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Multi-taxa trait and functional responses to physical disturbance

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Scott M. Pedley* • Paul M. Dolman

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6 School of Environmental Sciences

7 University of East Anglia

8 Norwich

9 NR4 7TJ, UK

10 Email addresses:

11 smpedley@gmail.com; p.dolman@uea.ac.uk

12

13 * Corresponding Author:

14 Tel: +44 1603 591341

15 Fax: +44 1603 591327

16 smpedley@gmail.com

17 Running headline:

18 Multi-taxa trait responses to physical disturbance

1 **Summary**

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

6

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

15

16 3. We sampled 197 arthropod species (14738 individuals) and 164 species of plant.
17 The strength of association between each trait and the disturbance intensity was
18 quantified by correlating matrices of species by traits, species abundance by sites,
19 and sites by environment, with significance assessed by comparison with a null
20 model.

21

22 4. Responses of biological traits varied among taxa but could be consistently
23 interpreted in terms of dispersal ability. Trait shifts for carabid and plant
24 assemblages were as predicted and correspond to those observed in other

1 disturbance regimes. Assemblages after disturbance comprised smaller and winged
2 carabids, and smaller plants with wind-dispersed seed, consistent with selection for
3 species with better dispersal ability. In contrast, aerial dispersal did not appear
4 important in spider recolonisation, instead terrestrial dispersal ability was suggested
5 by the increased abundance of larger-bodied and cursorial species. However, larger
6 spider body-size was also associated with an active-hunting strategy, also favoured
7 in the post-disturbance environment.

8

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

17

18 Key-words: assembly rules, body-size, brachypterous, colonisation, community-
19 weighted mean trait, dispersal ability, environmental filters, functional response,
20 macropterous.

1 **Introduction**

2 There is a need to better understand how biodiversity will respond to increasing
3 anthropogenic environmental change and perturbation (MEA 2005; McGill *et al.*
4 2006). But examining responses of species composition only provides information
5 that is context and bioregion specific, while measures such as richness or diversity do
6 not inform ecological function (Vandewalle *et al.* 2010). There is, therefore, growing
7 interest in trait- and function-based approaches that offer a mechanistic
8 understanding across multiple species (McGill *et al.* 2006). Within ecosystems or
9 habitats, biological and functional trait responses to ecological processes may be
10 robust to geographic turn-over in species composition, allowing generality across
11 bioregions (Statzner *et al.* 2001; Pont *et al.* 2006; Vandewalle *et al.* 2010). For
12 example, generalising responses of aquatic assemblages across regions provided
13 indices quantifying human modification of river channel states or pollution loads,
14 allowing the development of continent-wide monitoring criteria (Vandewalle *et al.*
15 2010).

16

17 For trait studies to go beyond the description of patterns and be predictive or
18 provide mechanistic understanding requires the testing of explicit *a priori*
19 hypotheses in terms of assemblage trait responses to environmental drivers (McGill
20 *et al.* 2006). Furthermore, biological traits (e.g. morphological, phenological or
21 behavioural) selected for investigation should represent meaningful ecological or
22 demographic functions (McGill *et al.* 2006; Gray *et al.* 2007; Vandewalle *et al.* 2010),
23 such as dispersal, trophic role, fecundity or rates of population increase. However,
24 the link between morphological or life history traits and ecological function may be

1 complex as commonly measured traits may be associated with multiple ecological
2 and functional attributes. For example, body size may be associated with dispersal
3 ability, feeding niche, fecundity and also competitive dominance (Kotze & O'Hara
4 2003; McGill *et al.* 2006; Williams *et al.* 2010). Therefore, to support mechanistic
5 understanding in a particular ecosystem or landscape, it is important to identify the
6 key environmental pressures or effects and from these, the expected ecological and
7 functional responses (McGill *et al.* 2006). This allows directional tests of
8 morphological or ecophysiological trait responses.

9

10 In fragmented and anthropogenically perturbed habitats, assemblages may be
11 filtered by species dispersal ability (Heino & Hanski 2001; Ribera *et al.* 2001), with
12 dispersal one of the most important traits for assemblage recovery after disturbance
13 in both arthropods (Roff 1990; Mullen *et al.* 2008; Malmstrom 2012) and plants (Kyle
14 & Leishman 2009; Moretti & Legg 2009). However, disturbed ecosystems have also
15 been found to select for smaller and more fecund species, while larger slow-growing
16 species are better suited to stable habitats (Statzner & Beche 2010; Chiu & Kuo
17 2012). Disturbance and subsequent successional recovery also affect vegetation
18 structure, microclimates, environmental stressors such as aridity, and resource
19 spectra such as soil fauna or plant seeds, with implications for other functional traits
20 (Entling *et al.* 2007; Schirmel & Buchholz 2011). Therefore, trait responses to
21 disturbance may be complex and mediated by multiple environmental effects in
22 addition to filters of dispersal ability. To understand such complex trait responses
23 and explore the degree to which they may be generalised, approaches that examine

1 community assembly across environmental gradients have been recommended
2 (McGill *et al.* 2006).

3

4 We created an experimental gradient of physical disturbance, embedded in an
5 extensive network of open-habitats within a forested landscape that permits re-
6 colonisation from regional source populations (Pedley *et al.* 2013b). We used this
7 experiment to examine whether assemblage response of attributes associated with
8 dispersal (e.g. body size or aerial flight) were consistent across taxonomic groups.

9 We also examine responses of biological traits for diet, foraging strategy and
10 environmental tolerance, and the inter-correlation between these and attributes
11 associated with dispersal.

12

13 We contrast the trait responses of two arthropod groups (carabids and spiders) to
14 those of vascular plants. Simultaneous examination of both arthropod groups and
15 plants permits exploration of the extent that trait responses may be generalised
16 across taxonomic groups (Moretti & Legg 2009), facilitating the search for general
17 rules in community ecology (MacArthur 1972; McGill *et al.* 2006). Carabid life
18 histories are known for European species and have been used to examine trait
19 responses to disturbance and landscape change (Ribera *et al.* 2001; Desender *et al.*
20 2010); in comparison, trait analysis of spiders has been more limited (though see
21 Langlands *et al.* 2011; Lambeets *et al.* 2008). Vascular plants provided an excellent
22 comparative group as species traits are well known (Cornelissen *et al.* 2003) and
23 trait-disturbance responses have been generalised (e.g. Keith *et al.* 2007; McIntyre &
24 Lavorel 2001).

1

2 Physical disturbance treatments ranged along a gradient of intensity to enable us to
3 address the following questions: 1) does disturbance cause trait shifts? 2) Are trait
4 responses similar across contrasting taxonomic groups, particularly responses of size,
5 dispersal ability, and phenology? 3) Do trait shifts in response to physical disturbance
6 concur with responses to other disturbance types such as fire, flooding and
7 management intensification? Based on trait response in other disturbance regimes,
8 we hypothesised that assemblages that developed after high intensities of
9 disturbance would have a reduced representation of arthropod species with large
10 bodies and poorer powers of dispersal (Ribera *et al.* 2001; Cole *et al.* 2002; Langlands
11 *et al.* 2011). We also test the hypothesis that disturbance would reduce the relative
12 abundance of plant species with slow maturation, short-lived seed banks and lacking
13 mechanisms for medium- or long-distance seed dispersal (McIntyre, Lavorel &
14 Tremont 1995; Lavorel *et al.* 1998; Kyle & Leishman 2009).

15

16 **Materials and methods**

17 Study design

18 Our study was conducted within Thetford Forest, a conifer-dominated plantation
19 established in the early 20th century, occupying 185 km² of Breckland, eastern
20 England (0°40'E, 52°27'N). This region is characterised by sandy soils and historically
21 supported species associated with heathland and ruderal land-uses (Dolman &
22 Sutherland 1992). Present forest management consists of clear-felling (typically at
23 60-80 years) and replanting of even-aged patches of tree crop (mean 9.0 ha ± 8.6
24 SD). These patches are subdivided by a network of forestry trackways (with a central

1 part occasionally used by forestry vehicles, flanked on both sides by wide vegetated
2 verges) that support diverse carabid and spider assemblages, comprising both open-
3 habitat and forest species (Pedley, Bertoneclj & Dolman 2013a; Pedley *et al.* 2013b;
4 Bertoneclj & Dolman 2013a).

5

6 Six mechanical disturbance treatments were applied together with a set of untreated
7 controls, each were replicated nine times in February 2009 (Fig. 1). Treatments
8 represented a gradient of disturbance severity, ranked as: 1) sward cutting (cutting
9 of standing vegetation without removal); 2) sward cutting with removal of clippings;
10 3) disc harrowing (that vertically cuts through vegetation, litter and roots, killing
11 some plants, but without inverting litter or soil horizons); 4) parallel individual
12 plough lines that inverted vegetation and litter, exposing mineral soil, separated by
13 an undisturbed strip of vegetation approximately 0.5 m wide; 5) agricultural
14 ploughing that chopped up and inverted all vegetation exposing mineral soil across
15 the entire plot; and 6) 'bulldozing' to remove all above-ground plant material and
16 root mass, litter and organic soil horizons to expose mineral soil. Each treatment
17 replicate comprised a single plot 150 m long with a mean width of 4 m, located
18 within a forest trackway (minimum width 9 m, mean 13.5 m \pm 3.7 SD, range 9-24 m)
19 verge, adjacent to planted forest. We acknowledge that, although invertebrates can
20 show marked behavioural responses to habitat boundaries (Bertoneclj & Dolman
21 2013b), the narrow plot dimension and associated edge effect may result in
22 oversampling of more mobile eurytopic species; however, it was not practical to
23 increase plot size sufficiently to exclude this. Trackways for treatment placement
24 were located within tree crops aged 10-25 years to avoid confounding effects of

1 shade and insolation, with treatments placed at least 100 m from plantation edges,
2 recently felled areas or other open habitats. Treatments and untreated controls
3 were allocated randomly across 63 suitable trackways; the resulting distribution of
4 treatments was spatially random within the forest as shown by Analysis of Variance
5 of longitude ($F_{6, 56}=1.396, P=0.232$) and latitude ($F_{6, 56}=1.014, P=0.426$). Spatial
6 autocorrelation in assemblage composition was examined separately for each taxa
7 by Mantel tests (Legendre & Legendre 1998) performed on the first two axes of a
8 non-metric multidimensional scaling (NMDS) ordination. NMDS was performed on
9 species abundance data using the vegan package (Oksanen *et al.* 2010) in R (R
10 Development Core Team 2012).

11

12 Sampling protocol

13 In each plot, abundance of each vascular plant species was quantified as its
14 frequency of presence across 20 independent replicate 1 m x 1 m quadrats placed
15 along the main axis of the plot, sampled once during May to August 2010. Ground
16 living carabids and epigeic (surface dwelling) spiders were sampled in each
17 treatment plot with pitfall traps set in May, June and late July/early August 2010, 15
18 to 17 months after the application of disturbance treatments. Traps were set in a
19 single transect along the centre of each treatment plot, 37.5 m in from each end,
20 with six individual traps (each 7.5 cm deep, 6.5 cm in diameter, filled with 50 ml of
21 70% ethylene glycol) set 15 m apart and opened for seven consecutive days in each
22 period. Traps in each transect were combined to give one composite sample of
23 material for identification, and data from each trapping period were combined to
24 give a composite sample for analysis, comprising 126 trap-days per treatment plot.

1 Pitfall trap catches, as with any trapping method, have inherent biases and can be
2 influenced by factors including habitat structure, weather conditions and animal
3 activity (Topping & Sunderland 1992). However, pitfall trapping successfully reflects
4 ecological differences among areas, as long as it is remembered that interpretation is
5 not based on population density but on the actual catch (Luff & Eyre 1988). In our
6 study, standardized pitfall trapping is an appropriate collection method as we aimed
7 to compare trait responses of ground-active invertebrates as affected by disturbance
8 and not to provide complete site inventories.

9

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

14

15 Species' traits

16 Attributes of morphology, life history, phenology, trophic guild, ecophysiological
17 tolerance and behaviours such as migration (e.g. Pont *et al.* 2006; Vandewalle *et al.*
18 2010) are phenotypic traits. Although considered in some trait studies, we excluded
19 local abundance or range extent (e.g. Davies *et al.* 2000; Henle *et al.* 2004; Gray *et al.*
20 2007; Barbaro & van Halder 2009) and habitat association (e.g. Davies *et al.* 2010;
21 Vandewalle *et al.* 2010), as we did not consider these to be strict biological traits, but
22 rather to be ecological attributes that may vary across a species range (Gaston *et al.*
23 1997) or with regional climate (Davies *et al.* 2006).

24

1 For carabids, spiders and vascular plants, we selected life-history traits that were
2 considered likely to respond to disturbance, and for which species-specific
3 information was available from published literature. It was not possible to develop
4 identical sets of traits for each of the contrasting taxonomic groups; rather we aimed
5 to quantify consistent morphological (e.g. life form, body size, winged), behavioural
6 and life-history (e.g. phenology), feeding strategy and ecophysiological (e.g.
7 tolerance of aridity or of shade) traits. Although scores for aridity tolerance were
8 available for plants and spiders, equivalent information was not available for
9 carabids; we did not wish to infer this trait from published information on carabid
10 habitat associations. Traits used in the analysis are detailed in Table 1.

11

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

21

22 Environmental parameters

23 Disturbance intensity was quantified in terms of the resulting vegetation structure,
24 measured at 40 points distributed along the centre of each treatment plot. At each

1 point vegetation height was measured using a sward stick (diameter 90 mm, weight
2 250 g, following Dolman and Sutherland (1992)) and the percentage cover of bare
3 substrate and of moss were visually estimated within 20 cm x 20 cm; plot means
4 were used in analysis. Cutting did not alter plant species composition (Pedley *et al.*
5 2013b), so that vegetation height could be considered separately from the trait of
6 potential maximum plant height. Moss largely comprised shade-tolerant
7 pleurocarpous species, rather than early-successional acrocarpous species, and
8 indicated moister microhabitats.

9

10 A compound measure of disturbance intensity at each plot was calculated as the first
11 axis of an unrotated Principal Component Analysis (PCA) performed on the
12 correlation matrix of the three vegetation structure variables (bare ground, moss
13 and vegetation height). These variables were inter-correlated (vegetation height and
14 moss, $r = 0.578$, $P < 0.001$; vegetation height and bare ground, $r = -0.701$, $P < 0.001$;
15 bare ground and moss, $r = -0.675$, $P < 0.001$); however, each responded non-linearly
16 to the intensity of disturbance treatment. Although the extent of bare ground
17 increased across the four soil disturbance treatments (Fig. S1), it changed negligibly
18 between untreated controls, cutting or cutting with removal. In contrast, cutting
19 treatments reduced vegetation height (Fig. S1). Thus, the combined PCA responded
20 to disturbance across the entire range of treatments (Fig. S1).

21

22 Trait Analysis

23 Trait responses to disturbance intensity were examined separately for each
24 taxonomic group using fourth-corner analysis (Dray & Legendre 2008). This

1 procedure tests whether the observed degree of trait-environment linkage differs
2 from that expected by chance, providing a mechanistic understanding in contrast to
3 emergent group analysis that describes species clustering based on shared traits
4 (Aubin *et al.* 2009), or 'RLQ' analysis that provides descriptive grouping of species,
5 traits and environmental variables (Brind'Amour *et al.* 2011). The strength of trait-
6 environment linkage was assessed against a null model, randomising species
7 incidence relative to disturbance parameters with 9999 permutations, following Dray
8 & Legendre (2008). Analyses were conducted in R using the ade4 package (Dray &
9 Dufour 2007). To compensate for reduced spider abundance with greater
10 disturbance, following Aubin *et al.* (2009) spider data were Hellinger transformed
11 (Legendre & Gallagher 2001), whereby the abundance of each species recorded per
12 site is first standardised by the total site abundance and then square-root
13 transformed. To control table-wide type 1 error rates of fourth-corner results across
14 each taxon, we applied sequential Bonferroni correction (Holm 1979; following
15 Aubin *et al.* 2009). For those that remained significant, the trait-environment
16 relation was visualised by plotting abundance-weighted mean trait values per
17 treatment plot against the PCA score of disturbance intensity. As fully resolved
18 phylogenetic trees are not available for spiders and beetles we applied no
19 phylogenetic correction.

20

1 **Results**

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

14

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

19

20 **Carabids**

21 Five of the ten carabid traits had significant links to the disturbance gradient when
22 examined by fourth-corner analysis (Table 2). Mean body size decreased and the
23 abundance of herbivores was greater with greater disturbance intensity (Fig. 2a, b).

24 Macropterous (winged) species were more abundant with greater disturbance

1 intensity, while the abundance of brachypterous (with vestigial wings) species in the
2 most intense treatment was reduced compared to controls (Fig. 2c). Surprisingly, the
3 frequency of wing dimorphic species was not related to disturbance intensity (Table
4 2). Of the 72 species only nine (from six different tribes) were wing dimorphic; of
5 these two were relatively numerous (*Bembidion lampros* and *Syntomus truncatellus*,
6 with 112 and 100 individuals recorded respectively) and were found in small
7 numbers across all treatments. Relations among traits are shown in Appendix S3.

8

9 Time of breeding related to activity period and body size, with autumn breeders
10 tending to be larger (mean body length $11.5 \text{ mm} \pm 5.2$) and spring breeders (mean
11 body length $7.4 \text{ mm} \pm 3.6 \text{ SD}$) having longer activity length (Appendix S3, Fig. S3a).
12 The herbivorous species were largely macropterous (31 of 33), while carnivorous and
13 omnivorous species showed a mix of winged traits (of 24 carnivores, 10 were
14 macropterous, five dimorphic, nine brachypterous; of seven omnivores, one, two
15 and four respectively). Small- to medium-sized species had a range of diets, so that
16 body size was largely independent of diet (Appendix S3, Fig. S3a); nevertheless, most
17 of the largest species were carnivorous (herbivores: mean $8.5 \text{ mm} \pm 2.1 \text{ SD}$, range
18 $4.4 - 13.5 \text{ mm}$; carnivores: mean 10.5 ± 6.4 , range $3.4 - 25.0$). Body size was related
19 to winged traits also, with brachypterous species tending to be larger
20 (macropterous: mean $8.4 \text{ mm} \pm 2.6 \text{ SD}$, range $3.2-14.5 \text{ mm}$; dimorphic: 4.9 ± 1.4 ,
21 range $3.1-7.0$, brachypterous mean 12.4 ± 7.2 , range $2.6-25.0$).

22

23 Herbivory was only found in the Zabrinini (*Amara* and *Curtonotus*) and Harpalini
24 (*Harpalus*, *Bradycellus*, *Ophonus*), which also tended to be macropterous. Winged

1 traits did not appear to be strongly phylogenetically conserved (Appendix S3, Fig.
2 S3a); 45 of the 72 carabid species were macropterous, across 14 of the 17 tribes, but
3 with brachyptery found in 18 species across nine tribes.

4

5 Spiders

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

13

14 Body size was related to hunting strategy, with web hunting spiders tending to be
15 smaller (mean body length $3.1 \text{ mm} \pm 1.8$) than active hunters (mean body length 6.4
16 $\text{mm} \pm 2.5$). Aerial dispersal (ballooning) was present in both web and active hunting
17 species (27 of 67 and 23 of 58, respectively) and was not related to body size
18 (Appendix S3, Fig. S3b). Web hunting was found in seven of the 19 spider families
19 recorded, with 49 of the 67 web hunting species coming from the Linyphiidae family.
20 There was a greater range (12 families) and more even distribution of families
21 comprising active hunting species. Running hunters made up the majority of active
22 hunting spiders with 37 species; ambush and stalking hunters comprised 13 and
23 eight species respectively.

24

1 Vascular plants

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

12

1 **Discussion**

2

3 Dispersal ability

4 For both carabids and vascular plants, trait responses to disturbance were consistent
5 with our hypothesis that disturbance would favour species with greater dispersal
6 ability. Abundance of macropterous carabids increased with disturbance intensity,
7 corresponding with responses to management intensity (Ribera *et al.* 2001; Mullen
8 *et al.* 2008) and fire (Moretti & Legg 2009; Samu *et al.* 2010). Small-seeded and
9 wind-dispersed vascular plant species increased with disturbance, as did species with
10 persistent seed banks (representing temporal rather than spatial dispersal). This
11 concurs with the general pattern that greater dispersal ability allows quicker
12 response following disturbance, as found for terrestrial arthropods (Lambeets *et al.*
13 2008; Malmstrom 2012), aquatic invertebrates (Matthaei & Townsend 2000; Smale
14 2008) and plants (McIntyre, Lavorel & Tremont 1995). Interestingly, wing
15 dimorphism in carabids, a trait expected to benefit species colonising new habitat
16 (Niemela & Spence 1991) or occupying heterogeneous and disturbed landscapes
17 (Kotze & O'Hara 2003), was not significantly related to disturbance intensity.
18 Compared to both brachypterous and macropterous carabids, wing-dimorphic
19 species are comparatively scarce in the regional source fauna (Pedley *et al.* 2013b),
20 and instead may be selected in landscapes or habitats subject to infrequent
21 disturbance. Following rare disturbance events winged individuals are expected to
22 have a dispersal advantage, but after settlement the reabsorption of wing muscles or
23 production of non-winged generations provides an advantage to form a larger
24 sedentary population (Roff 1990; Desender 2000).

1

2 In contrast to plants and carabids, interpreting spider assemblage responses to
3 disturbance was less straightforward. We found no evidence that physical
4 disturbance favoured spider species able to disperse aerially by ballooning, differing
5 from our original predictions and findings from inundation disturbance (Lambeets *et*
6 *al.* 2008), but consistent with post-fire response of grassland spiders (Langlands *et al.*
7 2011). Whether dispersal by ballooning allows species to colonise suitable sites
8 within heterogeneous landscapes will depend on their habitat requirements relative
9 to both landscape composition and structure. Ballooning has been found to be a
10 significant source of colonists in large areas of barren habitat, such as after volcanic
11 eruption (Crawford, Sugg & Edwards 1995). But among wolf-spiders of the genus
12 *Pardosa*, ballooning propensity was lower in species from abundant and stable
13 habitats (Richter 1970), while Bonte *et al.* (2003a) found dune habitat specialists
14 were less likely to balloon. The apparent lack of response of this trait to disturbance
15 in our experiment could also be affected by limited understanding of ballooning
16 behaviours. To assign aerial dispersal ability our and other recent studies (e.g.
17 Lambeets *et al.* 2008; Langlands *et al.* 2011) have considered positive evidence of
18 ballooning activity collated by Bell *et al.* (2005). This does not identify false negatives
19 or the effectiveness of species' ballooning behaviour for dispersal and site
20 colonisation, for example, although Thomisidae spiderlings balloon, they may land
21 just a few meters from the nest (Morse 1993). For such species the ballooning 'trait'
22 may not represent effective dispersal at the spatial scale of our experiment.

23

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

18

19 Size, phenology and foraging strategy

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

1

2 For carabids, body size is often linked with dispersal ability (Ribera *et al.* 2001; Kotze
3 & O'Hara 2003) and we found larger body size was associated with brachypterous
4 species that declined with disturbance, while macropterous species increased.

5 However, the response of body size cannot solely be interpreted in terms of
6 dispersal and the ability to colonise perturbed habitats. Longer life cycles require
7 stable habitats (Blake *et al.* 1994; Cole *et al.* 2002) with the larval stage particularly
8 vulnerable to physical disturbance owing to reduced mobility, weak chitinization and
9 the need to find sufficient food to develop (Lovei & Sunderland 1996). Smaller
10 carabid species are often spring breeders, with faster growing larvae (Mullen *et al.*
11 2008) that over-winter as adults (Ribera *et al.* 2001); similarly we found smaller
12 carabid body size correlated with spring breeding. Conversely, larger carabids are
13 generally longer-lived autumn breeders with overwintering larvae (Lovei &
14 Sunderland 1996). Not surprisingly, therefore, larger carabid body size has often
15 been associated with stable habitats (Cole *et al.* 2002; Blake *et al.* 2003; Kotze &
16 O'Hara 2003). Our results accord with other studies that found small carabid size and
17 spring breeding after greater disturbance (Ribera *et al.* 2001; Cole *et al.* 2002).

18

19 Vascular plant maximum height was also less with greater disturbance, although
20 functional mechanisms likely differed to those acting on carabids. Plant height was
21 weakly correlated with growth form, and responses were consistent with other
22 studies where disturbance favoured shorter stature, or rosette growth forms that
23 favour quick resource exploitation (McIntyre, Lavorel & Tremont 1995; Kyle &
24 Leishman 2009). Plant height was also weakly negatively related to therophyte life

1 history; therophytes, adapted to rapid resource acquisition and reproduction,
2 increased in abundance with high intensity of disturbance, consistent with responses
3 to soil, inundation and grazing disturbance (McIntyre, Lavorel & Tremont 1995;
4 Lavorel *et al.* 1998; Kyle & Leishman 2009).

5

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

16

17 Conclusions

18 Morphological trait responses to disturbance were not consistent among the three
19 groups, although they could universally be interpreted in terms of selection for
20 dispersal ability. The contrast between spiders and carabids in how traits related to
21 dispersal function highlights the need for trait-based studies to examine a range of
22 arthropod groups before generalisations can be accepted. Advocates of trait-based
23 analyses have emphasised the functional understanding that this can provide (e.g.
24 Dray & Legendre 2008; Barbaro & van Halder 2009). Nevertheless, functional

1 interpretation of trait responses remains challenging due to covariance among traits
2 (Langlands *et al.* 2011) and the mapping of individual traits to multiple functions. In
3 particular, body size responses potentially reflected correlations with life history,
4 physical susceptibility to disturbance, and dispersal ability that were inconsistent
5 between the two arthropod groups. When monitoring assemblage responses to
6 environmental change, arthropod body size offers a simple metric that can be
7 assessed by individuals without the need for strong biological or taxonomic expertise
8 (Vandewalle *et al.* 2010). But its usefulness may be limited owing to difficulties in
9 interpreting any change. Selection of traits for measurement should focus on taxa-
10 specific features for which functional or ecological significance of assembly level
11 changes can be understood.

12

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22

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1 **Figure legends**

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

4

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

9

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

14

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

1 Table 1. Coding and description for biological traits of each taxonomic group. For sources of
2 trait data see Table S2.

Carabids	Attribute
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 speices
Macropterous	1=macropterous species

Spiders	Attribute
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	Standardised niche parameters (0-1)
Shade score	Standardised niche parameters (0-1)
Ballooning	1=exact species is listed as ballooning in Bell et al. (2005)
Active hunter	1=active hunting strategy
Running hunter	1=running hunters
Ambush hunter	1=ambush hunters
Stalking hunter	1=stalking hunters

Plants	Attribute
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

3

1 Table 2. Fourth-corner correlation coefficients from analyses performed on plant, carabid
 2 and spider assemblages, with increasing disturbance intensity (increasing PCA 1 scores)
 3 related to species traits (see Table 1 for trait descriptions). Significant relationships ($p < 0.05$,
 4 after Holm's correction performed separately on each taxon) are indicated in bold.

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

5

- 1 **Supporting Information:**
- 2 Additional Supporting Information is available for this article online.
- 3 **Table S1.** Recorded species and their traits
- 4 **Table S2.** Trait details and source references
- 5 **Fig. S1.** Disturbance parameters (vegetation structure and PCA scores) in relation to
- 6 experimental treatments
- 7 **Fig. S2.** Abundance weighted means and ratios of significant fourth corner vascular plant
- 8 traits against the increasing disturbance gradient (PCA 1)
- 9 **Appendix S3.** PCoA of trait covariance for each taxa
- 10 **Fig. S3.** PCoA showing trait covariance for each taxa
- 11 **Table S3.** PCoA trait loadings