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

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20

21 **Abstract**

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

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

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

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

46 **Introduction**

47 Episodic disturbance of a habitat patch can re-organise and structure plant-insect communities
48 (Gerisch *et al.*, 2012; Jonsson *et al.*, 2009; Lambeets *et al.*, 2008c). Disturbance effects on
49 insect communities are often mediated by directly eliminating organisms and by modifying
50 local vegetation and the food and breeding resources therein (Brose, 2003a; Tews *et al.*, 2004;
51 Vanbergen *et al.*, 2014). Riparian habitats are highly dynamic environments due to
52 hydrogeomorphological processes and episodic disturbance by flood waters, either driven by
53 the management of discharge or as predicted to increase under global climate change (Gurnell
54 *et al.*, 2012; IPCC, 2013). Flooding of terrestrial environments are known to affect invertebrate
55 diversity and abundance (Brose, 2003b; Ellis *et al.*, 2001; Gerisch *et al.*, 2012; Lambeets *et al.*,
56 2008c; Rothenbacher & Schaefer, 2006). For example, in a lowland riparian bankside
57 assemblage, spider species richness reduced with increased flood intensity, whereas carabid
58 beetle species richness peaked at intermediate levels of flooding (Lambeets *et al.*, 2008c).
59 Disturbance from floods is thus likely to be important driver of species presence and
60 community structure in riparian habitats.

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

71 community-scale patterns in diversity and abundance (Fournier *et al.*, 2015; Leibold *et al.*,
72 2004; Sydenham *et al.*, 2014; Tews *et al.*, 2004).

73 Invertebrate community assembly in spatially heterogeneous and highly disturbed
74 environments is likely to be maintained through dynamic species extinction or colonisation of
75 habitat patches, as predicted by island biogeographical, metapopulation or metacommunity
76 processes (Leibold *et al.*, 2004; Vandermeer & Carvajal, 2001; Warren *et al.*, 2015). Species
77 either persist, perish or migrate when the environment is flooded, whilst populations can re-
78 establish through immigration as flood waters recede (Brose, 2003b; Rothenbucher & Schaefer,
79 2006). This can influence the species composition or diversity of flooded habitat, although
80 effects vary with taxonomic identity. This is because species extinctions or other biodiversity
81 changes tend to be non-random with species possessing certain traits (e.g. higher trophic level,
82 low intrinsic abundance, low dispersal ability) prone to be vulnerable to particular
83 environmental stressors (Raffaelli, 2004). A variety of metacommunity processes may
84 influence species demography and interactions, and hence community diversity (Leibold *et al.*,
85 2004). For instance, where habitat patches are in a different state over time and are adequately
86 connected, species dispersal can result in source-sink dynamics or mass effects, whereby
87 species are rescued from competitive exclusion in a patch by repeated immigration (Leibold *et*
88 *al.*, 2004). Whether such spatial dynamics pre-dominate will vary with the extent that species
89 in the assemblage are habitat specialists or generalists, as this will affect the organism's
90 perception of the size and isolation of the habitat patch (Leibold *et al.*, 2004; Tews *et al.*, 2004).

91 The landscape context of a given habitat patch is also likely to influence diversity and
92 abundance within it because the composition of the landscape matrix within dispersal range is
93 likely to dictate the pool of available colonists. Indeed landscape structure is known to
94 influence the species richness and abundance of many invertebrate taxa, including soil

95 invertebrates (Eggleton *et al.*, 2005; Sousa *et al.*, 2006), beetles and spiders (Billeter *et al.*,
96 2008; Driscoll & Weir, 2005; Vanbergen *et al.*, 2010), pollinators (Kennedy *et al.*, 2013) and
97 their interspecific interactions (Thies *et al.*, 2003; Vanbergen *et al.*, 2014).

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

102 Insular or island habitats are a microcosm of organisms and processes that due to their relative
103 size and isolation represent distinct ecosystem replicates embedded in a wider landscape
104 matrix. Hence they are a useful platform to understand the factors governing spatial patterns in
105 diversity (Gonzalez *et al.*, 1998; Jonsson *et al.*, 2009; Warren *et al.*, 2015). River islands are
106 highly dynamic ecosystems, ranging from mid-channel bars to vegetated islands, affected by
107 episodic disturbance from river flows (Gurnell *et al.*, 2012; Gurnell *et al.*, 2001; Mikuś *et al.*,
108 2013). Consequently, they offer an opportunity to understand the interplay between episodic
109 disturbance, habitat area, vegetation structure, and landscape context of islands in shaping
110 invertebrate communities.

111 Here, we tested how terrestrial invertebrate communities (millipedes–Diplopoda; ground
112 beetles–Carabidae; spiders–Araneae) occupying distinct ecological niches in riparian island
113 ecosystems responded to *i*) disturbance from episodic floods, *ii*) island area, *iii*) island
114 vegetation structure, and *iv*) surrounding landscape structure. Profound ecological differences
115 exist amongst these taxa. For instance, spiders are obligate predators and highly dispersive,
116 either overland through terrestrial locomotion or by aerial ballooning on silk threads (Hayashi
117 *et al.*, 2015; Lambeets *et al.*, 2008c; Pedley & Dolman, 2014). Ground beetle assemblages
118 often comprise species from all trophic levels, include habitat specialists and generalists, and

119 vary greatly in body size and flight ability (Kotze & O'Hara, 2003; Pedley & Dolman, 2014;
120 Vanbergen *et al.*, 2010). Millipedes are obligate detritivores, have limited mobility and are very
121 sensitive to disturbance and microclimate (Blower, 1985; Dauber *et al.*, 2005; Eggleton *et al.*,
122 2005). Accordingly, we predicted taxon-specific responses in abundance and species richness
123 to these different sources of environmental heterogeneity (*i-iv*). We also predicted abundance
124 and species richness in this dynamic riparian ecosystem would be governed by species'
125 dispersal ability (aerial & terrestrial vs terrestrial locomotion only), which shapes the capacity
126 for migration to sustain community structure.

127 **Methods**

128 *Island sites*

129 Twenty-eight islands were surveyed in 2010 and 2011 across four rivers (Earn = 6 islands, Tay
130 = 6, Tummel = 5 and Tweed = 11) within three catchments in central and southern Scotland
131 (Figure 1). Islands were mid channel bars formed by hydrological deposition of sediments and
132 subsequent stabilisation by vegetation (Gurnell *et al.*, 2012; Mikuš *et al.*, 2013). The perimeter
133 coordinates of each island were mapped with a GPS (Garmin 12) and subsequently the area
134 (m²) of each island determined using ArcGIS™ (version 9.3.1, ESRI®). The geographical co-
135 ordinates and area of each island are found in Table S1 (Appendix S1). A standardised transect
136 (20m long) was haphazardly situated in the centre of each island orientated along the up-down
137 stream axis of the island. Along the transect, 10 sampling points were located at 2m intervals
138 along which invertebrate communities and vegetation structure were quantified (see below).

139 *Invertebrate communities*

140 Island invertebrate assemblages were sampled with 10 pitfall traps distributed among the
141 sampling points on each transect. Each trap comprised a polypropylene cup (8.5 cm diameter,
142 10 cm deep), part filled with 70% propylene glycol as a preservative and killing agent. Traps

143 were run continuously (emptied fortnightly) for 16 weeks in both 2010 and 2011 (3-7th May to
144 30th August) to provide as complete a sample of the communities as logistically possible. Adult
145 beetle, spider and millipede specimens were identified to species (Blower, 1985; Luff, 2007;
146 Roberts, 1987) and counted to provide activity density per species (juvenile spider counts were
147 included in overall spider density estimate, but not species richness). Species identifications
148 were confirmed against reference collections, doubtful specimens were corroborated by
149 taxonomic experts as required (Oxford University Museum of Natural History, National
150 Museum of Scotland) and voucher specimens are held at CEH. Activity density is proportional
151 to the interaction between abundance and activity and is used as a proxy of true abundance
152 (Thiele, 1977).

153 From the literature, invertebrate species were classified according to whether they were limited
154 to terrestrial dispersal or also had the capacity for aerial dispersal, first pooling data from all
155 taxa and then for the sole taxon (Carabidae) with sufficient numbers (for analysis) of species
156 capable of either dispersal mode (Appendix S1, Table S3). For the Carabidae, there was much
157 published information and potential aerial dispersal ability was scored according to the
158 presence (macropterous or dimorphic) or absence (brachypterous) of wings (Barbaro & van
159 Halder, 2009; Kotze & O'Hara, 2003; Lambeets *et al.*, 2008c; Luff, 2007; Ribera *et al.*, 1999;
160 Woodcock *et al.*, 2010). For the Araneae, species were scored by their ability to disperse as
161 adults or juveniles by ballooning on silk threads (Hayashi *et al.*, 2015; Lambeets *et al.*, 2008a;
162 Lambeets *et al.*, 2008c; Roberts, 1987), where information on ballooning potential was lacking
163 (17% of total) then species were conservatively classified as being only capable of terrestrial
164 locomotion. Diplopoda are only capable of terrestrial locomotion (Blower, 1985; Dauber *et al.*,
165 2005). This meant the terrestrial dispersal group included: 100% of millipedes, 21% (18/84) of
166 carabid species and 17% (10/57) of spider species, although the latter were of very low
167 abundance (Appendix S1, Table S3).

168 *Island vegetation structure*

169 The community composition and structure of the herbaceous plant understory was surveyed in
170 each island (July 2010 & 2011) in a series of quadrats (1m²) assigned randomly to six of the
171 sampling points. Within each quadrat, the identity and percentage cover of the vascular and
172 non-vascular plant species was determined visually and the mean height (cm) understorey
173 sward measured at four random points. Tree canopy density (% cover) over each quadrat was
174 estimated using a concave spherical densitometer (Forestry suppliers Inc. USA). Values of
175 vegetation parameters for each island are found in Table S1 (Appendix S1) and were fitted in
176 subsequent models.

177 *Flood peak and intensity*

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

181 Total stream power is defined as:

182 $\Omega = \gamma QS$

183 where Ω is total stream power per unit length of channel (Wm⁻¹), γ is the specific weight of
184 water (9807 Nm⁻²), Q is discharge (m³ s⁻¹) and S is the energy slope (Barker *et al.*, 2009;
185 Knighton, 1999; Lawler *et al.*, 1999). As a surrogate for energy slope (S) we derived valley
186 slope measured over 500m upstream to 500m downstream of each site. Again this derivation
187 was automated using established methods (Dawson *et al.*, 2002) and applied to a digital terrain
188 model derived from interpolation of Ordnance Survey of Great Britain contour data, with a
189 resolution of 50m x 50m x 0.1m (Morris & Flavin, 1990). We screened the derived slopes for
190 outliers, arising for example from artefacts in the digital terrain model and presence of dams
191 within 500m upstream.

192 The total stream power was evaluated for discharge values S equal to the median annual
193 maximum flood peak (QMED) to characterise the high flow for each river (Knighton, 1999).
194 Estimates of QMED were obtained for each island site using a published equation
195 (Environment Agency, 2008) that predicts QMED for ungauged sites using four different
196 catchment descriptors (catchment area, annual average rainfall, degree of flow attenuation from
197 upstream lakes and reservoirs, and baseflow characteristics as predicted from soils data). The
198 initial estimates of QMED were subsequently refined by the degree to which the equation
199 under- or over-estimates at similar, preferably local, gauged catchments (Kjeldsen & Jones,
200 2010).

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

$$204 \omega = \Omega/W$$

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

208 *Landscape structure*

209 We quantified landscape structure from the UK Land Cover Map (LCM 2007). This map is
210 derived from satellite-based multispectral scanners combined with ground-truthing of broad
211 habitat classes and represents a comprehensive and high resolution land use map for the UK
212 (Morton *et al.*, 2011). Using ArcGIS™ (version 9.3.1, ESRI®) we defined within a 1 km radius
213 around each island: i) the percentage cover of forest (broadleaf and coniferous), ii) agricultural
214 land (arable, horticulture, improved grassland), open semi-natural land (acid grassland, rough
215 low productivity grassland, heather grassland, heather and dwarf shrub) and the habitat richness

216 (total count of distinct habitats present). Many or all of these habitats are utilised by the studied
217 invertebrate taxa, who are often quite generalised in their habitat associations, for feeding,
218 breeding or overwintering (Blower, 1985; Thiele, 1977). Due to inter-correlation among
219 landscape descriptors, we used a Principal Components Analysis (PCA) of these landscape
220 metrics to derive orthogonal PC axes scores (PC1 & PC2) that describe landscape structure
221 gradients and which were then fitted to subsequent LMMs. Values of landscape structure
222 around each island are found in Table S2 (Appendix S1).

223 *Statistical analysis*

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

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

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

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

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

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

267

268 **Results**

269 *Patterns in invertebrate assemblage composition*

270 A total of 14,014 individuals from 84 carabid species, 11,374 spiders from 59 species, and
271 11,278 millipedes from 13 species were collected from the islands over the two years: see
272 Appendix S1-Table S3 for a breakdown of species and abundance per river and Appendix S3
273 for rarefaction curves per island site for each taxon and dispersal mode. Of the 25 species that
274 dominated the carabid assemblage in these islands (equivalent to 95% of the total carabid
275 abundance), 48% are eurytopic species, often locally abundant, but associated with dry habitat
276 conditions (e.g. *Pterostichus niger*, *P. oblongopunctatus*, *Bembidion tetracolum*). Another
277 20% are considered highly eurytopic (e.g. *P. strenuus*, *P. nigrita*, *Clivina fossor*) and 8% are
278 known woodland (e.g. *Calathus spp.*, *Platynus assimilis*, *Cychrus caraboides*) species,
279 sometimes associated with moist conditions (Luff, 2007; Thiele, 1977). In contrast, only 24%
280 of these numerically dominant species are hygrophilic and frequently recorded in riparian
281 habitats (e.g. *Agonum fuliginosum*, *A. micans*, *Patrobus atrorufus*) or habitat specialists
282 associated with riparian shingle and gravel bar areas (i.e. *Bembidion atrocaeruleum*, *B.*
283 *geniculatum*, *B. prasinum*, *B. punctulatum*) (Luff, 2007; Thiele, 1977).

284 In the case of the spiders, 54% of the species dominating these island assemblages (equivalent
285 to 95% of the total spider abundance) are known to be capable of ballooning (i.e. *Pardosa*
286 *amentata*, *Erigone atra/dentipalpis*, *Leptorhoptrum robustum*, *Pardosa agricola*,
287 *Bathyphantes gracilis*, *Bathyphantes nigrinus* and *Oedothorax spp.*) and hence can rapidly

288 recolonize flooded habitat (Lambeets *et al.*, 2008c). In contrast to the carabid assemblages
289 where habitat generalists dominated, 47% of the spider species recorded are known to inhabit
290 riparian habitat (e.g. *P. amentata*, *L. robustum* and *O. apicatus*), and the most abundant spider
291 species in this study (*Halorates distinctus* - 22% of total spider abundance) is a riparian or
292 wetland specialist (Lambeets *et al.*, 2008a; Lambeets *et al.*, 2008c). Millipedes were mainly
293 concentrated in islands supporting forest or woody vegetation and 80% of the most abundant
294 species (95% of the total) were forest or tree-climbing specialists (e.g. *Ommatoiulus sabulosus*,
295 *Tachypodoiulus niger*) (Blower, 1985).

296 *Impact of flood peak and intensity on island invertebrates*

297 Flood peak (QMED) was related negatively to carabid beetle abundance (Table 1, Fig.2c), but
298 did not influence the abundance of spiders ($F_{1,20}=3.93$, $P=0.06$) or millipedes ($F_{1,17}=0.61$, P
299 $=0.45$). Flood intensity (SSP) had no impact on the abundance of millipedes ($F_{1,16}=0.18$, P
300 $=0.68$), spiders ($F_{1,19}=0.81$, $P=0.38$) or carabid beetles ($F_{1,20}=1.34$, $P=0.26$).

301 When invertebrate taxa data were pooled and analyzed by capacity for aerial dispersal, no effect
302 of flood peak (QMED) or flood intensity (SSP) was detected on overall invertebrate abundance
303 according to aerial (QMED $F_{1,19}=0.16$, $P=0.70$; SSP $F_{1,19}=0.20$, $P=0.66$) or terrestrial
304 (QMED $F_{1,18}=0.01$, $P=0.94$; SSP $F_{1,22}=0.58$, $P=0.45$) dispersal capacity. However, the
305 negative relationship between beetle abundance and flood peak was greatest for flightless
306 carabid species compared with winged species (Table 3, Fig.2c). Flood intensity (SSP) had no
307 impact on abundance of carabid species with aerial ($F_{1,21}=0.75$, $P=0.40$) or terrestrial ($F_{1,17}=$
308 0.69 , $P=0.42$) dispersal capacity.

309 Flood peak (QMED) and flood intensity (SSP) had no detectable influence on the species
310 richness of invertebrates capable of aerial (QMED $F_{1,21}=1.90$, $P=0.18$; SSP $F_{1,16}=0.50$, $P=$
311 0.49) or solely terrestrial (QMED $F_{1,11}=0.49$, $P=0.50$; SSP $F_{1,3}<0.01$, $P>0.90$) dispersal.

312 *Relationships with island area*

313 Island area related positively to spider (Araneae) and beetle (Carabidae) abundance (Table 1),
314 and species capable of aerial dispersal across these taxa (Fig. 2a, Table 2) and within the
315 Carabidae (Fig.2a, Table 3). There was no detectable effect of island area on the abundance of
316 millipedes ($F_{1,20} = 0.88, P = 0.36$) or invertebrate ($F_{1,20} = <0.01, P >0.90$) and carabid ($F_{1,19} =$
317 $1.03, P = 0.32$) assemblages limited to terrestrial locomotion. Island area had no effect on the
318 species richness of assemblages grouped by aerial ($F_{1,18} = 0.65, P = 0.43$) or terrestrial ($F_{1,3}$
319 $=0.02, P = 0.90$) dispersal mode.

320 *Effects of local vegetation structure on island invertebrates*

321 The vegetation structure of the islands was an important predictor of both invertebrate
322 abundance and species richness. The presence of a dense tree canopy was positively related to
323 the abundance of millipedes (Diplopoda) and beetles (Carabidae) (Fig. 3b, Table 1); species
324 capable of aerial dispersal, either across taxa (Araneae & Carabidae) (Fig. 3a, Table 2) or within
325 the Carabidae (Fig. 3a, Table 3); and the species richness of terrestrial dispersers (Fig. 3c, Table
326 2). The diversity and cover of understorey vegetation on the islands also affected invertebrate
327 abundance. Plant species richness related positively to spider abundance (Table 1), the
328 abundance of both aerial and terrestrial dispersers (Table 2, Fig.2b) and richness of terrestrial
329 dispersers (Table 2). The abundance of carabid beetle species that could disperse through flight
330 related positively to the percentage cover of graminoid plants (grasses and sedges) (Table 3).
331 The species richness of aerial dispersers across taxa (Araneae & Carabidae) related negatively
332 to the cover of herbaceous vegetation (Table 2). This particular final model, however, had high
333 levels of spatial autocorrelation and random and residual variance (Table 2). Terrestrial
334 dispersers were unaffected by herbaceous cover ($F_{1,8} = 0.64, P = 0.44$). The species richness of
335 aerial dispersers was not influenced by plant species richness ($F_{1,8} = 0.29, P = 0.60$) and

336 graminoid cover had no influence over richness of aerial dispersers ($F_{1,17} = 0.19$, $P = 0.67$) or
337 terrestrial dispersers ($F_{1,7} = 0.29$, $P = 0.60$).

338 *Influence of landscape structure on island invertebrates*

339 Overall the landscapes were dominated by agricultural lands (mean proportion of 1 km buffer
340 = 0.51, SD = 0.21, range = 0.18-0.85) with forests (mean = 0.28, SD = 0.17, range = 0.03-0.82)
341 and open semi-natural habitats (mean = 0.13, SD = 0.12, range = 0.01-0.41) making up a lower
342 proportion of landscape cover. Principal components analysis revealed that the first and second
343 axes of landscape structure explained 84% of the variance (PC1 eigenvalue=2.33, proportion
344 variance = 0.58; PC2 eigenvalue=1.02, proportion variance = 0.26). PC1 was related positively
345 to the proportional cover of forest (eigenvector = 0.50), open semi-natural habitats (eigenvector
346 = 0.32), and habitat richness (eigenvector = 0.50) in the landscape and negatively with
347 agricultural land cover (eigenvector = -0.63). PC2 was positively related to the cover of open
348 semi-natural habitats (eigenvector = 0.83) and negatively with forest cover (eigenvector = -
349 0.55) and only weakly with agricultural land (eigenvector = 0.00) and habitat richness
350 (eigenvector = 0.02). As predictors in the GLMMs, these gradients in landscape structure (PC1
351 or PC2) had no effect on the invertebrates grouped by dispersal mode either in terms of their
352 abundance (aerial: PC1 $F_{1,19} = 0.12$, $P = 0.73$, PC2 $F_{1,19} = 0.38$, $P = 0.54$; terrestrial: PC1 $F_{1,22} =$
353 2.44 , $P = 0.13$, PC2 $F_{1,21} = 0.56$, $P = 0.46$) or species richness (aerial: PC1 $F_{1,14} = 0.02$, $P = 0.89$,
354 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
355 was there any effect on abundance according to dispersal mode within a single taxon, the
356 Carabidae (aerial: PC1 $F_{1,24} = 0.96$, $P = 0.34$, PC2 $F_{1,17} = 0.02$, $P = 0.88$; terrestrial: PC1 $F_{1,16} =$
357 0.20 , $P = 0.66$, PC2 $F_{1,18} = 0.17$, $P = 0.69$).

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

361 **Discussion**

362 In this study we sought to establish how terrestrial invertebrate taxa that occupy distinct
363 ecological niches in riparian island ecosystems responded to disturbance from episodic floods,
364 the size and vegetation structure of the island habitat, and the surrounding landscape structure.
365 Species dispersal capacity shaped responses of community richness and abundance to sources
366 of environmental variability operating at local scales, namely vegetation structure, island area
367 and, for one taxon, flood disturbance. It is also notable that these island assemblages comprised
368 a mix of habitat generalist and riparian specialist species. Altogether, this community
369 composition and the role of species dispersal traits in governing responses to environmental
370 gradients implies that the island assemblages are subsidized through spatio-temporal dispersal
371 (e.g. mass effects) from the species pool in the surrounding landscape (Leibold *et al.*, 2004;
372 Tews *et al.*, 2004). This would likely reduce the influence of island biogeographical processes
373 and ameliorate the impact of disturbance from floods on these assemblages (Warren *et al.*,
374 2015).

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

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

390 We found no evidence that flooding directly affected spider abundance or richness, which
391 concurs with some earlier studies (Ballinger *et al.*, 2005; Bonn *et al.*, 2002) but contrasts with
392 other studies that showed decreased spider abundance/diversity following riparian or
393 floodplain inundation (Ellis *et al.*, 2001; Lambeets *et al.*, 2008c). A possible explanation for
394 the lack of a direct impact of floods on spiders is that their adaptations may aid persistence in
395 these highly dynamic habitats. Many spider species can tolerate submersion in water bodies
396 (Hayashi *et al.*, 2015; Lambeets *et al.*, 2008b; Rothenbacher & Schaefer, 2006) and post-flood
397 spider population sizes rapidly increase through re-colonization of the habitat by aerial
398 ballooning on silk threads or rafting on flood debris (Ballinger *et al.*, 2005; Braccia & Batzer,
399 2001). Recent research has also shown that aeronaut spider species when alighting on water
400 adopt elaborate sailing and anchoring behaviour to traverse this hazard and reach terrestrial
401 habitat (Hayashi *et al.*, 2015). The domination of these riparian spider assemblages by such
402 aeronaut species, is consistent with the hypotheses that spatial dynamics (e.g. mass effects,
403 source-sink dynamics) continually subsidize these spider populations and, together with
404 vegetation features (see below), aid species persistence in the local habitat.

405 Flooding did not affect millipede (Diplopoda) richness or abundance, nor that of the
406 assemblages of species limited to terrestrial dispersal, mostly comprising millipedes (Appendix
407 S1, Table S3). The intolerance of submersion, restricted mobility and limited range size of
408 millipede species (Dauber *et al.*, 2005; Plum, 2005; Uetz *et al.*, 1979) meant they were unlikely

409 to either persist in, or rapidly recolonize, frequently flooded habitat. Millipede occurrence was
410 thus strictly limited to riparian habitat where vegetation features existed (tree cover - see below)
411 that allowed species persistence.

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

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

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

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

474 Multiple ecological processes (e.g. spatial dynamics, niche structure, resource concentration)
475 may be operating in the assembly of these riparian island communities as indicated by
476 correlations with vegetation features, island area and in some cases episodic flood disturbance.
477 Differences in dispersal capacity often influenced the observed patterns in abundance: island
478 size and tree cover were direct predictors of the abundance of more mobile species. Lower
479 dispersal capacity also exacerbated the negative impact of floods on the abundance of a single
480 taxon (Carabidae). It is likely that these island communities are highly connected to other parts
481 of the landscape through repeated immigrations, which reduces the influence of island
482 biogeographical processes (area and isolation) and may subsidize these communities in the face

483 of flood disturbance events (Warren *et al.*, 2015). The overall insensitivity of these riparian
484 invertebrate assemblages to episodic disturbance from floodwater implies a degree of resilience
485 imparted by spatial community dynamics and particular habitat features (e.g. trees).

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

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

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

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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) <i>Random effect</i> = 3.19 <i>Autocorrelation</i> = 0.00 <i>Residual</i> = 1.03	River	MPE	3.12	3,23	<0.05
	Tree canopy	0.0211	4.58	1,23	<0.05
Carabidae					
Activity density (log) <i>Random effect</i> = 0.32 <i>Autocorrelation</i> = 0.00 <i>Residual</i> = 0.58	Year (2010 or 2011)	MPE	7.31	1,26	0.01
	QMED	-0.0048	15.59	1,23	<0.001
	Island Area (log)	0.4747	14.84	1,23	<0.001
	Tree canopy	0.0149	12.87	1,23	<0.001
	Graminoid plant	0.0302	7.32	1,41	<0.001
Araneae					
Activity density (log) <i>Random effect</i> = 0.15 <i>Autocorrelation</i> = 0.00 <i>Residual</i> = 0.86	Year (2010 or 2011)	MPE	3.83	1,27	0.06
	River	MPE	4.49	3,22	0.01
	Island Area (log)	0.3381	6.34	1,23	<0.05
	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) <i>Random effect</i> = 0.048 <i>Autocorrelation</i> = 0.00 <i>Residual</i> = 0.57	Year (2010 or 2011)	MPE	10.40	1,27	<0.01
	River	MPE	6.05	3,21	<0.01
	Island Area (log)	0.4471	21.68	1,21	<0.001
	Plant <i>S</i>	0.0394	7.14	1,35	0.01
	Tree canopy	0.0068	5.27	1,20	<0.05
Species richness <i>Random effect</i> = 27.26 <i>Autocorrelation</i> = 8.06 <i>Residual</i> = 11.31	Herb	-0.3113	12.87	1,7	<0.01
Terrestrial dispersers (Diplopoda, Carabidae, Araneae)					
Activity density (log) <i>Random effect</i> = 2.63 <i>Autocorrelation</i> = 0.00 <i>Residual</i> = 0.34	Plant <i>S</i>	0.0403	5.78	1,35	<0.05
	Tree canopy	0.0366	9.98	1,12	<0.01
	Plant <i>S</i>	-0.1989	4.76	1,12	0.05
Species richness <i>Random effect</i> = 0.00 <i>Autocorrelation</i> = 0.00 <i>Residual</i> = 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) <i>Random effect</i> = 0.41 <i>Autocorrelation</i> = 0.00 <i>Residual</i> = 0.57	Year (2010 or 2011)	MPE	9.87	1,26	<0.01
	QMED	-0.0047	13.60	1,23	0.001
	Island Area (log)	0.5068	14.91	1,23	<0.001
	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) <i>Random effect</i> = 0.80 <i>Autocorrelation</i> = 0.00 <i>Residual</i> = 0.39	River	MPE	8.85	3,23	<0.001
	QMED	-0.00948	11.59	1,23	<0.01

Figure 1

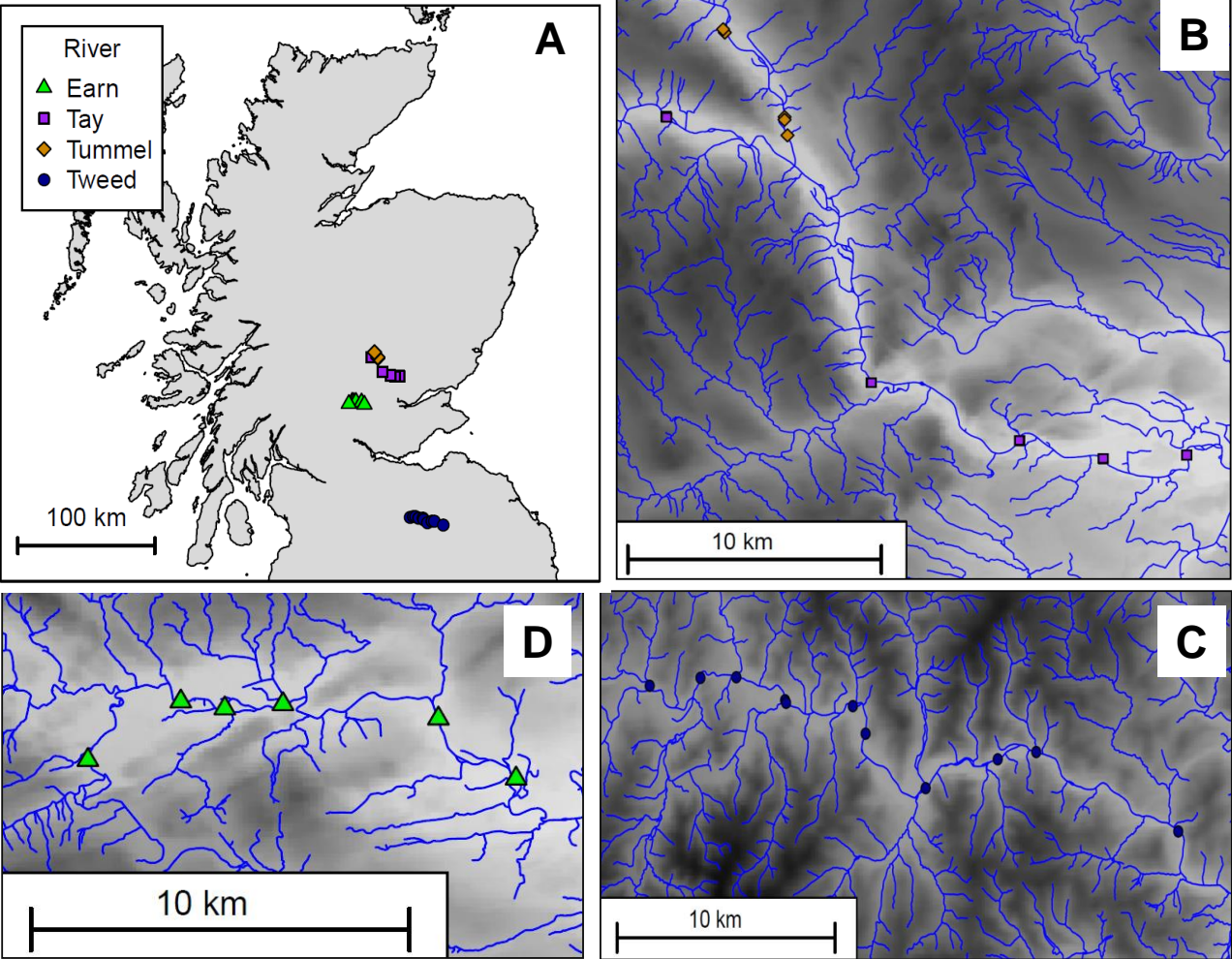


Figure 2

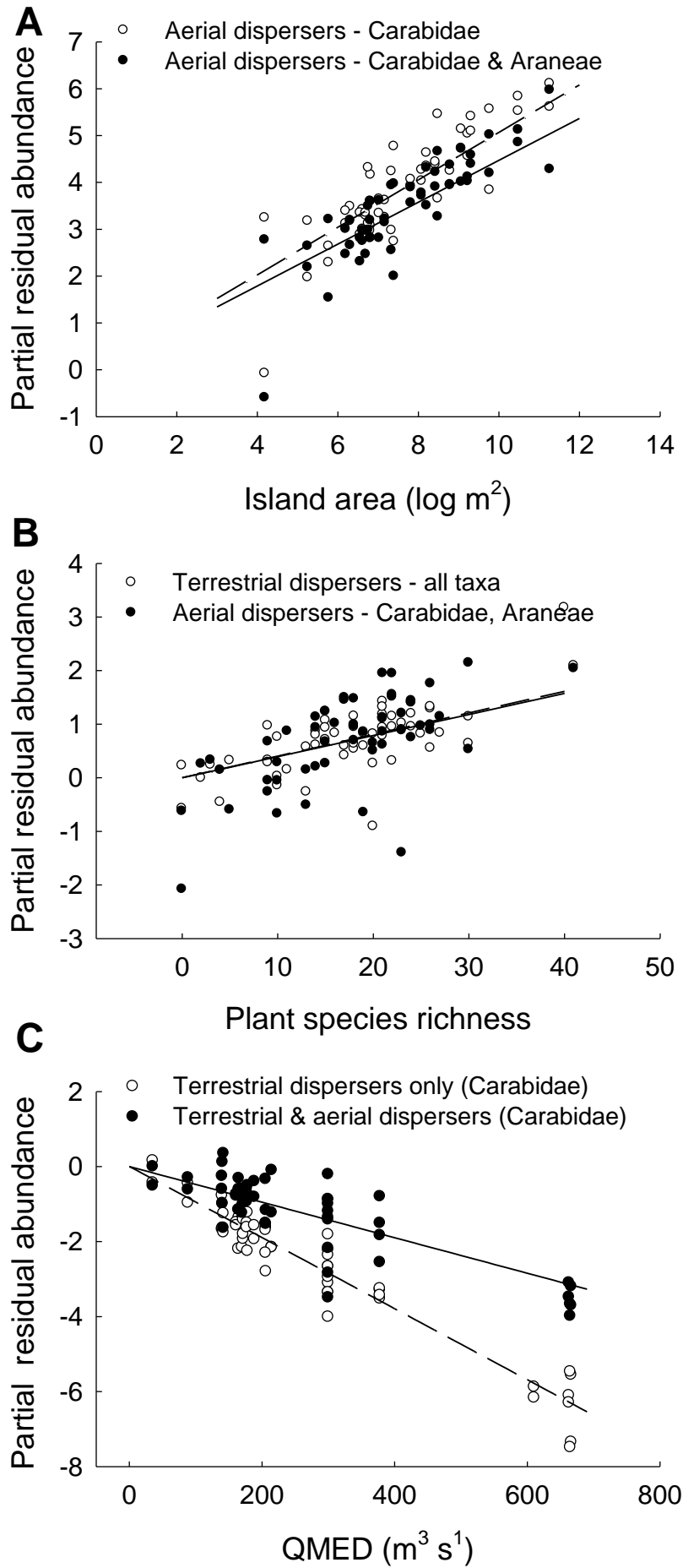


Figure 3

