This is the peer reviewed version of the following article: Vanbergen, A. J., Woodcock, B. A., Gray, A. , Andrews, C. , Ives, S. , Kjeldsen, T. R., Laize, C. L., Chapman, D. S., Butler, A. and O'Hare, M. T. (2017), Dispersal capacity shapes responses of river island invertebrate assemblages to vegetation structure, island area, and flooding. *Insect Conservation and Diversity*, 10: 341-353, which has been published in final form at https://doi.org/10.1111/icad.12231. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for self-archiving.

Dispersal capacity shapes responses of river island invertebrate assemblages to vegetation structure, island area, and flooding.

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Running title: *Invertebrate biodiversity of riparian islands*

Keywords: *dispersal, niche, disturbance, riparian, trait, habitat structure*

Word count: 7447 excluding abstract, figure and table legends

Abstract

1. Riparian invertebrate communities occupy a dynamic ecotone where hydrogeomorphological (e.g. river flows) and ecological (e.g. succession) processes may govern assemblage structure by filtering species according to their traits (e.g. dispersal capacity, niche).

2. We surveyed terrestrial invertebrate assemblages (millipedes, carabid beetles, spiders) in 28 river islands across four river catchments over two years. We predicted that distinct ecological niches would produce taxon-specific responses of abundance and species richness to: *i*) disturbance from episodic floods, *ii*) island area, *iii*) island vegetation structure and *iv*) landscape structure. We also predicted that responses would differ according to species' dispersal ability (aerial vs terrestrial only), indicating migration was sustaining community structure.

3. Invertebrate abundance and richness was affected by different combinations of vegetation structure, island area and flood disturbance according to species' dispersal capacity. Carabid abundance related negatively to episodic floods, particularly for flightless species, but the other taxa were insensitive to this disturbance. Larger islands supported greater abundance of carabids and all invertebrates able to disperse aerially. Vegetation structure, particularly tree canopy density and plant richness, related positively to invertebrate abundance across all taxa and aerial dispersers, whereas terrestrial disperser richness related positively to tree cover. Landscape structure did not influence richness or abundance.

4. Multiple ecological processes govern riparian invertebrate assemblages. Overall insensitivity to flood disturbance and responses contingent on dispersal mode imply that spatial dynamics subsidize the communities through immigration. Particular habitat features (e.g. trees, speciose vegetation) may provide refuges from disturbance and concentration of niches and food resources.

Introduction

Episodic disturbance of a habitat patch can re-organise and structure plant-insect communities (Gerisch *et al.*, 2012; Jonsson *et al.*, 2009; Lambeets *et al.*, 2008c). Disturbance effects on insect communities are often mediated by directly eliminating organisms and by modifying local vegetation and the food and breeding resources therein (Brose, 2003a; Tews *et al.*, 2004; Vanbergen *et al.*, 2014). Riparian habitats are highly dynamic environments due to hydrogeomorphological processes and episodic disturbance by flood waters, either driven by the management of discharge or as predicted to increase under global climate change (Gurnell *et al.*, 2012; IPCC, 2013). Flooding of terrestrial environments are known to affect invertebrate diversity and abundance (Brose, 2003b; Ellis *et al.*, 2001; Gerisch *et al.*, 2012; Lambeets *et al.*, 2008c; Rothenbucher & Schaefer, 2006). For example, in a lowland riparian bankside assemblage, spider species richness reduced with increased flood intensity, whereas carabid beetle species richness peaked at intermediate levels of flooding (Lambeets *et al.*, 2008c). Disturbance from floods is thus likely to be important driver of species presence and community structure in riparian habitats.

In addition to disturbance, habitat successional processes can produce spatial environmental gradients or heterogeneity to affect species persistence and community composition. For example, in riparian systems the natural or anthropogenic modification of river channels or flows affects the hydrological deposition of sediments and the degree of stabilization by vegetation (Gurnell *et al.*, 2012; Mikuś *et al.*, 2013). Such hydrogeomorphological processes will produce riparian and in-stream terrestrial habitats (e.g. islands or mid-channel bars) varying in vegetation structure and their capacity to support terrestrial invertebrate communities (Gurnell *et al.*, 2012; Gurnell *et al.*, 2001; Mikuś *et al.*, 2013). Such gradients in vegetation structure will sort species assemblages according to traits (e.g. ecological niche or dispersal capacity) facilitating niche partitioning, species coexistence and generating community-scale patterns in diversity and abundance (Fournier *et al.*, 2015; Leibold *et al.*, 2004; Sydenham *et al.*, 2014; Tews *et al.*, 2004).

Invertebrate community assembly in spatially heterogeneous and highly disturbed environments is likely to be maintained through dynamic species extinction or colonisation of habitat patches, as predicted by island biogeographical, metapopulation or metacommunity processes (Leibold *et al.*, 2004; Vandermeer & Carvajal, 2001; Warren *et al.*, 2015). Species either persist, perish or migrate when the environment is flooded, whilst populations can re-establish through immigration as flood waters recede (Brose, 2003b; Rothenbucher & Schaefer, 2006). This can influence the species composition or diversity of flooded habitat, although effects vary with taxonomic identity. This is because species extinctions or other biodiversity changes tend to be non-random with species possessing certain traits (e.g. higher trophic level, low intrinsic abundance, low dispersal ability) prone to be vulnerable to particular environmental stressors (Raffaelli, 2004). A variety of metacommunity processes may influence species demography and interactions, and hence community diversity (Leibold *et al*., 2004). For instance, where habitat patches are in a different state over time and are adequately connected, species dispersal can result in source-sink dynamics or mass effects, whereby species are rescued from competitive exclusion in a patch by repeated immigration (Leibold *et al.*, 2004). Whether such spatial dynamics pre-dominate will vary with the extent that species in the assemblage are habitat specialists or generalists, as this will affect the organism's perception of the size and isolation of the habitat patch (Leibold *et al.*, 2004; Tews *et al.*, 2004).

The landscape context of a given habitat patch is also likely to influence diversity and abundance within it because the composition of the landscape matrix within dispersal range is likely to dictate the pool of available colonists. Indeed landscape structure is known to influence the species richness and abundance of many invertebrate taxa, including soil invertebrates (Eggleton *et al.*, 2005; Sousa *et al.*, 2006), beetles and spiders (Billeter *et al.*, 2008; Driscoll & Weir, 2005; Vanbergen *et al.*, 2010), pollinators (Kennedy *et al.*, 2013) and their interspecific interactions (Thies *et al.*, 2003; Vanbergen *et al.*, 2014).

The species assemblage of a given habitat patch is thus likely to be governed by a combination of the area and vegetation structure of the habitat, the level of disturbance, and spatio-temporal dispersal dynamics that link the assemblage to the wider species pool in the surrounding landscape (Driscoll & Weir, 2005; Leibold *et al.*, 2004; Vandermeer & Carvajal, 2001).

Insular or island habitats are a microcosm of organisms and processes that due to their relative size and isolation represent distinct ecosystem replicates embedded in a wider landscape matrix. Hence they are a useful platform to understand the factors governing spatial patterns in diversity (Gonzalez *et al.*, 1998; Jonsson *et al.*, 2009; Warren *et al.*, 2015). River islands are highly dynamic ecosystems, ranging from mid-channel bars to vegetated islands, affected by episodic disturbance from river flows (Gurnell *et al.*, 2012; Gurnell *et al.*, 2001; Mikuś *et al.*, 2013). Consequently, they offer an opportunity to understand the interplay between episodic disturbance, habitat area, vegetation structure, and landscape context of islands in shaping invertebrate communities.

Here, we tested how terrestrial invertebrate communities (millipedes–Diplopoda; ground beetles–Carabidae; spiders–Araneae) occupying distinct ecological niches in riparian island ecosystems responded to *i*) disturbance from episodic floods, *ii*) island area, *iii*) island vegetation structure, and *iv*) surrounding landscape structure. Profound ecological differences exist amongst these taxa. For instance, spiders are obligate predators and highly dispersive, either overland through terrestrial locomotion or by aerial ballooning on silk threads (Hayashi *et al.*, 2015; Lambeets *et al.*, 2008c; Pedley & Dolman, 2014). Ground beetle assemblages often comprise species from all trophic levels, include habitat specialists and generalists, and vary greatly in body size and flight ability (Kotze & O'Hara, 2003; Pedley & Dolman, 2014; Vanbergen *et al.*, 2010). Millipedes are obligate detritivores, have limited mobility and are very sensitive to disturbance and microclimate (Blower, 1985; Dauber *et al.*, 2005; Eggleton *et al.*, 2005). Accordingly, we predicted taxon-specific responses in abundance and species richness to these different sources of environmental heterogeneity (*i*-*iv*). We also predicted abundance and species richness in this dynamic riparian ecosystem would be governed by species' dispersal ability (aerial & terrestrial vs terrestrial locomotion only), which shapes the capacity for migration to sustain community structure.

Methods

Island sites

Twenty-eight islands were surveyed in 2010 and 2011 across four rivers (Earn = 6 islands, Tay = 6, Tummel = 5 and Tweed =11) within three catchments in central and southern Scotland (Figure 1). Islands were mid channel bars formed by hydrological deposition of sediments and subsequent stabilisation by vegetation (Gurnell *et al.*, 2012; Mikuś *et al.*, 2013). The perimeter coordinates of each island were mapped with a GPS (Garmin 12) and subsequently the area (m^2) of each island determined using ArcGIS™ (version 9.3.1, ESRI®). The geographical co-ordinates and area of each island are found in Table S1 (Appendix S1). A standardised transect (20m long) was haphazardly situated in the centre of each island orientated along the up-down stream axis of the island. Along the transect, 10 sampling points were located at 2m intervals along which invertebrate communities and vegetation structure were quantified (see below).

Invertebrate communities

Island invertebrate assemblages were sampled with 10 pitfall traps distributed among the sampling points on each transect. Each trap comprised a polypropylene cup (8.5 cm diameter, 10 cm deep), part filled with 70% propylene glycol as a preservative and killing agent. Traps were run continuously (emptied fortnightly) for 16 weeks in both 2010 and 2011 (3-7th May to 30th August) to provide as complete a sample of the communities as logistically possible. Adult beetle, spider and millipede specimens were identified to species (Blower, 1985; Luff, 2007; Roberts, 1987) and counted to provide activity density per species (juvenile spider counts were included in overall spider density estimate, but not species richness). Species identifications were confirmed against reference collections, doubtful specimens were corroborated by taxonomic experts as required (Oxford University Museum of Natural History, National Museum of Scotland) and voucher specimens are held at CEH. Activity density is proportional to the interaction between abundance and activity and is used as a proxy of true abundance (Thiele, 1977).

From the literature, invertebrate species were classified according to whether they were limited to terrestrial dispersal or also had the capacity for aerial dispersal, first pooling data from all taxa and then for the sole taxon (Carabidae) with sufficient numbers (for analysis) of species capable of either dispersal mode (Appendix S1, Table S3). For the Carabidae, there was much published information and potential aerial dispersal ability was scored according to the presence (macropterous or dimorphic) or absence (brachypterous) of wings (Barbaro & van Halder, 2009; Kotze & O'Hara, 2003; Lambeets *et al.*, 2008c; Luff, 2007; Ribera *et al.*, 1999; Woodcock *et al.*, 2010). For the Araneae, species were scored by their ability to disperse as adults or juveniles by ballooning on silk threads (Hayashi *et al.*, 2015; Lambeets *et al.*, 2008a; Lambeets *et al.*, 2008c; Roberts, 1987), where information on ballooning potential was lacking (17% of total) then species were conservatively classified as being only capable of terrestrial locomotion. Diplopoda are only capable of terrestrial locomotion (Blower, 1985; Dauber *et al.*, 2005). This meant the terrestrial dispersal group included: 100% of millipedes, 21% (18/84) of carabid species and 17% (10/57) of spider species, although the latter were of very low abundance (Appendix S1, Table S3).

Island vegetation structure

The community composition and structure of the herbaceous plant understory was surveyed in each island (July 2010 & 2011) in a series of quadrats ($1m^2$) assigned randomly to six of the sampling points. Within each quadrat, the identity and percentage cover of the vascular and non-vascular plant species was determined visually and the mean height (cm) understorey sward measured at four random points. Tree canopy density (% cover) over each quadrat was estimated using a concave spherical densitometer (Forestry suppliers Inc. USA). Values of vegetation parameters for each island are found in Table S1 (Appendix S1) and were fitted in subsequent models.

Flood peak and intensity

The disturbance to islands from river flow was characterised using the median annual maximum flood peak (QMED) and specific stream power (SSP) as a descriptor of the stream energy at a particular flow and given set of geographic co-ordinates.

Total stream power is defined as:

$\Omega = \gamma QS$

where Ω is total stream power per unit length of channel (Wm^{-1}), γ is the specific weight of water (9807 Nm^{-2}), Q is discharge ($m^3\ s^{-1}$) and S is the energy slope (Barker *et al.*, 2009; Knighton, 1999; Lawler *et al.*, 1999). As a surrogate for energy slope (S) we derived valley slope measured over 500m upstream to 500m downstream of each site. Again this derivation was automated using established methods (Dawson *et al.*, 2002) and applied to a digital terrain model derived from interpolation of Ordnance Survey of Great Britain contour data, with a resolution of 50m x 50m x 0.1m (Morris & Flavin, 1990). We screened the derived slopes for outliers, arising for example from artefacts in the digital terrain model and presence of dams within 500m upstream.

The total stream power was evaluated for discharge values *S* equal to the median annual maximum flood peak (QMED) to characterise the high flow for each river (Knighton, 1999). Estimates of QMED were obtained for each island site using a published equation (Environment Agency, 2008) that predicts QMED for ungauged sites using four different catchment descriptors (catchment area, annual average rainfall, degree of flow attenuation from upstream lakes and reservoirs, and baseflow characteristics as predicted from soils data). The initial estimates of QMED were subsequently refined by the degree to which the equation under- or over-estimates at similar, preferably local, gauged catchments (Kjeldsen & Jones, 2010).

As a measure of stream energy and hence flood intensity across river channels of different size, we calculated specific stream power (SSP) across the bankfull channel width at each island location:

$$\omega = \Omega/W$$

where ω is specific stream power (SSP = Wm^{-2}) and W is the bankfull width of the channel (m). Both QMED and SSP were fitted as predictor variables in subsequent LMMs (see below) and values for each island are found in Table S1 (Appendix S1).

Landscape structure

We quantified landscape structure from the UK Land Cover Map (LCM 2007). This map is derived from satellite-based multispectral scanners combined with ground-truthing of broad habitat classes and represents a comprehensive and high resolution land use map for the UK (Morton *et al.*, 2011). Using ArcGIS™ (version 9.3.1, ESRI®) we defined within a 1 km radius around each island: i) the percentage cover of forest (broadleaf and coniferous), ii) agricultural land (arable, horticulture, improved grassland), open semi-natural land (acid grassland, rough low productivity grassland, heather grassland, heather and dwarf shrub) and the habitat richness (total count of distinct habitats present). Many or all of these habitats are utilised by the studied invertebrate taxa, who are often quite generalised in their habitat associations, for feeding, breeding or overwintering (Blower, 1985; Thiele, 1977). Due to inter-correlation among landscape descriptors, we used a Principal Components Analysis (PCA) of these landscape metrics to derive orthogonal PC axes scores (PC1 & PC2) that describe landscape structure gradients and which were then fitted to subsequent LMMs. Values of landscape structure around each island are found in Table S2 (Appendix S1).

Statistical analysis

Invertebrate species richness and abundance was summed per island per year for each taxon (Diplopoda, Carabidae, Araneae), and pooling all taxa according to species dispersal mode (aerial vs terrestrial), and within the single taxon (Carabidae) with sufficient numbers of individuals (for analysis) capable of each mode of dispersal. Rarefaction (package ‘vegan’ R version 2.14.1) was used to assess sampling completeness (Appendix S3) and standardise invertebrate species richness (set to 200 individuals), thereby controlling for the varying number of individuals recorded (sampling effort) across different island sites (Gotelli & Colwell, 2001). Rarefaction eliminated sites with < 200 individuals, which meant there was sufficient data to analyze species richness of aerial and terrestrial dispersers pooling all taxa, but precluded analysis of the separate taxa and carabid beetle dispersal groups.

Species richness (rarefaction) and abundance data were dependent variables in linear mixed models (LMM, proc mixed, SAS v9.1) with a Gaussian error distribution, with island site fitted as a random effect and year × catchment as a repeated measure statement. Where required, data were log transformed and checked with proc univariate (SAS v9.1) to ensure that model assumptions of residual homogeneity of variance and normality were met.

We restricted the candidate list of potential explanatory variables in view of the limited sample size (56 observations: 28 islands observed in each of 2 years). We avoided fitting highly correlated predictors by inspecting Pearson correlation coefficients or in the case of the landscape structure fitting orthogonal PC axis scores. Consequently, the maximal model contained 11 fixed effects describing at each island location: flood peak (1. annual median flood peak – QMED); flood intensity (2. specific stream power - SSP); island size (3. area); island vegetation (4. total plant species richness *S*; 5. mean percent cover of herbaceous plants; 6. mean graminoid plant cover; 7. tree canopy density) and landscape structure (8. PC1 and 9. PC2). The final two categorical predictors were 'sampling year' (2010 or 2011) and 'river' (Tay, Tummel, Earn or Tweed), which were included to capture inter-annual and spatial structure in data according to the particular stretch of river.

To allow our analyses to account for spatial autocorrelation mediated by river network distances, we adjusted the island spatial coordinates so that pairwise Euclidean distances calculated from the adjusted coordinates preserved, as best as possible, the along-river distances within catchments and the geographic distances between catchments (see Appendix S2 for detail). The mixed models accounted for residual spatial autocorrelation by assuming that correlation decays exponentially in relation to the Euclidean distances between adjusted coordinates (see code in Appendix S2). In all models, spatial autocorrelation was always either zero or very close to zero (e.g. Tables 1-3), suggesting it was either not a significant influence or that the sample size was too small to meaningfully estimate the actual magnitude.

Model selection was by stepwise backward elimination of least significant term starting from a maximal model containing all eleven fixed effects. F-ratios and p–values reported are adjusted (SAS type III) for the other significant parameters retained in the final reduced model. In one case (Table 3-Araneae activity density) a marginally non-significant term improved overall model fit (AICc) and so was retained. Degrees of freedom were estimated using

Sattherthwaite's approximation. Partial residual plots derived from final GLMMs to show the effect of the significant explanatory variables conditional on other fixed and random effects in the final model for each analysis.

Results

Patterns in invertebrate assemblage composition

A total of 14,014 individuals from 84 carabid species, 11,374 spiders from 59 species, and 11,278 millipedes from 13 species were collected from the islands over the two years: see Appendix S1-Table S3 for a breakdown of species and abundance per river and Appendix S3 for rarefaction curves per island site for each taxon and dispersal mode. Of the 25 species that dominated the carabid assemblage in these islands (equivalent to 95% of the total carabid abundance), 48% are eurytopic species, often locally abundant, but associated with dry habitat conditions (e.g. *Pterostichus niger*, *P. oblongopunctatus*, *Bembidion tetracolum*). Another 20% are considered highly eurytopic (e.g. *P. strenuus*, *P. nigrita*, *Clivina fossor*) and 8% are known woodland (e.g. *Calathus spp.*, *Platynus assimilis, Cychrus caraboides*) species, sometimes associated with moist conditions (Luff, 2007; Thiele, 1977). In contrast, only 24% of these numerically dominant species are hygrophilic and frequently recorded in riparian habitats (e.g. *Agonum fuliginosum*, *A. micans*, *Patrobus atrorufus*) or habitat specialists associated with riparian shingle and gravel bar areas (i.e. *Bembidion atrocaeruleum, B. geniculatum, B. prasinum, B. punctulatum*) (Luff, 2007; Thiele, 1977).

In the case of the spiders, 54% of the species dominating these island assemblages (equivalent to 95% of the total spider abundance) are known to be capable of ballooning (i.e. *Pardosa amentata*, *Erigone atra/dentipalpis*, *Leptorhoptrum robustum*, *Pardosa agricola, Bathyphantes gracilis*, *Bathyphantes nigrinus* and *Oedothorax spp.*) and hence can rapidly recolonize flooded habitat (Lambeets *et al.*, 2008c). In contrast to the carabid assemblages where habitat generalists dominated, 47% of the spider species recorded are known to inhabit riparian habitat (e.g. *P. amentata, L. robustum* and *O. apicatus*), and the most abundant spider species in this study (*Halorates distinctus* - 22% of total spider abundance) is a riparian or wetland specialist (Lambeets *et al.*, 2008a; Lambeets *et al.*, 2008c). Millipedes were mainly concentrated in islands supporting forest or woody vegetation and 80% of the most abundant species (95% of the total) were forest or tree-climbing specialists (e.g. *Ommatoiulus sabulosus, Tachypodoiulus niger*) (Blower, 1985).

Impact of flood peak and intensity on island invertebrates

Flood peak (QMED) was related negatively to carabid beetle abundance (Table 1, Fig.2c), but did not influence the abundance of spiders ($F_{1, 20}$ =3.93, P =0.06) or millipedes ($F_{1, 17}$ =0.61, P =0.45). Flood intensity (SSP) had no impact on the abundance of millipedes ($F_{1, 16}$ =0.18, P =0.68), spiders ($F_{1, 19}$ =0.81, P =0.38) or carabid beetles ($F_{1, 20}$ = 1.34, P =0.26).

When invertebrate taxa data were pooled and analyzed by capacity for aerial dispersal, no effect of flood peak (QMED) or flood intensity (SSP) was detected on overall invertebrate abundance according to aerial (QMED $F_{1, 19}$= 0.16, P = 0.70; SSP $F_{1, 19}$= 0.20, P = 0.66) or terrestrial (QMED $F_{1, 18}$= 0.01, P = 0.94; SSP $F_{1, 22}$= 0.58, P =0.45) dispersal capacity. However, the negative relationship between beetle abundance and flood peak was greatest for flightless carabid species compared with winged species (Table 3, Fig.2c). Flood intensity (SSP) had no impact on abundance of carabid species with aerial ($F_{1, 21}$= 0.75, P = 0.40) or terrestrial ($F_{1, 17}$= 0.69, P = 0.42) dispersal capacity.

Flood peak (QMED) and flood intensity (SSP) had no detectable influence on the species richness of invertebrates capable of aerial (QMED $F_{1, 21}$ =1.90, P =0.18; SSP $F_{1, 16}$ =0.50, P = 0.49) or solely terrestrial (QMED $F_{1, 11}$ = 0.49, P = 0.50; SSP $F_{1, 3}$ <0.01, P >0.90) dispersal.

Relationships with island area

Island area related positively to spider (Araneae) and beetle (Carabidae) abundance (Table 1), and species capable of aerial dispersal across these taxa (Fig. 2a, Table 2) and within the Carabidae (Fig.2a, Table 3). There was no detectable effect of island area on the abundance of millipedes ($F_{1, 20}$ = 0.88, P = 0.36) or invertebrate ($F_{1, 20}$ = <0.01, P >0.90) and carabid ($F_{1, 19}$ = 1.03, P = 0.32) assemblages limited to terrestrial locomotion. Island area had no effect on the species richness of assemblages grouped by aerial ($F_{1, 18}$ = 0.65, P = 0.43) or terrestrial ($F_{1, 3}$ =0.02, P = 0.90) dispersal mode.

Effects of local vegetation structure on island invertebrates

The vegetation structure of the islands was an important predictor of both invertebrate abundance and species richness. The presence of a dense tree canopy was positively related to the abundance of millipedes (Diplopoda) and beetles (Carabidae) (Fig. 3b, Table 1); species capable of aerial dispersal, either across taxa (Araneae & Carabidae) (Fig. 3a, Table 2) or within the Carabidae (Fig. 3a, Table 3); and the species richness of terrestrial dispersers (Fig. 3c, Table 2). The diversity and cover of understorey vegetation on the islands also affected invertebrate abundance. Plant species richness related positively to spider abundance (Table 1), the abundance of both aerial and terrestrial dispersers (Table 2, Fig.2b) and richness of terrestrial dispersers (Table 2). The abundance of carabid beetle species that could disperse through flight related positively to the percentage cover of graminoid plants (grasses and sedges) (Table 3). The species richness of aerial dispersers across taxa (Araneae & Carabidae) related negatively to the cover of herbaceous vegetation (Table 2). This particular final model, however, had high levels of spatial autocorrelation and random and residual variance (Table 2). Terrestrial dispersers were unaffected by herbaceous cover ($F_{1, 8}$ = 0.64, P = 0.44). The species richness of aerial dispersers was not influenced by plant species richness ($F_{1, 8}$ = 0.29, P = 0.60) and graminoid cover had no influence over richness of aerial dispersers ($F_{1,17} = 0.19$, $P = 0.67$) or terrestrial dispersers ($F_{1,7} = 0.29$, $P = 0.60$).

Influence of landscape structure on island invertebrates

Overall the landscapes were dominated by agricultural lands (mean proportion of 1 km buffer = 0.51, SD = 0.21, range = 0.18-0.85) with forests (mean =0.28, SD = 0.17, range = 0.03-0.82) and open semi-natural habitats (mean =0.13, SD = 0.12, range =0.01-0.41) making up a lower proportion of landscape cover. Principal components analysis revealed that the first and second axes of landscape structure explained 84% of the variance (PC1 eigenvalue=2.33, proportion variance =0.58; PC2 eigenvalue=1.02, proportion variance =0.26). PC1 was related positively to the proportional cover of forest (eigenvector = 0.50), open semi-natural habitats (eigenvector = 0.32), and habitat richness (eigenvector = 0.50) in the landscape and negatively with agricultural land cover (eigenvector = -0.63). PC2 was positively related to the cover of open semi-natural habitats (eigenvector = 0.83) and negatively with forest cover (eigenvector = -0.55) and only weakly with agricultural land (eigenvector = 0.00) and habitat richness (eigenvector = 0.02). As predictors in the GLMMs, these gradients in landscape structure (PC1 or PC2) had no effect on the invertebrates grouped by dispersal mode either in terms of their abundance (aerial: PC1 $F_{1,19} = 0.12$, $P = 0.73$, PC2 $F_{1,19} = 0.38$, $P = 0.54$; terrestrial: PC1 $F_{1,22} = 2.44$, $P = 0.13$, PC2 $F_{1,21} = 0.56$, $P = 0.46$) or species richness (aerial: PC1 $F_{1,14} = 0.02$, $P = 0.89$, PC2 $F_{1,12} = 0.01$, $P = 0.93$; terrestrial: PC1 $F_{1,3} = 0.05$, $P = 0.83$, PC2 $F_{1,3} = 0.64$, $P = 0.48$). Nor was there any effect on abundance according to dispersal mode within a single taxon, the Carabidae (aerial: PC1 $F_{1,24} = 0.96$, $P = 0.34$, PC2 $F_{1,17} = 0.02$, $P = 0.88$; terrestrial: PC1 $F_{1,16} = 0.20$, $P = 0.66$, PC2 $F_{1,18} = 0.17$, $P = 0.69$).

The abundance of invertebrates capable of aerial dispersal, flightless carabids, millipedes and spiders were all significantly affected by the stretch of river in which the islands were situated (Table 1-3).

Discussion

In this study we sought to establish how terrestrial invertebrate taxa that occupy distinct ecological niches in riparian island ecosystems responded to disturbance from episodic floods, the size and vegetation structure of the island habitat, and the surrounding landscape structure. Species dispersal capacity shaped responses of community richness and abundance to sources of environmental variability operating at local scales, namely vegetation structure, island area and, for one taxon, flood disturbance. It is also notable that these island assemblages comprised a mix of habitat generalist and riparian specialist species. Altogether, this community composition and the role of species dispersal traits in governing responses to environmental gradients implies that the island assemblages are subsidized through spatio-temporal dispersal (e.g. mass effects) from the species pool in the surrounding landscape (Leibold *et al.*, 2004; Tews *et al.*, 2004). This would likely reduce the influence of island biogeographical processes and ameliorate the impact of disturbance from floods on these assemblages (Warren et al., 2015).

There was no evidence that flood peak (QMED) or intensity (SSP) affected invertebrate abundance or species richness differentially according to dispersal mode, when pooling all taxa (Diplopoda, Carabidae and Araneae). However, a flood-biodiversity relationship was revealed by analysis of the ground beetles (Carabidae), the only taxon with sufficient abundance data for a within taxon comparison of dispersal mode. Carabid beetle abundance related negatively to flood peak – a proxy for inundation of the riparian habitat – especially for carabid species limited to terrestrial locomotion for dispersal. Therefore, for this taxon only, there is evidence that a potential capability for aerial dispersal reduced the impact of flood disturbance on population sizes. The sensitivity of the abundance of the carabid assemblage might be explained by the overall dominance of these communities not by riparian specialists (e.g. many

Bembidion spp.), but instead by habitat generalists that are less adapted to riparian floods. This preponderance of habitat generalists implies that repeated immigrations, through flight or downstream transportation aboard plant debris, from mainland source habitats are important processes underpinning the assembly of this community in this dynamic ecosystem (Braccia & Batzer, 2001; Leibold *et al.*, 2004).

We found no evidence that flooding directly affected spider abundance or richness, which concurs with some earlier studies (Ballinger *et al.*, 2005; Bonn *et al.*, 2002) but contrasts with other studies that showed decreased spider abundance/diversity following riparian or floodplain inundation (Ellis *et al.*, 2001; Lambeets *et al.*, 2008c). A possible explanation for the lack of a direct impact of floods on spiders is that their adaptations may aid persistence in these highly dynamic habitats. Many spider species can tolerate submersion in water bodies (Hayashi *et al.*, 2015; Lambeets *et al.*, 2008b; Rothenbucher & Schaefer, 2006) and post-flood spider population sizes rapidly increase through re-colonization of the habitat by aerial ballooning on silk threads or rafting on flood debris (Ballinger *et al.*, 2005; Braccia & Batzer, 2001). Recent research has also shown that aeronaut spider species when alighting on water adopt elaborate sailing and anchoring behaviour to traverse this hazard and reach terrestrial habitat (Hayashi *et al.*, 2015). The domination of these riparian spider assemblages by such aeronaut species, is consistent with the hypotheses that spatial dynamics (e.g. mass effects, source-sink dynamics) continually subsidize these spider populations and, together with vegetation features (see below), aid species persistence in the local habitat.

Flooding did not affect millipede (Diplopoda) richness or abundance, nor that of the assemblages of species limited to terrestrial dispersal, mostly comprising millipedes (Appendix S1, Table S3). The intolerance of submersion, restricted mobility and limited range size of millipede species (Dauber *et al.*, 2005; Plum, 2005; Uetz *et al.*, 1979) meant they were unlikely to either persist in, or rapidly recolonize, frequently flooded habitat. Millipede occurrence was thus strictly limited to riparian habitat where vegetation features existed (tree cover - see below) that allowed species persistence.

Different elements of island vegetation structure were the most frequent and important predictor of invertebrate abundance across different taxa and species dispersal groupings. Tree cover related positively to the abundance of millipedes, ground beetles and species capable of aerial dispersal (certain Araneae & Carabidae) and the species richness of terrestrial dispersers. Plant species richness of the understorey vegetation related positively to the abundance of spiders and both aerial and terrestrial dispersers, whilst graminoid cover was related positively to the abundance of carabid species able to fly. Vegetation structure influences terrestrial invertebrate communities either directly by providing niches or plant foods or indirectly through prey abundance (Vanbergen *et al.*, 2010; Woodcock *et al.*, 2007). For instance, many seed feeding carabid species are from the flight capable carabid genera *Amara* and *Harpalus* (Thiele, 1977; Vanbergen *et al.*, 2010). The relationships between riparian vegetation and the abundance of terrestrial invertebrates imply that the concentration of food resources and/or niche space supported riparian specialists and habitat generalists alike (Leibold *et al.*, 2004; Root, 1973; Tews *et al.*, 2004). Trees are a keystone habitat feature known to maintain community structure (Tews *et al.*, 2004) and likely ameliorated the impact of floods through provision of physical refugia and perhaps aided colonization by intercepting aerial dispersers. The millipedes recorded were forest or tree-climbing specialists that were concentrated in the forested islands, which met their niche requirement for a dense litter layer (Blower, 1985; Uetz *et al.*, 1979). As millipedes are limited to terrestrial dispersal, the most likely mode of immigration to these wooded islands was through downstream transportation on rafts of woody debris (Braccia & Batzer, 2001; Mikuś *et al.*, 2013) observed to be deposited by flood water in these sites.

Island area was positively related to the abundance of species that could disperse by air (spider and carabid beetles), which concurs with earlier studies that have shown a variety of population density responses to island area (Connor *et al.*, 2000; Jonsson *et al.*, 2009). Larger islands may be more apparent to actively flying beetle species or simply represent a higher probability of landfall for them and passively ballooning spiders. Contrary to predictions of island biogeographical theory (Warren *et al.*, 2015), we found no effect of island area on species richness, but this is consistent with neutral or negative species-area effects seen in other island ecosystems (Jonsson *et al.*, 2009; Wardle *et al.*, 2003). One explanation is that these river islands are simply insufficiently isolated by the river channel (never > 80 m to nearest bankside) for species-area effects to prevail over multiple dispersal processes (flight, ballooning & sailing, rafting) operating in riparian systems (Braccia & Batzer, 2001; Hayashi *et al.*, 2015; Lambeets *et al.*, 2008c; Warren *et al.*, 2015). Another possibility is that some un-vegetated gravel bars that were among the larger islands often supported lower invertebrate species richness than equally large forested islands. This might have complicated detection of species-area effects, but also points to the role of vegetation structure (Tews *et al.*, 2004) in maintaining diversity in these riparian systems.

There was no direct evidence that the landscape structure surrounding these islands affected the abundance or richness of these invertebrate communities through immigration from nearby habitats (Leibold *et al.*, 2004). This was unexpected as proximity to source habitat influences re-colonization rates and community recovery following disturbance, especially for species with limited mobility such as millipedes and micro-arthropods (Gongalsky & Persson, 2013; Perdomo *et al.*, 2012; Redi *et al.*, 2005). Moreover, this departs from other studies that showed the sensitivity of beetle and spider communities to landscape-scale habitat structure (Billeter *et al.*, 2008; Vanbergen *et al.*, 2010).

Nonetheless, the highly significant and divergent effects of vegetation structure, flood peak (for beetles), and island area on assemblages defined by dispersal capacity suggest that spatial dynamics is an important mechanism underpinning invertebrate community structure in islands. Around the majority of island sites the landscapes tended to be dominated by an agriculture-forest mosaic, which may have meant the environmental gradient in the local landscape was insufficiently acute to elicit a shift in overall community structure in these sites. It remains possible that the abundance of particular species in one or many islands was influenced by the pool of source habitats in the local landscape, but if so then these were not strong enough responses to landscape structure to shape the overall size or diversity of the assemblage. Another possibility is that the invertebrates dispersing aerially may emanate from habitat at distances greater than 1km from the island, making the resolution of our landscape analysis a caveat to these results. While landscape structure as measured here did not predict the richness or abundance of these assemblages, the river in which the islands were situated often explained variation in invertebrate abundance. This may point to unidentified local geographic factors structuring the species pool and population sizes, and potentially the occurrence of regional patterns in community assembly (Leibold *et al.*, 2004).

Multiple ecological processes (e.g. spatial dynamics, niche structure, resource concentration) may be operating in the assembly of these riparian island communities as indicated by correlations with vegetation features, island area and in some cases episodic flood disturbance. Differences in dispersal capacity often influenced the observed patterns in abundance: island size and tree cover were direct predictors of the abundance of more mobile species. Lower dispersal capacity also exacerbated the negative impact of floods on the abundance of a single taxon (Carabidae). It is likely that these island communities are highly connected to other parts of the landscape through repeated immigrations, which reduces the influence of island biogeographical processes (area and isolation) and may subsidize these communities in the face of flood disturbance events (Warren *et al.*, 2015). The overall insensitivity of these riparian invertebrate assemblages to episodic disturbance from floodwater implies a degree of resilience imparted by spatial community dynamics and particular habitat features (e.g. trees).

Acknowledgements

Many thanks to the landowners who allowed us access to field sites. This paper was a co-funded output of CEH national capability projects (NEC04358, NEC04654) and the EU FP7 REFORM project (Restoring rivers for effective catchment management - ENV.2011.2.1.2-1 Grant Agreement 282656). Data are accessible from the NERC Environmental Information Data Centre.

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Figure 1. (A) Geographic distribution of 28 river islands situated within the Rivers Tay, Tummel, Earn and Tweed in Scotland. Panels B-D are digital elevation maps (SRTM 50x50m) of catchments showing the spatial distribution of islands within the rivers (B) Tay (n= 6 islands) & Tummel (5), (C) Tweed (11) and (D) Earn (6), increasing elevation (mean above sea level) is indicated by darker shading.

Figure 2. The effects on invertebrate abundance according to aerial or terrestrial dispersal mode of: (A) island area, (B) island plant species richness and (C) annual average flood peak (QMED). Plots are partial residuals on the linear predictor scale accounting for other predictors and random effects. Dashed fitted line = open symbols, solid line = closed symbols.

Figure 3. The effect of island tree canopy density (%) on (A) abundance of invertebrate taxa able to disperse aerially, (B) carabid beetle and diplopod abundance, (C) rarefied species richness of invertebrates limited to terrestrial locomotion. Plots are partial residuals on the linear predictor scale accounting for other predictors and random effects. Dashed fitted line = open symbols, solid line = closed symbols.

Table 1. Final linear mixed models of river island abundance of each taxon (Diplopoda, Carabidae, Araneae) in response to floods, island size and habitat structure and landscape structure. Twenty-eight islands were sampled over two years. Island site was fitted as a random effect and spatial autocorrelation modelled using an exponential function describing island position within a catchment: parameter estimates shown. MPE: indicates multiple parameter estimates for categorical variables.

Taxon/model	**Predictor**	**Slope**	**F**	**df**	**P**
Diplopoda					
Activity density (log)	River	MPE	3.12	3,23	<0.05
Random effect = 3.19	Tree canopy	0.0211	4.58	1,23	<0.05
Autocorrelation = 0.00					
Residual = 1.03					
Carabidae					
Activity density (log)	Year (2010 or 2011)	MPE	7.31	1,26	0.01
Random effect = 0.32	QMED	-0.0048	15.59	1,23	<0.001
Autocorrelation = 0.00	Island Area (log)	0.4747	14.84	1,23	<0.001
Residual =0.58	Tree canopy	0.0149	12.87	1,23	<0.001
	Graminoid plant	0.0302	7.32	1,41	<0.001
Araneae					
Activity density (log)	Year (2010 or 2011)	MPE	3.83	1,27	0.06
Random effect = 0.15	River	MPE	4.49	3,22	0.01
Autocorrelation = 0.00	Island Area (log)	0.3381	6.34	1,23	<0.05
Residual = 0.86	Plant *S*	0.0409	4.25	1,40	<0.05

Table 2. Final linear mixed models of abundance and species richness of river island invertebrates grouped according to mode of dispersal (pooling taxa) in response to floods, island size and habitat structure and landscape structure. Twenty-eight islands were sampled over two years. Island site was fitted as a random effect and spatial autocorrelation modelled using an exponential function describing island position within a catchment: parameter estimates shown. MPE: indicates multiple parameter estimates for categorical variables.

Dispersal mode (Taxa)	**Predictor**	**Slope**	**F**	**df**	**P**
Aerial dispersers (Carabidae, Araneae)					
Activity density (log)	Year (2010 or 2011)	MPE	10.40	1,27	<0.01
Random effect = 0.048	River	MPE	6.05	3,21	<0.01
Autocorrelation = 0.00	Island Area (log)	0.4471	21.68	1,21	<0.001
Residual = 0.57	Plant *S*	0.0394	7.14	1,35	0.01
	Tree canopy	0.0068	5.27	1,20	<0.05
Species richness	Herb	-0.3113	12.87	1,7	<0.01
Random effect = 27.26					
Autocorrelation = 8.06					
Residual = 11.31					
Terrestrial dispersers (Diplopoda, Carabidae, Araneae)					
Activity density (log)	Plant *S*	0.0403	5.78	1,35	<0.05
Random effect = 2.63					
Autocorrelation = 0.00					
Residual = 0.34					
Species richness					
Random effect = 0.00	Tree canopy	0.0366	9.98	1,12	<0.01
Autocorrelation = 0.00	Plant *S*	-0.1989	4.76	1,12	0.05
Residual = 3.64					

Table 3 Final linear mixed models of river island carabid beetle abundance according to mode of dispersal in response to floods, island size and habitat structure and landscape structure. Twenty-eight islands were sampled over two years. Island site was fitted as a random effect and spatial autocorrelation modelled using an exponential function describing island position within a catchment: parameter estimates shown. MPE: indicates multiple parameter estimates for categorical variables.

Dispersal mode (Taxon)	**Predictor**	**Slope**	**F**	**df**	**P**
Aerial dispersers (Carabidae)					
Activity density (log)	Year (2010 or 2011)	MPE	9.87	1,26	<0.01
Random effect = 0.41	QMED	-0.0047	13.60	1,23	0.001
Autocorrelation =0.00	Island Area (log)	0.5068	14.91	1,23	<0.001
Residual = 0.57	Graminoid plant	0.0271	5.48	1,43	<0.05
	Tree canopy	0.0165	14.09	1,23	0.001
Terrestrial dispersers (Carabidae)					
Activity density (log)	River	MPE	8.85	3,23	<0.001
Random effect =0.80	QMED	-0.00948	11.59	1,23	<0.01
Autocorrelation =0.00					
Residual = 0.39					

Figure 1

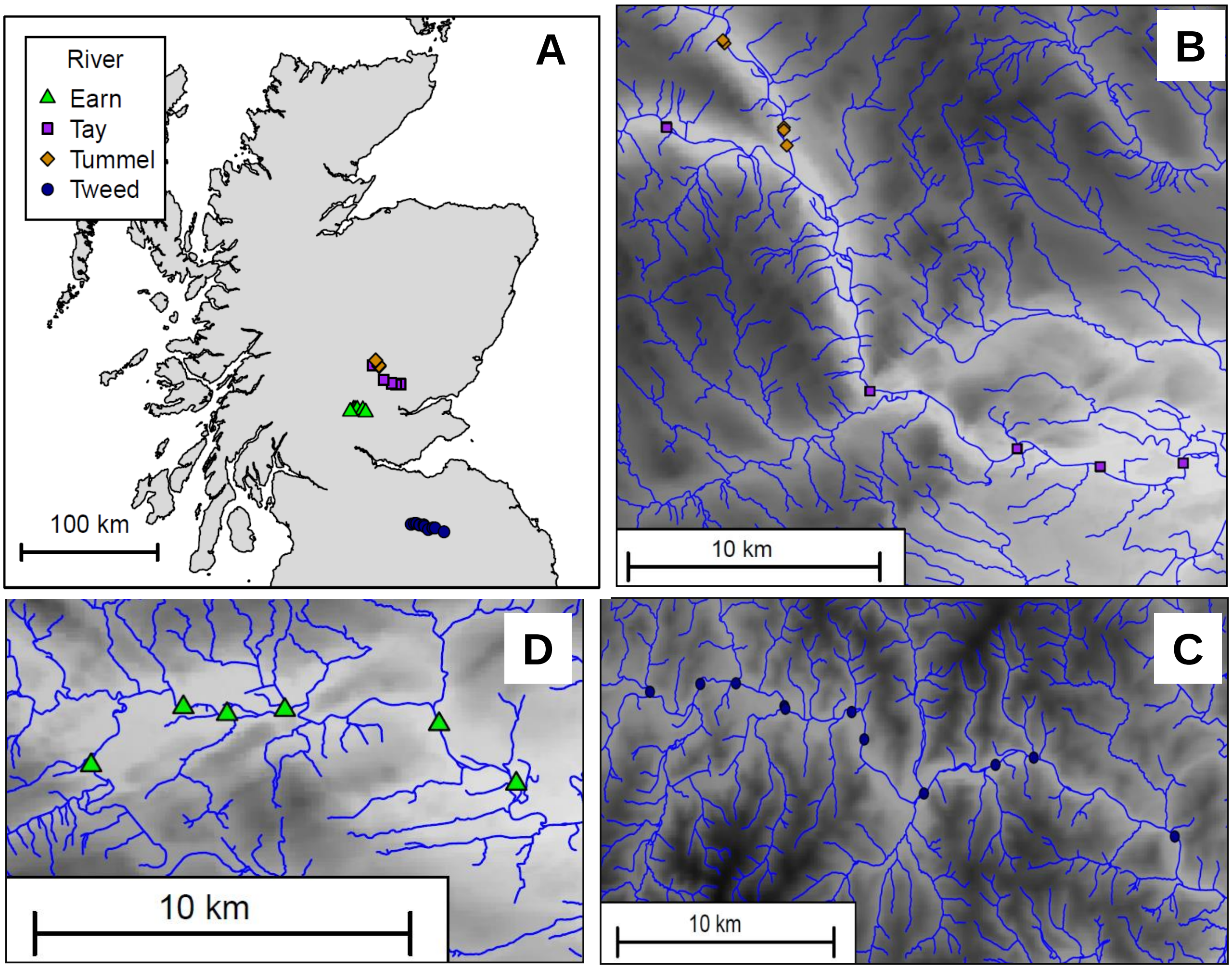


Figure 2

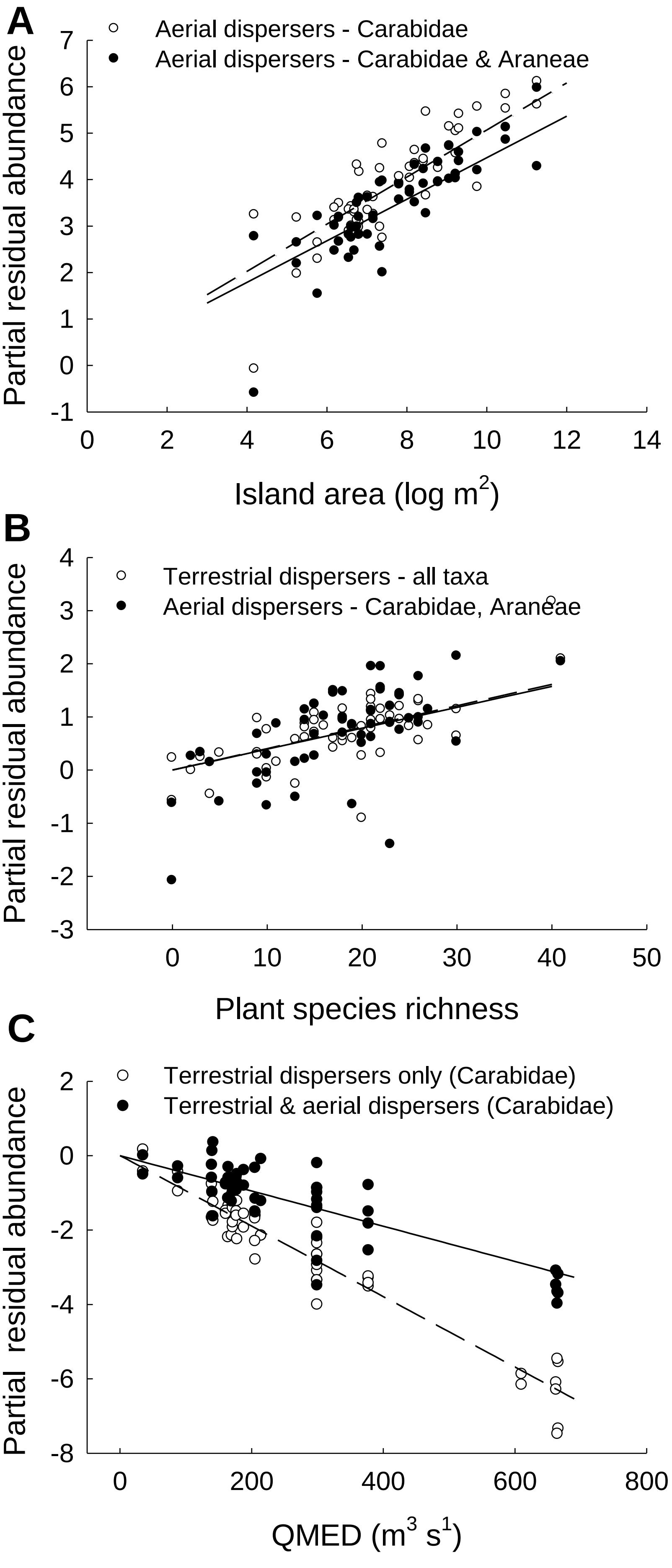
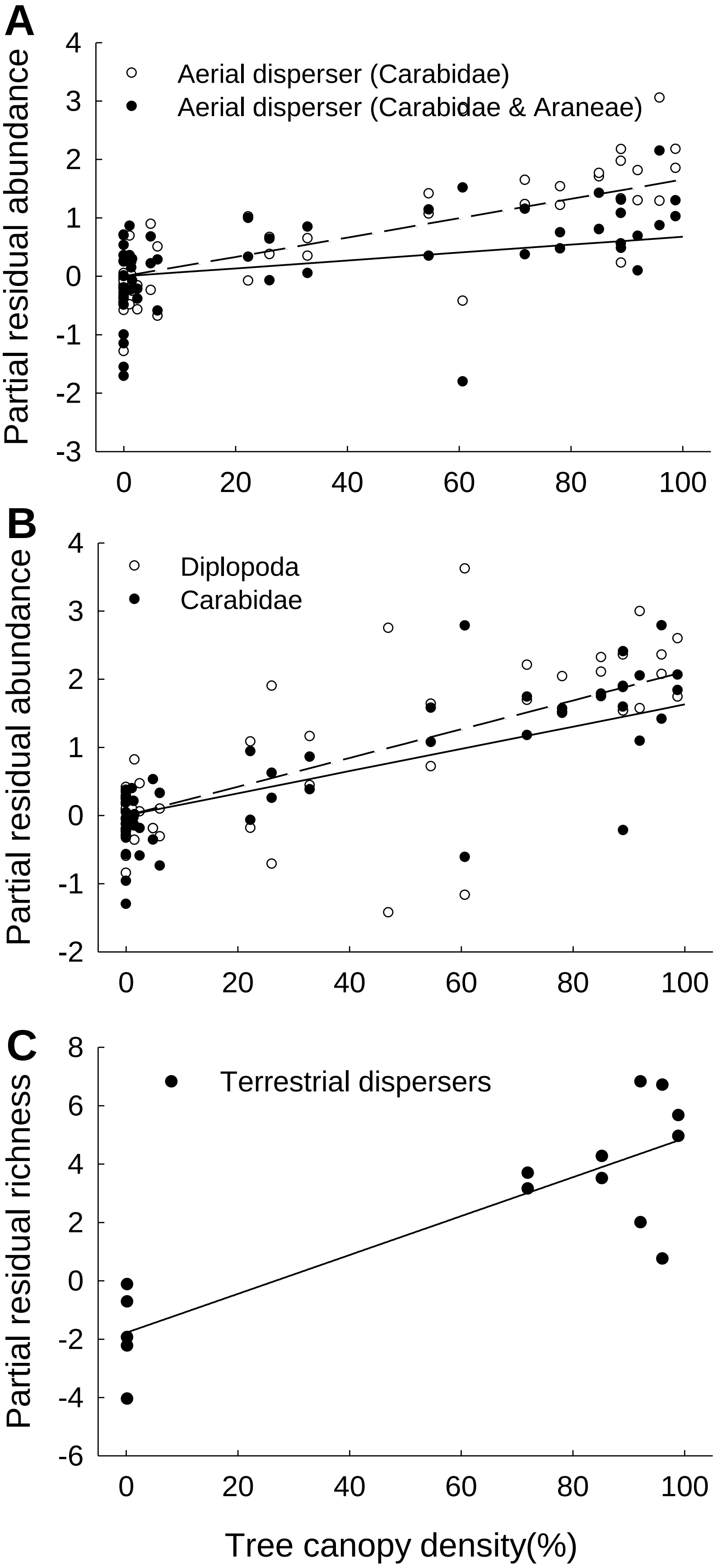

A
Aerial dispersers - Carabidae
Aerial dispersers - Carabidae & Araneae
Partial residual abundance
7
6
5
4
3
2
1
0
-1
0
2
4
6
8
10
12
14
Island area (log m^2)
B
Terrestrial dispersers - all taxa
Aerial dispersers - Carabidae, Araneae
Partial residual abundance
4
3
2
1
0
-1
-2
-3
0
10
20
30
40
50
Plant species richness
C
Terrestrial dispersers only (Carabidae)
Terrestrial & aerial dispersers (Carabidae)
Partial residual abundance
2
0
-2
-4
-6
-8
0
200
400
600
800
QMED (m^3 s^1)

Figure 3


A
Partial residual abundance
Aerial disperser (Carabidae)
Aerial disperser (Carabidae & Araneae)
4
3
2
1
0
-1
-2
-3
0
20
40
60
80
100
B
Partial residual abundance
Diplopoda
Carabidae
4
3
2
1
0
-1
-2
0
20
40
60
80
100
C
Partial residual richness
Terrestrial dispersers
8
6
4
2
0
-2
-4
-6
0
20
40
60
80
100
Tree canopy density(%)