (Richter 1970); similarly, Bonte *et al.* (2003a) found high variation in tip-toe behaviour in controlled conditions among 29 species from a range of families. We therefore considered reported ballooning behaviour as an indicator of dispersal ability.

#### ENVIRONMENTAL PARAMETERS

Disturbance intensity was quantified in terms of the resulting vegetation structure, measured at 40 points distributed along the centre of each treatment plot. At each point, vegetation height was measured using a sward stick (diameter 90 mm, weight 250 g, following Dolman & Sutherland 1992), and the percentage cover of bare substrate and of moss was visually estimated within  $20 \times 20$  cm; plot means were used in analysis. Cutting did not alter plant species composition (Pedley *et al.* 2013b), so that vegetation height could be considered separately from the trait of potential maximum plant height. Moss largely comprised shade-tolerant pleurocarpous species, rather than early-successional acrocarpous species, and indicated moister microhabitats.

A compound measure of disturbance intensity at each plot was calculated as the first axis of an unrotated principal component analysis (PCA) performed on the correlation matrix of the three vegetation structure variables (bare ground, moss and vegetation height). These variables were intercorrelated (vegetation height and moss,  $r = 0.578$ ,  $P < 0.001$ ; vegetation height and bare ground,  $r = -0.701$ ,  $P < 0.001$ ; bare ground and moss,  $r = -0.675$ ,  $P < 0.001$ ); however, each responded nonlinearly to the intensity of disturbance treatment. Although the extent of bare ground increased across the four soil disturbance treatments (Fig. S1, Supporting information), it changed negligibly between untreated controls, cutting or cutting with removal. In contrast, cutting treatments reduced vegetation height (Fig. S1, Supporting information). Thus, the combined PCA responded to disturbance across the entire range of treatments (Fig. S1, Supporting information).

#### TRAIT ANALYSIS

Trait responses to disturbance intensity were examined separately for each taxonomic group using fourth-corner analysis (Dray & Legendre 2008). This procedure tests whether the observed degree of trait–environment linkage differs from that expected by chance, providing a mechanistic understanding in contrast to emergent group analysis that describes species clustering based on shared traits (Aubin *et al.* 2009), or 'RLQ' analysis that



**Table 1.** Coding and description for biological traits of each taxonomic group. For sources of trait data, see Table S2 (Supporting information)

	Attribute
<b>Carabids</b>	
Body size	Average body size in mm
Activity length	1 = short (1–3 months); 2 = medium (4 months); 3 = long (>5 months)
Activity period	Main period of activity, either foraging or breeding. 1 = spring (early); 2 = summer (mid); 3 = autumn (late)
Spring breeding	Either spring or autumn breeding.
Carnivorous	1 = carnivore
Herbivorous	1 = herbivore
Omnivores	1 = omnivore
Brachypterous	1 = brachypterous species
Wing-dimorphic	1 = wing-dimorphic species
Macropterous	1 = macropterous species
<b>Spiders</b>	
Body size	Female body size in mm
Activity length	Number of months adult females active 1 = short (3–5 months); 2 = medium (6–7 months); 3 = long (>7 months)
Aridity score	Standardized niche parameters (0–1)
Shade score	Standardized niche parameters (0–1)
Ballooning	1 = exact species is listed as ballooning in Bell <i>et al.</i> (2005)
Active hunter	1 = active-hunting strategy
Running hunter	1 = running hunters
Ambush hunter	1 = ambush hunters
Stalking hunter	1 = stalking hunters
<b>Plants</b>	
Height	Maximum plant height in cm
Primary life-form	1 = Mega/meso/microphanerophyte; 2 = Chamaephyte; 3 = Hemicryptophyte; 4 = Non-bulbous geophyte; 5 = Therophyte
Life history	1 = perennial; 2 = biennial; 3 = annual
Woodiness	1 = woody species
Light score	Ellenberg indicator (1–9)
Moisture score	Ellenberg indicator (1–9)
Animal dispersed	1 = seeds dispersed by animals
Wind-dispersed	1 = seeds dispersed by wind
Dispersule weight	1 = too small to be measured easily; 2 = ≤0.20 mg; 3 = 0.21–0.50 mg; 4 = 0.51–1.00 mg; 5 = 1.01–2.00 mg; 6 = 2.01–10.00 mg; 7 = ≥10 mg
Lateral spread	1–4 little or no vegetative spread to far-creeping rhizome
Seed bank	1–4 transient seed bank to large bank of long persistent seeds

provides descriptive grouping of species, traits and environmental variables (Brind'Amour *et al.* 2011). The strength of trait–environment linkage was assessed against a null model, randomizing species incidence relative to disturbance parameters with 9999 permutations, following Dray & Legendre (2008). Analyses were conducted in R using the ADE4 package (Dray & Dufour 2007). To compensate for reduced spider abundance with greater disturbance, following Aubin *et al.* (2009), spider data were Hellinger-transformed (Legendre & Gallagher 2001),

whereby the abundance of each species recorded per site is first standardized by the total site abundance and then square root-transformed. To control table-wide type I error rates of fourth-corner results across each taxon, we applied sequential Bonferroni correction (Holm 1979; following Aubin *et al.* 2009). For those that remained significant, the trait–environment relation was visualized by plotting abundance-weighted mean trait values per treatment plot against the PCA score of disturbance intensity. As fully resolved phylogenetic trees are not available for spiders and beetles, we applied no phylogenetic correction.

## Results

We collated traits for 72 carabid, 125 spider and 164 vascular plant species (Table S1, Supporting information), the majority of the 73 carabid, 138 spider and 181 vascular plant species identified from the experiment. The 361 species for which we obtained trait data were represented by 3356 carabids, 11 382 spiders and 10 624 plant observations (summed across replicate quadrats within plots). Assemblage composition of each taxa was geographically structured, with the first axis of a NMDS ordination (performed on species abundance data) significantly related to latitude and longitude (Mantel tests:  $P < 0.001$  for both invertebrate taxa and  $P < 0.01$  for plants); for carabids, the second NMDS axis was also spatially autocorrelated ( $P = 0.024$ ). However, treatment distribution and thus trait responses were not confounded by this underlying spatial heterogeneity (see Materials and methods).

The first PCA axis explained 84.1% of the variance in the three structural variables, was negatively related to both sward height and moss, and positively related to extent of bare ground. Thus, the PCA 1 score was positively related to increasing intensity of disturbance across the range of treatments (Fig. S1, Supporting information).

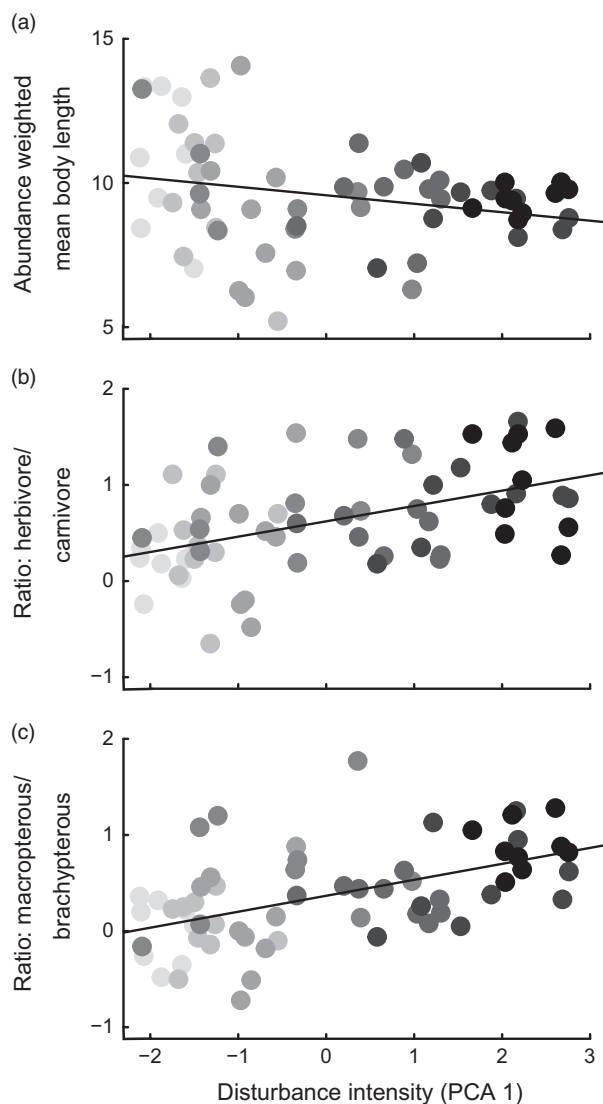
## CARABIDS

Five of the 10 carabid traits had significant links to the disturbance gradient when examined by fourth-corner analysis (Table 2). Mean body size decreased, and the abundance of herbivores was greater with greater disturbance intensity (Fig. 2a,b). Macropterous (winged) species were more abundant with greater disturbance intensity, while the abundance of brachypterous (with vestigial wings) species in the most intense treatment was reduced compared to controls (Fig. 2c). Surprisingly, the frequency of wing-dimorphic species was not related to disturbance intensity (Table 2). Of the 72 species, only nine (from six different tribes) were wing dimorphic; of these, two were relatively numerous (*Bembidion lampros* and *Syntomus truncatellus*, with 112 and 100 individuals recorded, respectively) and were found in small numbers across all treatments. Relations among traits are shown in Appendix S3 (Supporting information).

**Table 2.** Fourth-corner correlation coefficients from analyses performed on plant, carabid and spider assemblages, with increasing disturbance intensity (increasing Principal Component Analysis 1 scores) related to species traits (see Table 1 for trait descriptions)

Carabids	Coefficient	Spiders	Coefficient	Plants	Coefficient
Body size	<b>-0.157</b>	Body size	<b>0.073</b>	Height	<b>-0.053</b>
Activity length	0.121	Activity length	-0.025	Primary life-form	<b>0.093</b>
Activity period	-0.142	Aridity score	0.039	Life history	<b>0.104</b>
Spring breeding	0.087	Shade score	-0.028	Woodiness	<b>-0.102</b>
Carnivorous	<b>-0.144</b>	Ballooning	0.019	Light score	<b>0.118</b>
Herbivorous	<b>0.236</b>	Active hunter	<b>0.095</b>	Moisture score	<b>-0.114</b>
Omnivores	-0.172	Running hunter	<b>0.059</b>	Animal dispersed	<b>-0.100</b>
Brachypterous	<b>-0.233</b>	Ambush hunter	0.015	Wind-dispersed	<b>0.084</b>
Wing-dimorphic	-0.005	Stalking hunter	0.025	Dispersule weight	-0.077
Macropterous	<b>0.220</b>			Lateral spread	<b>-0.094</b>
				Seed bank	0.047

Significant relationships ( $P < 0.05$ , after Holm's correction performed separately on each taxon) are indicated in bold.

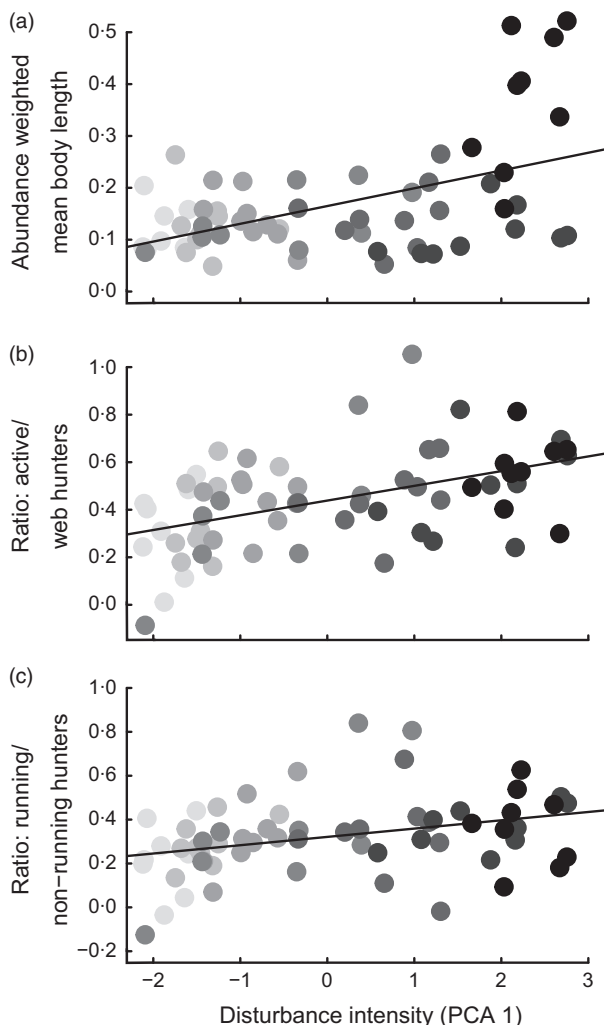
**Fig. 2.** Abundance-weighted mean and ratios of significant fourth-corner carabid traits against the increasing disturbance gradient [principal component analysis (PCA) 1]. Individual treatment types are plotted in separate shades from light grey, for non-intervention controls, to black for the most intensive disturbance treatment.

Time of breeding related to activity period and body size, with autumn breeders tending to be larger (mean body length  $11.5 \text{ mm} \pm 5.2$ ) and spring breeders (mean body length  $7.4 \text{ mm} \pm 3.6 \text{ SD}$ ) having longer activity length (Appendix S3, Fig. S3a, Supporting information). The herbivorous species were largely macropterous (31 of 33), while carnivorous and omnivorous species showed a mix of winged traits (of 24 carnivores, 10 were macropterous, five dimorphic, nine brachypterous; of seven omnivores, one, two and four, respectively). Small- to medium-sized species had a range of diets, so that body size was largely independent of diet (Appendix S3, Fig. S3a, Supporting information); nevertheless, most of the largest species were carnivorous (herbivores: mean  $8.5 \text{ mm} \pm 2.1 \text{ SD}$ , range  $4.4\text{--}13.5 \text{ mm}$ ; carnivores: mean  $10.5 \pm 6.4$ , range  $3.4\text{--}25.0$ ). Body size was related to winged traits also, with brachypterous species tending to be larger (macropterous: mean  $8.4 \text{ mm} \pm 2.6 \text{ SD}$ , range  $3.2\text{--}14.5 \text{ mm}$ ; dimorphic:  $4.9 \pm 1.4$ , range  $3.1\text{--}7.0$ , brachypterous mean  $12.4 \pm 7.2$ , range  $2.6\text{--}25.0$ ).

Herbivory was only found in the Zabrinini (Amara and Curtonotus) and Harpalini (Harpalus, Bradycellus, Ophonus), which also tended to be macropterous. Winged traits did not appear to be strongly phylogenetically conserved (Appendix S3, Fig. S3a, Supporting information); 45 of the 72 carabid species were macropterous, across 14 of the 17 tribes, but with brachyptery found in 18 species across nine tribes.

#### SPIDERS

Three spider traits from the nine tested were significantly related to the disturbance gradient (Table 2), although correlations were weaker than for carabids. In contrast to trait responses of carabids, mean body size increased with greater disturbance intensity (Fig. 3a). The abundance of active-hunting spiders increased and web-hunting species decreased with greater disturbance (Fig. 3b). Of the active-hunting spiders, running hunters



**Fig. 3.** Abundance-weighted means (Hellinger-transformed) and ratios of significant fourth-corner spider traits against the increasing disturbance gradient [principal component analysis (PCA) 1]. Individual treatment types are plotted in separate shades from light grey, for non-intervention controls, to black for the most intensive disturbance treatment.

increased in abundance more than ambush and stalking species (Fig. 3c).

Body size was related to hunting strategy, with web-hunting spiders tending to be smaller (mean body length  $3.1 \text{ mm} \pm 1.8$ ) than active hunters (mean body length  $6.4 \text{ mm} \pm 2.5$ ). Aerial dispersal (ballooning) was present in both web- and active-hunting species (27 of 67 and 23 of 58, respectively) and was not related to body size (Appendix S3, Fig. S3b, Supporting information). Web hunting was found in seven of the 19 spider families recorded, with 49 of the 67 web-hunting species coming from the Linyphiidae family. There was a greater range (12 families) and more even distribution of families comprising active-hunting species. Running hunters made up the majority of active-hunting spiders with 37 species; ambush and stalking hunters comprised 13 and eight species, respectively.

#### VASCULAR PLANTS

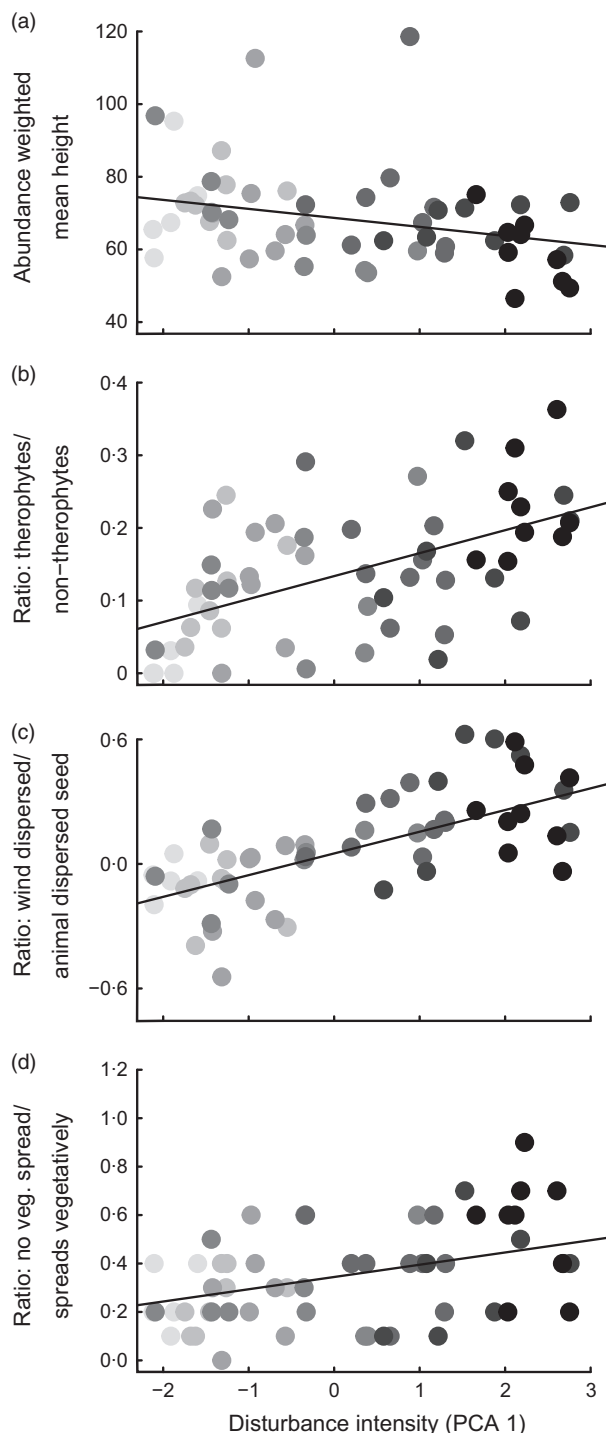
Nine of the 11 vascular plant traits were significantly related to the gradient of disturbance (Table 2). With greater disturbance, mean maximum plant height was lower (Fig. 4a), the ratio of therophytes to non-therophytes greater (Fig. 4b), the ratio of plants with wind-dispersed seed increased compared to those with animal dispersed seeds (Fig. 4c), and plants with no or little lateral spread increased in abundance (Fig. 4d). In the most intensive disturbance treatments, mean Ellenberg light score was higher, mean Ellenberg moisture score lower, and the abundance of woody plants decreased (Table 2, Fig. S2, Supporting information). Although dispersal ability was largely independent, plant traits of growth form and life history were intercorrelated, although independent of vascular plant family (Appendix S3, Fig. S3c, Supporting information).

#### Discussion

##### DISPERSAL ABILITY

For both carabids and vascular plants, trait responses to disturbance were consistent with our hypothesis that disturbance would favour species with greater dispersal ability. Abundance of macropterous carabids increased with disturbance intensity, corresponding with responses to management intensity (Ribera *et al.* 2001; Mullen *et al.* 2008) and fire (Moretti & Legg 2009; Samu *et al.* 2010). Small-seeded and wind-dispersed vascular plant species increased with disturbance, as did species with persistent seed banks (representing temporal rather than spatial dispersal). This concurs with the general pattern that greater dispersal ability allows quicker response following disturbance, as found for terrestrial arthropods (Lambeets *et al.* 2008; Malmstrom 2012), aquatic invertebrates (Matthaei & Townsend 2000; Smale 2008) and plants (McIntyre, Lavorel & Tremont 1995). Interestingly, wing dimorphism in carabids, a trait expected to benefit species colonizing new habitat (Niemela & Spence 1991) or occupying heterogeneous and disturbed landscapes (Kotze & O'Hara 2003), was not significantly related to disturbance intensity. Compared to both brachypterous and macropterous carabids, wing-dimorphic species are comparatively scarce in the regional source fauna (Pedley *et al.* 2013b), and instead may be selected in landscapes or habitats subject to infrequent disturbance. Following rare disturbance events, winged individuals are expected to have a dispersal advantage, but after settlement, the re-absorption of wing muscles or production of non-winged generations provides an advantage to form a larger sedentary population (Roff 1990; Desender 2000).

In contrast to plants and carabids, interpreting spider assemblage responses to disturbance was less straightforward. We found no evidence that physical disturbance favoured spider species able to disperse aurally by ballooning, differing from our original predictions and



**Fig. 4.** Abundance-weighted means and ratios of significant fourth-corner vascular plant traits against the increasing disturbance gradient [principal component analysis (PCA) 1]. For brevity, we only include those traits that relate to competitive establishment and dispersal ability; for plots of all significant traits–disturbance relationships listed in Table 2, see Fig. S2 (Supporting information). Individual treatment types are plotted in separate shades from light grey, for non-intervention controls, to black for the most intensive disturbance treatment.

findings from inundation disturbance (Lambeets *et al.* 2008), but consistent with post-fire response of grassland spiders (Langlands *et al.* 2011). Whether dispersal by bal-

looning allows species to colonize suitable sites within heterogeneous landscapes will depend on their habitat requirements relative to both landscape composition and structure. Ballooning has been found to be a significant source of colonists in large areas of barren habitat, such as after volcanic eruption (Crawford, Sugg & Edwards 1995). But among wolf spiders of the genus *Pardosa*, ballooning propensity was lower in species from abundant and stable habitats (Richter 1970), while Bonte *et al.* (2003a) found dune habitat specialists were less likely to balloon. The apparent lack of response of this trait to disturbance in our experiment could also be affected by limited understanding of ballooning behaviours. To assign aerial dispersal ability, our and other recent studies (e.g. Lambeets *et al.* 2008; Langlands *et al.* 2011) have considered positive evidence of ballooning activity collated by Bell *et al.* (2005). This does not identify false negatives or the effectiveness of species' ballooning behaviour for dispersal and site colonization, for example, although Thomisidae spiderlings balloon, they may land just a few metres from the nest (Morse 1993). For such species, the ballooning 'trait' may not represent effective dispersal at the spatial scale of our experiment.

Although disturbance did not select for ballooning, we interpret other aspects of spider trait responses in terms of dispersal function. Active-hunting spiders, in particular cursorial species (running, rather than stalking or ambush hunters), increased in abundance with greater disturbance intensity. Post-disturbance vegetation structure is particularly suitable for this foraging mode, as sparse and/or shorter vegetation structure may facilitate the movement of running predatory invertebrates (Bonte *et al.* 2003b; Harvey *et al.* 2008). However, this hunting mode can also enhance adult dispersal ability. For one of the dominant cursorial species in this study (*Pardosa monticola*), terrestrial movements have been estimated as 280 m over a lifetime (Bonte *et al.* 2003b), 30–40 m per day for female natal dispersal (Bonte, Van Belle & Maelfait 2007) or mean and maxima of 11.8 and 50 m per day within our study landscape (Waiboonya 2010). Such movements may be sufficient for local- to medium-scale colonization after disturbance; for example, Langlands *et al.* (2011) suggested that terrestrial movements may have been sufficient to colonize study patches of 300 × 300 m after fire. Running and body size were linked in our study, and it is likely that larger cursorial species may be able to colonize quicker after disturbance.

#### SIZE, PHENOLOGY AND FORAGING STRATEGY

Increasing disturbance intensity selected for smaller carabid and vascular plant species, but the opposite response was found for spiders. Interpretation of these responses was complicated by the covariance of size with other biological traits that differed among taxa and also as the functional mechanisms by which disturbance selected size traits may have differed.



For carabids, body size is often linked with dispersal ability (Ribera *et al.* 2001; Kotze & O'Hara 2003), and we found larger body size was associated with brachypterous species that declined with disturbance, while macrop-terous species increased. However, the response of body size cannot solely be interpreted in terms of dispersal and the ability to colonize perturbed habitats. Longer life cycles require stable habitats (Blake *et al.* 1994; Cole *et al.* 2002) with the larval stage particularly vulnerable to physical disturbance owing to reduced mobility, weak chitini-zation and the need to find sufficient food to develop (Lovei & Sunderland 1996). Smaller carabid species are often spring breeders, with faster-growing larvae (Mullen *et al.* 2008) that overwinter as adults (Ribera *et al.* 2001); similarly, we found smaller carabid body size correlated with spring breeding. Conversely, larger carabids are generally longer-lived autumn breeders with overwintering larvae (Lovei & Sunderland 1996). Not surprisingly, therefore, larger carabid body size has often been associ-ated with stable habitats (Cole *et al.* 2002; Blake *et al.* 2003; Kotze & O'Hara 2003). Our results accord with other studies that found small carabid size and spring breeding after greater disturbance (Ribera *et al.* 2001; Cole *et al.* 2002).

Vascular plant maximum height was also less with greater disturbance, although functional mechanisms likely differed to those acting on carabids. Plant height was weakly correlated with growth form, and responses were consistent with other studies where disturbance favoured shorter stature, or rosette growth forms that favour quick resource exploitation (McIntyre, Lavorel & Tremont 1995; Kyle & Leishman 2009). Plant height was also weakly neg-atively related to therophyte life history; therophytes, adapted to rapid resource acquisition and reproduction, increased in abundance with high intensity of disturbance, consistent with responses to soil, inundation and grazing disturbance (McIntyre, Lavorel & Tremont 1995; Lavorel *et al.* 1998; Kyle & Leishman 2009).

In contrast, spider body size was larger with greater dis-turbance intensity. We attribute this to better terrestrial dispersal ability, although it may also reflect open-habitat structure that favours larger cursorial hunters. Larger spi-der body length found immediately after fire may be a functional attribute not of dispersal, but of a relation between body size and burrowing (Langlands *et al.* 2011) so that large size favours survival through perturbation. While after flooding disturbance, two spider groups showed contrasting responses with larger Linyphiidae and smaller Lycosidae (Lambeets *et al.* 2008). Again, func-tional interpretation of size–trait responses is not straight-forward, with disturbance acting on different ecological functions of body size.

## Conclusions

Morphological trait responses to disturbance were not consistent among the three groups, although they could

universally be interpreted in terms of selection for dis-persal ability. The contrast between spiders and carabids in how traits related to dispersal function highlights the need for trait-based studies to examine a range of arthro-pod groups before generalizations can be accepted. Advoc-ates of trait-based analyses have emphasized the functional understanding that this can provide (e.g. Dray & Legendre 2008; Barbaro & van Halder 2009). Neverthe-less, functional interpretation of trait responses remains challenging due to covariance among traits (Langlands *et al.* 2011) and the mapping of individual traits to multi-ple functions. In particular, body size responses poten-tially reflected correlations with life history, physical susceptibility to disturbance and dispersal ability that were inconsistent between the two arthropod groups. When monitoring assemblage responses to environmental change, arthropod body size offers a simple metric that can be assessed by individuals without the need for strong biological or taxonomic expertise (Vandewalle *et al.* 2010). But its usefulness may be limited owing to difficul-ties in interpreting any change. Selection of traits for mea-surement should focus on taxa-specific features for which functional or ecological significance of assembly-level changes can be understood.

## Acknowledgements

Experimental treatments were applied by the Forestry Commission. Fund-ing was provided by the British Ecological Society, Forestry Commission, Natural Environment Research Council, Norfolk Biodiversity Partnership and Suffolk Biodiversity Partnership. We thank Dr H. Mossman and Dr A. Franco for comments and three anonymous referees whose perceptive criticism greatly improved the manuscript. We are very grateful to Tim Pankhurst (Plant life) for vegetation surveying, Martin Collier and Jake Stone for identification of carabid beetles and Neal Armour-Chelu (For-estry Commission) for help and support during the study.

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Received 15 April 2013; accepted 8 May 2014

Handling Editor: Ben Woodcock

## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** Recorded species and their traits.

**Table S2.** Trait details and source references.

**Fig. S1.** Disturbance parameters (vegetation structure and PCA scores) in relation to experimental treatments.

**Fig. S2.** Abundance-weighted means and ratios of significant fourth-corner vascular plant traits against the increasing disturbance gradient (PCA 1).

**Appendix S3.** PCoA of trait covariance for each taxa.