

Local-scale attributes determine the suitability of woodland creation sites for Diptera

Journal:	<i>Journal of Applied Ecology</i>
Manuscript ID	JAPPL-2017-00502.R1
Manuscript Type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Fuller, Lauren; University of Stirling, Biological and Environmental Sciences Fuentes-Montemayor, Elisa; University of Stirling, Biological and Environmental Sciences Watts, Kevin; Forest Research, Macgregor, Nicholas; Natural England Bitenc, Katja; University of Stirling Park, Kirsty; University of Stirling,
Key-words:	Biodiversity, Ecological networks, Forest, Fragmentation, Habitat creation, Insect, Natural experiment, Local-scale, WrEN project, Landscape-scale conservation

1 Local-scale attributes determine the suitability of woodland creation sites for Diptera

2

3 Lauren Fuller^{*1}, Elisa Fuentes-Montemayor¹, Kevin Watts^{1,4}, Nicholas A. Macgregor^{2,3}, Katja

4 Bitenc¹, Kirsty J. Park¹

5

6 *Corresponding author: laurenvfuller@gmail.com

7 ¹Biological and Environmental Sciences, University of Stirling, FK9 4LA, UK

8 ²Natural England, Nobel House, 17 Smith Square, London, SW1P 3JR, UK

9 ³Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and
10 Conservation, University of Kent, Canterbury, Kent CT2 7NR, UK

11 ⁴Forest Research, Alice Holt Lodge, Farnham, GU10 4LH, UK

12

13 **Summary**

- 14 1. New native woodlands are typically created in a small and isolated configuration,
15 potentially reducing their value as a resource for biodiversity. The use of ecological
16 networks for habitat restoration and creation could be beneficial for woodland
17 biodiversity. This approach is conceptualised as local and landscape-scale
18 conservation actions to increase the area, quality, amount and connectivity of habitat
19 types. However, there is limited evidence about the value of secondary woodlands
20 and the relative or combined effects of network variables for woodland insects.
- 21 2. Seventy-eight woodland sites created in the last 160 years across England and
22 Scotland were sampled for hoverflies (Diptera: Syrphidae) and craneflies (Diptera:
23 Tipuloidea), using two Malaise net traps placed in the centre of each woodland. The
24 diversity of insects supported by created woodland patches was analysed using
25 measures of dissimilarity, and the relative direct and indirect effects of ecological
26 network variables on their abundance and species richness were assessed using
27 structural equation models.
- 28 3. We found 27% of British woodland hoverfly species and 43% of British woodland
29 cranefly species in the study sites, indicating that woodland insects are colonising
30 created native woodlands, despite their fragmented nature. However, these species
31 communities were highly variable across woodland patches.
- 32 4. Landscape-scale variables had no effect on woodland-associated hoverflies or
33 craneflies relative to local-scale variables. Local-scale variables relating to habitat
34 quality (i.e. structural heterogeneity of trees and understory cover) had the strongest
35 influence on abundance and species richness.
- 36 5. Synthesis and applications – To benefit woodland-associated Diptera, woodland
37 creation and restoration should maintain a focus on habitat quality. This should
38 include active management to facilitate a diverse tree and understorey vegetation

39 structure. Many woodlands in the UK are privately owned and landowners should be
40 encouraged to plant and actively manage their woodlands to increase structural
41 heterogeneity and resources for woodland insects.

42

43 Keywords: Biodiversity, ecological networks, forest, fragmentation, habitat creation, insect,
44 landscape-scale conservation, local-scale, natural experiment, WrEN project

45

46 **Introduction**

47 Habitat loss and fragmentation is a major contributor to the current biological diversity crisis
48 and, in particular, conversion of forests to agriculture is a leading cause of species
49 decline (Millennium Ecosystem Assessment 2005). Many temperate forest regions in Europe
50 have historically undergone large-scale deforestation followed by a more recent period of
51 forest creation (Forest Europe 2015). At the turn of the century the primary reason for forest
52 creation was timber production, generally in the form of non-native coniferous plantations,
53 but the value of native broadleaf woodlands for biodiversity conservation is now an important
54 driver of forest creation. Woodland is the term commonly used in the UK to describe any
55 forested area; for convenience, we use this term hereafter in the paper. However, many of
56 these newly-created areas of native broadleaf woodland are small, isolated from existing
57 woodlands and surrounded by urban or agricultural land (Quine & Watts 2009; Fuentes-
58 Montemayor *et al.* 2015). This potentially inhibits dispersal of woodland species across the
59 landscape (Villard & Metzger 2014) and reduces the value of created woodlands as a
60 resource for biodiversity. This issue affects many other natural ecosystems as well as
61 woodlands. To address this, policymakers and conservationists are increasingly
62 acknowledging the need to restore, reconnect and create native habitats to facilitate
63 ecosystem functioning, dispersal of species and gene flow in a changing environment
64 (United Nations 2012); a concept often referred to as creating 'ecological networks'.

65 In terms of physical design, ecological networks are conceived as a spatial network of core
66 habitat areas, corridors, stepping stones and buffer zones (Jongman & Pungetti 2004).

67 Within England, this has been translated into policy recommendations through four broad
68 components relating to local and landscape level conservation actions for habitat restoration
69 and creation (Lawton *et al.* 2010). The first two principles, increasing the area of core
70 habitats and increasing quality and structural heterogeneity of core habitats are local level
71 actions, while the other two, increasing the amount of habitat and increasing connectivity

72 between habitats, are landscape level actions. These principles are based on the underlying
73 concepts of habitat area, quality, amount and connectivity which have been adopted in many
74 landscape-scale conservation initiatives throughout the world (Worboys, Francis &
75 Lockwood 2010), meaning they are applicable to many similarly fragmented landscapes in
76 other geographical regions. Although the basic concepts of ecological networks are
77 appealing and based on sound ecological principles there is limited empirical evidence to
78 inform their implementation (Humphrey *et al.* 2015) and some have argued that ecological
79 networks offer little for biodiversity conservation beyond a simple conceptual framework
80 (Boitani *et al.* 2007). Furthermore, disentangling the related effects of habitat amount and
81 connectivity is the subject of much debate (Hodgson *et al.* 2009, 2011; Doerr, Barrett &
82 Doerr 2011; Fahrig 2013, 2015; Hanski 2015) and some question the additional value of
83 reducing isolation between habitat patches, with much effort spent on creating habitat
84 configurations which provide little benefit (Fahrig 2013).

85 Habitat creation and restoration projects face many challenges related to competing land-
86 use, socio-economic, and conservation priorities and must achieve the most cost-effective
87 gains, meaning policymakers and conservationists need to know where to prioritise
88 conservation efforts to optimise the biodiversity outcomes (Menz, Dixon & Hobbs 2013). The
89 prioritisation of conservation efforts in fragmented landscapes is further complicated by the
90 balance between “extinction debt”, where species are lost over time in response to past
91 habitat loss and fragmentation (Tilman *et al.* 1994), and the significant temporal lag in
92 biodiversity benefits from habitat restoration or creation (“colonisation credits”; Cristofoli *et al.*
93 2010). Much of the evidence used to inform landscape-scale restoration and creation is
94 currently drawn from studies of habitat fragmentation and it is unclear whether the effects of
95 these two processes are reciprocal. In addition, much of the previous research on habitat
96 restoration and creation focuses on the effects of habitat quality at the patch scale, with
97 limited evidence on landscape-scale processes (Brudvig 2011; Humphrey *et al.* 2015). There
98 is also a lack of information on successes and failures in landscape-scale restoration

99 projects (Brudvig 2011), with limited evidence from well-replicated studies of relative or
100 combined effects of local and landscape-scale variables on biodiversity at a range of spatial
101 and temporal scales (Humphrey *et al.* 2015).

102 A 'natural experiment' may be one way to address the spatial and temporal challenges
103 inherent in addressing the issues outlined above. Within the UK we have a unique
104 opportunity to tackle this problem, as the spatial composition and configuration of woodland
105 creation is particularly well-documented in historical maps. This allows the tracking of the
106 last 160 years of woodland planting in a largely agricultural landscape. The Woodland
107 Creation and Ecological Networks project (WrEN; wren-project.com) is a large-scale natural
108 experiment based in the UK which aims to test the ecological network concept for native
109 woodland restoration and creation (Watts *et al.* 2016). The WrEN project is studying
110 woodlands created in the last 160 years across two large, agriculturally-dominated
111 landscapes in lowland in England and Scotland. This spatio-temporal scale is much larger
112 than in many previous studies of ecosystem development, and the project's focus on
113 woodland creation complements the many studies of woodland fragmentation that have
114 been conducted in the past.

115 Emerging evidence on the relationships between species and local and landscape network
116 variables in woodland creation sites tends to focus on well-studied groups such as plants,
117 birds and mammals (Humphrey *et al.* 2015). However, woodlands also support a large
118 proportion of insect species, important for ecosystem processes through functional roles
119 such as pollinators, decomposers, and predators and prey in food webs (Didham *et al.*
120 1996). Hoverflies (Diptera: Syrphidae), which are strong fliers and play important functional
121 roles in pollination and biocontrol (Jauker *et al.* 2009; Meyer, Jauker & Steffan-Dewenter
122 2009), can be influenced by interactions between the amount and connectivity of woodlands,
123 as well as the diversity of patch scale microhabitats (Ouin *et al.* 2006; Herrault *et al.* 2016).
124 Heterogeneous landscapes with well-connected suitable habitats and hedgerows have been
125 shown to support higher hoverfly diversity (Burgio & Sommaggio 2007; Haenke *et al.* 2014).

126 In contrast, craneflies (Diptera: Tipuloidea: Cylindrotomidae, Limoniidae, Pediciidae,
127 Ptychopteridae, Tipulidae), are poor fliers (Service 1973) and have detritivorous larvae, with
128 many species associated with the decomposition of litter/ woody debris in woodlands
129 (Stubbs 1992). The abundance and distribution of cranefly larvae are influenced by soil
130 moisture and organic content, while adults are influenced by climate (Merritt & Lawson 1981;
131 McCracken, Foster & Kelly 1995). Additionally, relatively immobile invertebrates, such as
132 craneflies, have been shown to respond to vegetation structure at a small scale (Cole *et al.*
133 2010). This suggests that local-scale variables may have a strong influence on cranefly
134 diversity, but also that woodland specialist craneflies may require well-connected habitats,
135 which provide the climate preferred by adults and the substrate required for larvae, in order
136 to disperse. However, to the best of our knowledge, the relative importance of local and
137 landscape variables have not been examined for craneflies.

138 In this study, hoverflies and craneflies were selected due to their known woodland
139 association and differing dispersal abilities. The study used the WrEN sites to: 1) identify the
140 value of woodland creation sites for woodland-associated species; 2) determine the direct
141 and indirect effects of a range of local and landscape-scale variables on species diversity in
142 woodland creation sites; 3) compare the effect of local and landscape-scale variables on
143 insect groups with differing dispersal capabilities. In relation to aim 1, we hypothesise that
144 woodland creation sites would support a proportion of woodland-associated hoverfly and
145 cranefly species; populations within these woodland sites would also display high
146 nestedness, as smaller or younger woodlands should contain a subset of the communities in
147 larger or older sites which have accumulated more species over space and time. As these
148 insects are known to be strongly influenced by local-scale variables, we hypothesised (aim
149 2) that habitat quality at the local-scale would have the greatest influence on woodland
150 cranefly and hoverfly abundance and species richness compared to landscape variables
151 which relate to the amount or connectivity of woodland habitat. For aim 3, we hypothesised
152 that craneflies would be more influenced by woodland connectivity when compared to

153 hoverflies, as they are likely to require suitable habitat in the surrounding landscape to move
154 between patches, whereas hoverflies are strong fliers which allows them to move more
155 freely across fragmented habitats with poor connectivity.

156 **Methods**

157 *Site selection*

158 A total of 33 English and 45 Scottish broadleaved woodland patches were selected for
159 sampling from the WrEN project sites (see Appendix S1 in Supporting Information for map).
160 The patches had been planted on previously agricultural land within the last 160 years and
161 varied in age (10 – 160 years), patch size (0.5 – 32 hectares), proportion of broadleaved
162 woodland within 3km (0.4 – 17%) and distance to nearest broadleaved woodland (8m –
163 1.6km) (Appendix S2 in Supporting Information). The sites were chosen using the site
164 selection protocol defined in Watts *et al.* (2016).

165 *Insect sampling*

166 One Malaise net trap was placed in a suitable location as close to the centre of the woodland
167 as possible. A suitable location was defined as a clearing which received sun exposure for
168 the majority of the day. The collecting bottle was oriented south and filled with 100% ethanol
169 to kill and preserve the insects. The trap was left in place for a sampling period of seven
170 days each in June, July and August. In each week of sampling between 19 and 23 sites
171 were sampled at the same time and the traps were rotated around the sites over a three
172 week period. This was repeated three times, totalling 21 days of sampling at each site
173 across the summer period. A second trap was also placed at least 100m from the first
174 Malaise trap in each site for one sampling period of seven days to capture variation across
175 the site. The second trap was located in the same environmental conditions as the first trap,
176 i.e. same amount of vegetation and canopy cover. Hoverflies and craneflies were extracted
177 from the samples and identified to species level using Stubbs & Falk (2002) and Stubbs &
178 Kramer (2016).

179 *Local level variables*

180 The surveyed environmental variables were chosen for their likely importance for woodland
181 insect biodiversity based on the literature and their ability to be manipulated by management
182 actions. Historic Ordnance Survey maps (EDINA 2013) were used to calculate the ecological
183 continuity of each woodland patch (i.e. the time period that had elapsed since each
184 woodland patch 'appeared' in maps), hereafter referred to as patch age. The temporal
185 resolution of historic maps was 10 years, one for each decade from 1840 - 1990. Digital
186 maps (National Forest Inventory) were spatially analysed in ArcMap to measure the area of
187 each woodland. In each site the percentage cover and number of flowering vascular plant
188 species (angiosperms) were recorded in five quadrats placed in areas that were
189 representative of the woodland. Average angiosperm percentage cover and total species
190 richness per site were calculated from the five quadrats. Vegetation surveys were conducted
191 along an edge-to-interior transect in each woodland. At every 15m along the transect the
192 tree species, tree density and tree diameter at breast height (DBH) were recorded and a 5m
193 x 5m quadrat was established to measure percentage understorey cover and litter/ woody
194 debris (CWD) on the ground measured on an indicator scale of 0 – 3: 0 = no litter or woody
195 debris, 1 = leaf litter & twigs (≤ 1 cm), 2 = large branches (< 10 cm) and 3 = coarse woody
196 debris (≥ 10 cm diameter) (see Appendix S3 in Supporting Information for more detailed
197 descriptions).

198 *Landscape level variables*

199 ArcMap was used to analyse the proportion of land covered by broadleaf woodland within
200 five buffer scales (250m, 500m, 1000m, 1500m, 2000m), using the National Forest Inventory
201 (Forestry Commission 2012). Within each buffer we also measured the inter-patch
202 connectivity of broadleaf woodland based on a combination of area of surrounding woodland
203 and their distance to the focal patch (Appendix S4 in Supporting Information). The area of
204 semi-natural habitat (excluding woodland), urban areas and agricultural land was also
205 calculated within these buffer scales using UK Land Cover Maps 2007 (Morton *et al.* 2011).

206 These scales were chosen as previous studies of landscape variables have found effects on
207 Diptera at the scale of 250-2000m (Kleijn & van Langevelde 2006; Bommarco *et al.* 2014).

208 *Data analysis*

209 The online invertebrate traits database PANTHEON (Webb 2014) was used to classify
210 woodland-associated species (species code: A1 = arboreal, S1 = shaded, DW1 =
211 deadwood) and remaining species were classed as non-woodland. The abundance and
212 species richness of woodland-associated and non-woodland species were calculated for
213 each collection period and trap within each site. Hoverflies and craneflies were analysed
214 separately and the data were analysed in the statistical program R version 3.3.0 (R Core
215 Team 2016).

216 Species diversity metrics were calculated for woodland-associated species in England and
217 Scotland separately. The replacement of species between sites (turnover) was measured as
218 Simpson pair-wise dissimilarity, subsets of species communities between sites (nestedness)
219 was measured as the nestedness-fraction of Sorensen pair-wise dissimilarity, and beta
220 diversity between sites was calculated as Sorensen pair-wise dissimilarity. Subsets of 20
221 sites were resampled 100 times to produce density plots of the diversity values (Baselga *et*
222 *al.* 2013). The dissimilarity measures are on a 0 - 1 scale, and the analyses were conducted
223 using the betapart package (Baselga *et al.* 2013).

224 Environmental variables were divided into “local” and “landscape” scale variables which
225 relate to ecological network components (Table 1). Prior to model selection, the scales of
226 each landscape variable were run in separate generalised linear models (GLM) using the
227 MASS package (Venables & Ripley 2003) and AICc was used to select the best scale (250 -
228 2000m). The data from the two regions were pooled and region was used as a factor in the
229 models to test for differences between the regions. “Collection period” and “trap” were
230 initially included as random factors in generalised linear mixed models, but the variance
231 explained by these was negligible. Therefore we pooled the data for each collection and trap

232 and used the simplified model structure of the sum of all collection periods and traps for
233 each site.

234 The effect of these local and landscape-scale variables on woodland and non-woodland
235 species abundance and richness was tested using piecewise structural equation models
236 (SEM) in the piecewiseSEM package (Lefcheck 2015). SEM is a multivariate technique that
237 can be used to test if a-priori hypothesised direct and indirect causal relationships between
238 variables (presented as a series of GLMs) are supported by the observed data, and compare
239 relative effect sizes between variables. SEM also conducts tests for missing paths, to identify
240 relationships between variables that were not predicted. These relationships can then be
241 incorporated into the model or specified as correlated errors between variables and do not
242 form part of the model, i.e. they are not considered causative but do have a significant
243 correlation. A global conceptual model based on underlying theory and evidence was used
244 to guide the construction of hypotheses for species abundance and species richness. Here
245 we present our hypotheses and global conceptual model for woodland-associated species
246 only (Figure 1). Our hypotheses, global conceptual model and results for non-woodland
247 associated species are available in Appendix S6 in Supplementary Information.

248 Preliminary analysis showed that abundance and species richness were highly correlated
249 (woodland-associated hoverflies: Pearson's $r = 0.96$, $P < 0.001$; woodland-associated
250 craneflies: Pearson's $r = 0.76$, $P < 0.001$), suggesting that both response variables were
251 likely to exhibit similar relationships with environmental variables. Species richness is known
252 to increase with abundance (Gotelli & Colwell 2001) and we hypothesised that local and
253 landscape-scale variables indirectly affect species richness through direct effects on
254 abundance. Species abundance typically increases with the area of suitable habitat
255 (species-area relationship: MacArthur and Wilson, 1967; McGuinness, 1984) so we
256 expected woodland species richness to increase with woodland patch size. We expected
257 patch age to directly positively affect the abundance of woodland-associated species
258 because there is a time lag between habitat creation and colonisation (Cristofoli *et al.* 2010).

259 We also expected an indirect positive effect of patch age on woodland-associated species
260 as microhabitats provided by deadwood and structural diversity of trees develop as
261 woodlands mature (Hodge & Peterken 1998; Reay & Norton 1999). Specifically, we
262 expected a direct positive effect of the variation in tree diameter (tree DBH SD) and litter/
263 woody debris. Variation in tree diameter was also expected to be positively affected by tree
264 species richness as mean diameter differs between tree species; additionally, trees provide
265 nectar and pollen resources in spring, therefore tree species richness was expected to have
266 a direct positive effect on woodland-associated hoverflies. Angiosperms (flowering plants)
267 are an important resource for adult hoverflies; species which flower at different times of the
268 year increase resource provision of nectar and pollen and some hoverfly species show
269 preferences for particular plant species (Stubbs & Falk 2002). Therefore the species
270 richness and abundance of angiosperms were expected to have a positive effect on
271 woodland-associated hoverflies. However, we expected angiosperm richness and
272 abundance to be highly correlated and included this relationship in the model by testing for
273 an indirect effect of angiosperm abundance mediated through a direct effect of angiosperm
274 richness. Understory vegetation of trees and shrubs increases woodland-associated hoverfly
275 species richness (Gittings *et al.* 2006), providing higher structural complexity and greater
276 availability of important resources such as shelter and insect prey for larvae, therefore we
277 expected the cover of understory vegetation, i.e. trees and shrubs ≤ 7 cm DBH and/or ≤ 3 m
278 in height, to have a direct positive effect on woodland-associated species. While woodland-
279 associated species are adapted for shade created by the canopy layer, closely spaced tree
280 stems tend to result in very high levels of shade and lower structural diversity of trees (Vesk
281 *et al.* 2008), as well as fewer clear flight paths for Diptera. Therefore, we expected that high
282 tree density would negatively affect woodland-associated species. In turn, tree density was
283 expected to be negatively affected by patch age, as older woodlands have trees that have
284 died, creating gaps where they have fallen.

285 Broadleaf woodland cover, semi-natural habitat cover and broadleaf woodland connectivity
286 in the landscape were expected to have direct positive effects on woodland species by
287 facilitating their dispersal across the landscape (Herrault *et al.* 2016). The amount of
288 agricultural land was expected to have an indirect negative effect on woodland-associated
289 species mediated through a direct negative effect on the amount and connectivity of
290 broadleaf woodland. Our measure of broadleaf connectivity necessarily includes the amount
291 of broadleaf cover as a component (see Methods section), since these two variables are
292 typically intrinsically related (Hanski 2015). To disentangle these effects, we tested for direct
293 effects of woodland amount *per se* and connectivity (i.e. a combination of both woodland
294 amount and configuration). We hypothesised that if broadleaf connectivity was more
295 important than broadleaf cover then connectivity would have a direct effect on hoverfly and
296 crane fly species abundance, and broadleaf cover would only have an indirect effect
297 mediated through connectivity.

298 Variables were transformed where necessary and models were checked following Zuur &
299 Ieno (2016). SEM fit was evaluated using Fisher's C ($P > 0.05$ indicates good model fit).
300 Residuals from the models were examined for spatial autocorrelation by calculating Moran's
301 I using the program Spatial Analysis in Macroecology (SAM). There were no statistically
302 significant patterns in spatial autocorrelation ($P > 0.05$), so corrections to account for this in
303 the models were not necessary.

304 **Results**

305 *Value of woodland creation sites*

306 Hoverflies were caught at 32 of the 33 English sites and 42 of the 45 Scottish sites. Mean
307 abundance and richness of woodland-associated and non-woodland species were higher in
308 England than Scotland (Table 2). In total, we caught 25 species of woodland-associated
309 hoverflies. Approximately 33% of the 281 species of British hoverflies are associated with
310 woodland habitats (Webb 2014), meaning we sampled 27% of these woodland species.
311 However, the proportion of woodland-associated hoverflies caught compared to the total

312 catch was low in England (woodland-associated individuals = 10% and woodland-associated
313 species = 40%) and similarly low in Scotland (woodland-associated individuals = 11% and
314 woodland-associated species = 37%).

315 Craneflies were caught at all 33 English sites and all 45 Scottish sites. Mean abundance and
316 richness of woodland-associated and non-woodland species were higher in Scotland than
317 England (Table 2). In total, we caught 67 species of woodland-associated craneflies. Almost
318 half of the 334 species of British craneflies are associated with woodland (Webb 2014) and
319 we caught 43% of these woodland species. The proportion of woodland-associated
320 craneflies caught compared to the total catch was high in England (woodland-associated
321 individuals = 79% and woodland-associated species = 80%), but slightly lower in Scotland
322 (woodland-associated individuals = 57% and woodland-associated species = 63%).

323 In terms of species composition of these woodlands, the nestedness of woodland-associated
324 hoverfly and cranefly species communities was low whereas turnover was high in both
325 regions (Figure 2). Therefore, the woodland patches did not contain subsets of woodland-
326 associated species and species replacement between sites was high.

327 *Effects of local and landscape scale variables*

328 The initial model of hypothesised direct and indirect effects of local and landscape-scale
329 variables on woodland-associated hoverflies was not significantly different from the observed
330 data (Fisher C = 154.47, df = 136, P = 0.13). No additional missing paths were identified,
331 although tree density was correlated with log area and variation in tree DBH (Table 3). None
332 of the landscape-scale variables directly or indirectly influenced woodland-associated
333 hoverfly abundance and species richness. Surprisingly, patch age and litter/ woody debris
334 had direct negative effects on woodland hoverfly abundance and in turn species richness
335 (Table 3; Figure 2). The direct effect of age was equivalent to a 5.6% reduction in
336 abundance per 10% increase in patch age. The effect of litter/woody debris was equivalent
337 to a 3.5% reduction in abundance per 10% increase in litter/woody debris. Woodland age
338 also influenced woodland-associated hoverfly abundance indirectly by increasing litter/

339 woody debris. The abundance of woodland-associated hoverflies was also affected by
340 structural elements of the habitat, specifically a direct positive effect of understory cover and
341 variation in tree diameter. In turn, tree diameter variation was positively affected by
342 woodland age and tree species richness. The effect of understory cover was equivalent to a
343 3.9% increase in abundance per 10% increase in understory cover. The effect of variation in
344 tree DBH was equivalent to a 4.4% increase in abundance per 10% increase in variation in
345 tree DBH. The model specified for woodland-associated crane flies was not significantly
346 different from the observed data (Fisher C = 115.26, df = 94, P = 0.07) after a missing path
347 of a direct effect of region on crane fly species richness was incorporated into the model
348 (Table 4). Crane fly abundance and species richness was strongly influenced by region, with
349 higher numbers in Scotland than England. Again, patch age had a direct negative effect on
350 woodland-associated species, which was equivalent to a 2.4% decrease in abundance per
351 10% increase in patch age.

352 **Discussion**

353 *Value of woodland creation sites*

354 The created woodland patches used in this study are providing habitat for woodland insects
355 despite their small and fragmented configuration; we caught a quarter of all British woodland
356 hoverfly species and almost half of all British woodland crane fly species. In terms of species
357 composition, the woodland patches did not contain subsets of species and species
358 replacement between sites was high. We also caught a large number of agricultural and
359 grassland species which are more closely associated with the surrounding landscape. The
360 high mobility and low abundance of hoverflies could mean we caught many species that
361 were just passing through the woodland. Woodland crane fly species were more abundant
362 than hoverflies, possibly because their low mobility which makes them very dependent on
363 small-scale woodland microhabitats and more confined to the woodland interior.

364 Woodland-associated insects have been shown to begin colonising woodlands within the
365 first five years of creation (Fuller *et al.* 2013). However, while the sites in this study support

366 some woodland species, the relatively low abundance suggests that the habitat quality or
367 surrounding landscape is not suitable for large populations of woodland insect species to
368 persist. An alternative explanation relates to historical landscape change, as hoverflies have
369 been shown to respond more to past changes in habitat area at similar temporal scales to
370 our study, than to current landscape context (Bommarco *et al.* 2014; Herrault *et al.* 2016).
371 Past deforestation and removal of vegetated field margins and hedgerows in the UK
372 landscape (Benton, Vickery & Wilson 2003) might be why we found low diversity in these
373 woodland patches and few responses to landscape level variables. This could be a
374 manifestation of extinction debt, but there is no literature on the effect of historical landscape
375 changes on crane fly diversity, and it would be interesting to test this to determine the extent
376 to which they exhibit extinction debts or colonisation credits.

377 Although studies have demonstrated increases in biodiversity as a result of habitat
378 restoration, it is often harder to recreate ecosystems which function at the same level as
379 intact reference systems (Benayas *et al.* 2009), such as ancient woodlands. This could be
380 what is happening with insects in these secondary woodlands and has also been found for
381 other species groups in these study sites. For example, even in 160 year old woodlands
382 birds typically associated with ancient woodland such as Pied Flycatcher (*Ficedula*
383 *hypoleuca*) and Wood Warbler (*Phylloscopus sibilatrix*) were not found (Whytock *et al.* in
384 review). A comparison of secondary and ancient woodlands is required to test this theory for
385 these insect species, and this work is currently underway by the authors.

386 *Relative and combined effects of ecological network variables*

387 As expected, the local-scale variables related to habitat quality performed best at explaining
388 abundance and species richness of woodland-associated hoverfly and crane fly species
389 richness and abundance. A review of published evidence, for a range of taxa, suggested that
390 variation in habitat quality has bigger effects than habitat composition or configuration in the
391 landscape, because higher quality sites provide larger source populations and locations for
392 colonisation (Hodgson *et al.* 2011). The area of woodland patches played no significant role

393 in explaining insect abundance or species richness, which was unexpected as other studies
394 have shown a strong relationship with both historic and current patch area (Ouin *et al.* 2006;
395 Bommarco *et al.* 2014; Herrault *et al.* 2016). However, 81% of our sites were <5ha whereas
396 other studies have used a range of up to 200ha, so possibly the ranges of sizes were not
397 sufficient to detect a strong influence of patch size. The patch sizes used in this study were a
398 consequence of the woodlands available to us; 65% of woodlands in Britain are <2ha
399 (Forestry Commission 2012).

400 Hoverflies in our study were negatively influenced by increased levels of woody debris and
401 positively influenced by understory cover and variation in tree diameter. However, these
402 variables were involved in complex direct and indirect relationships mediated through patch
403 age. Patch age had a direct negative effect which was indirectly increased through large
404 woody debris, but was mitigated indirectly by increased variation in tree diameter. The
405 negative influence of woody debris might reflect the differing feeding habits of larval and
406 adult hoverflies. Many woodland hoverfly larvae depend on deadwood microhabitats;
407 however, Fayt *et al.* (2006) found that adult hoverflies were not influenced by the amount of
408 deadwood present, and were most diverse in open stands with large trees and abundant
409 floral resources which they require for reproduction. Alternatively, this result might also be
410 influenced by the way we recorded woody debris, using an indicator scale from twigs to large
411 pieces > 10 cm. Measuring the cover or volume of woody debris may provide more fine-
412 scale information on this microhabitat and we are currently in the process of collecting this
413 information in the WrEN sites. It should also be noted that Malaise traps are activity traps,
414 which sample species passively and can be affected by the density of vegetation, i.e. more
415 dense vegetation might mean species are less likely to encounter the trap. However, our
416 results suggest that the analysis was not confounded by vegetation density, as understory
417 cover (a measure of small trees and shrubs) had a positive effect on hoverfly species.
418 Woodland-associated craneflies were only affected by patch age and the effect was not
419 strong, probably because the regional differences in abundance and species richness were

420 more important. The lack of any other local-scale variable effects on craneflies makes it
421 difficult to compare the impacts of variable scales on Diptera with differing dispersal
422 capabilities. However, both species groups showed no relationships with landscape-scale
423 variables, suggesting that local-scale variables are more important regardless of their ability
424 to disperse across the landscape.

425 The lack of an effect of woodland cover and connectivity on hoverflies here contrasts with
426 other studies (Ouin *et al.* 2006; Sjödin, Bengtsson & Ekbohm 2007; Herrault *et al.* 2016).
427 However, the evidence is mixed as a number of others have also found no significant effects
428 of habitat fragmentation on hoverfly species and concluded their high mobility and non-
429 dependence of larvae on flower resources makes them less dependent on the surrounding
430 landscape matrix (Jauker *et al.* 2009; Ekroos, Rundlöf & Smith 2013). Alternatively, it is
431 possible that we did not detect any significant effects of landscape-scale variables because
432 the local-scale variables included in the models were relatively much more important.
433 Furthermore, the National Forest Inventory only contains data on woodlands over 0.5
434 hectares, and many insects respond to habitats at much finer scales than this. It is
435 acknowledged that hedgerows and large, individual trees outside of woodlands may provide
436 habitat for many Diptera species, with 33% of British hoverfly species and 22% of British
437 cranefly species being recorded in a British hedge (Wolton *et al.* 2014), and these areas of
438 connective habitat are likely to provide resources for woodland-associated insects (Burgio &
439 Sommaggio 2007). We require finer scale data on hedgerows, individual trees and small
440 patches of tree/ scrub vegetation under 0.5 hectares to determine if these contribute to how
441 woodland insects use the landscape and enable them to move between woodland patches.

442 **Synthesis and applications**

443 Secondary woodlands created over the past 160 years are providing resources for both
444 hoverflies and craneflies. Results from this study indicate that woodland-associated
445 hoverflies would benefit from conservation actions to improve the quality and structure within
446 woodland habitats. This can be achieved by managing the heterogeneity of woodlands for

447 greater structural diversity (i.e. a 10% increase in variation of tree DBH and cover of
448 understorey vegetation results in a 4.4% and 3.9% increase in abundance, respectively). In
449 terms of prioritising local-scale management actions, variation in tree DBH had a slightly
450 greater effect size than understorey cover but we consider both to be important. This is also
451 likely to benefit a range of other taxa and those reliant on woodland insects as a food
452 source. Many existing woodlands in the UK are planted on private lands using government
453 grants and are subsequently abandoned or have little management input (Lawrence &
454 Dandy 2014; Fuentes-Montemayor *et al.* 2015). Active woodland management could be
455 encouraged, such as thinning woodlands once they are established to allow trees to grow
456 and natural regeneration to occur, and maintaining open spaces within glades or rides.
457 These simple management strategies are likely to facilitate a diverse tree and understorey
458 vegetation structure associated with high insect abundance and species richness.

459 Our results demonstrate that the broad adoption of the principles from ecological networks,
460 no matter how appealing in practice, may not be the most effective basis for a landscape-
461 scale conservation strategy for these insect groups. However, we do acknowledge that the
462 configuration and composition of woodlands in agricultural landscapes may be important for
463 other species and ecosystem processes. The WrEN project (Watts *et al.* 2016) continues to
464 survey sites for a wide range of taxa which is likely to respond differently to patch and
465 landscape-scale variables at different spatial and temporal scales. Using this approach we
466 hope to identify potential differences in the requirements of different taxonomic or functional
467 groups and draw out general recommendations for conserving woodland biodiversity.

468 **Authors' Contributions**

469 LF, KP, EFM, KW and NM designed the study. LF and KB carried out data collection and
470 species identification. LF carried out analysis. LF, KP, EFM, KW and NM contributed to
471 writing.

472 **Data accessibility**

473 Data in this study is available from DataStorre at the University of Stirling.

474 **Acknowledgements**

475 Thanks to Roy Allen for assistance with fieldwork, Nadine Royle for assistance with sorting
476 samples, Geoff Hancock for assistance with crane fly identification, and Robbie Whytock for
477 the study site location map. Funding for this work was provided by the company Tarmac.

478 **References**

- 479 Baselga, A., Orme, D., Villeger, S., De Bortoli, J. & Leprieur, F. (2013) betapart: Partitioning
480 beta diversity into turnover and nestedness components. , R package version 1.3.
- 481 Benayas, J.M.R., Newton, A.C., Diaz, A. & Bullock, J.M. (2009) Enhancement of Biodiversity
482 and Ecosystem Services by Ecological Restoration: A Meta-Analysis. *Science*, **325**,
483 1121–1124.
- 484 Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat
485 heterogeneity the key? *Trends in Ecology & Evolution*, **18**, 182–188.
- 486 Boitani, L., Falucci, A., Maiorano, L. & Rondinini, C. (2007) Ecological Networks as
487 Conceptual Frameworks or Operational Tools in Conservation. *Conservation Biology*,
488 **21**, 1414–1422.
- 489 Bommarco, R., Lindborg, R., Marini, L. & Öckinger, E. (2014) Extinction debt for plants and
490 flower-visiting insects in landscapes with contrasting land use history ed M. van
491 Kleunen. *Diversity and Distributions*, **20**, 591–599.
- 492 Brudvig, L.A. (2011) The restoration of biodiversity: Where has research been and where
493 does it need to go? *American Journal of Botany* , **98**, 549–558.
- 494 Burgio, G. & Sommaggio, D. (2007) Syrphids as landscape bioindicators in Italian
495 agroecosystems. *Agriculture, Ecosystems & Environment*, **120**, 416–422.
- 496 Cole, L.J., Pollock, M.L., Robertson, D., Holland, J.P., McCracken, D.I. & Harrison, W.
497 (2010) The influence of fine-scale habitat heterogeneity on invertebrate assemblage

- 498 structure in upland semi-natural grassland. *Agriculture, Ecosystems & Environment*,
499 **136**, 69–80.
- 500 Cristofoli, S., Piqueray, J., Dufrêne, M., Bizoux, J.-P. & Mahy, G. (2010) Colonization Credit
501 in Restored Wet Heathlands. *Restoration Ecology*, **18**, 645–655.
- 502 Didham, R.K., Ghazoul, J., Stork, N.E. & Davis, A.J. (1996) Insects in fragmented forests: a
503 functional approach. *Trends in Ecology & Evolution*, **11**, 255–260.
- 504 Doerr, V., Barrett, T. & Doerr, E. (2011) Connectivity, dispersal behaviour and conservation
505 under climate change: a response to Hodgson et al. *Journal of Applied Ecology*, **48**,
506 143–147.
- 507 EDINA. (2013) Ancient Roam Service, <http://edina.ac.uk/digimap>
- 508 Ekroos, J., Rundlöf, M. & Smith, H.G. (2013) Trait-dependent responses of flower-visiting
509 insects to distance to semi-natural grasslands and landscape heterogeneity. *Landscape*
510 *Ecology*, **28**, 1283–1292.
- 511 Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis
512 ed K. Triantis. *Journal of Biogeography*, **40**, 1649–1663.
- 513 Fahrig, L. (2015) Just a hypothesis: a reply to Hanski. *Journal of Biogeography*, **42**, 993–
514 994.
- 515 Fayt, P., Dufrêne, M., Branquart, E., Hastir, P., Pontégnie, C., Henin, J.-M. & Versteirt, V.
516 (2006) Contrasting Responses of Saproxyllic Insects to Focal Habitat Resources: The
517 Example of Longhorn Beetles and Hoverflies in Belgian Deciduous Forests. *Journal of*
518 *Insect Conservation*, **10**, 129–150.
- 519 Forest Europe. (2015) *State of Europe's Forests 2015*.
- 520 Forestry Commission. (2012) National Forest Inventory – Great Britain,
521 www.forestry.gov.uk/datadownload
- 522 Fuentes-Montemayor, E., Peredo-Alvarez, V.M., Watts, K. & Park, K.J. (2015) Are woodland

- 523 creation schemes providing suitable resources for biodiversity? Woodland moths as a
524 case study. *Biodiversity and Conservation*, **24**, 3049–3070.
- 525 Fuller, L., Oxbrough, A., Gittings, T., Irwin, S., Kelly, T.C. & O'Halloran, J. (2013) The
526 response of ground-dwelling spiders (Araneae) and hoverflies (Diptera: Syrphidae) to
527 afforestation assessed using within-site tracking. *Forestry*, **87**, 301–312.
- 528 Gittings, T., O'Halloran, J., Kelly, T.T.C.T.C., Giller, P.S.P.S., Oxbrough, A.G. & O'Halloran,
529 J. (2006) The contribution of open spaces to the maintenance of hoverfly (Diptera,
530 Syrphidae) biodiversity in Irish plantation forests. *Forest Ecology and Management*,
531 **237**, 478–491.
- 532 Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity : procedures and pitfalls in the
533 measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.
- 534 Haenke, S., Kovács-Hostyánszki, A., Fründ, J., Batáry, P., Jauker, B., Tschardtke, T. &
535 Holzschuh, A. (2014) Landscape configuration of crops and hedgerows drives local
536 syrphid fly abundance ed J. Osborne. *Journal of Applied Ecology*, **51**, 505–513.
- 537 Hanski, I. (2015) Habitat fragmentation and species richness. *Journal of Biogeography*, **42**,
538 989–993.
- 539 Herrault, P.-A., Larrieu, L., Cordier, S., Gimmi, U., Lachat, T., Ouin, A., Sarthou, J.-P. &
540 Sheeren, D. (2016) Combined effects of area, connectivity, history and structural
541 heterogeneity of woodlands on the species richness of hoverflies (Diptera: Syrphidae).
542 *Landscape Ecology*, **31**, 877–893.
- 543 Hodge, S.J. & Peterken, G.F. (1998) Deadwood in British forests: priorities and a strategy .
544 *Forestry*, **71**, 99–112.
- 545 Hodgson, J.A., Moilanen, A., Wintle, B.A. & Thomas, C.D. (2011) Habitat area, quality and
546 connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology*,
547 **48**, 148–152.

- 548 Hodgson, J.A., Thomas, C.D., Wintle, B.A. & Moilanen, A. (2009) Climate change,
549 connectivity and conservation decision making: back to basics. *Journal of Applied*
550 *Ecology*, **46**, 964–969.
- 551 Humphrey, J.W., Watts, K., Fuentes-Montemayor, E., Macgregor, N.A., Peace, A.J. & Park,
552 K.J. (2015) What can studies of woodland fragmentation and creation tell us about
553 ecological networks? A literature review and synthesis. *Landscape Ecology*, **30**, 21–50.
- 554 Jauker, F., Diekötter, T., Schwarzbach, F. & Wolters, V. (2009) Pollinator dispersal in an
555 agricultural matrix: opposing responses of wild bees and hoverflies to landscape
556 structure and distance from main habitat. *Landscape Ecology*, **24**, 547–555.
- 557 Jongman, R.H.G. & Pungetti, G. (2004) *Ecological Networks and Greenways: Concepts,*
558 *Design, Implementation*. Cambridge University Press, Cambridge.
- 559 Kleijn, D. & van Langevelde, F. (2006) Interacting effects of landscape context and habitat
560 quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology*,
561 **7**, 201–214.
- 562 Lawrence, A. & Dandy, N. (2014) Private landowners' approaches to planting and managing
563 forests in the UK: What's the evidence? *Land Use Policy*, **36**, 351–360.
- 564 Lawton, J.H., Brotherton, P.N.M., Brown, V.K., Elphick, C., Fitter, A.H., Forshawm, J. & et al.
565 (2010) *Making Space for Nature: A Review of England's Wildlife Sites and Ecological*
566 *Network*. London.
- 567 Lefcheck, J.S. (2015) piecewiseSEM: Piecewise structural equation modeling in R for
568 ecology, evolution, and systematics. *Methods in Ecology and Evolution*, **7**, 573–579.
- 569 MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton
570 University Press, New Jersey.
- 571 McCracken, D.I., Foster, G.N. & Kelly, A. (1995) Factors affecting the size of leatherjacket
572 (Diptera: Tipulidae) populations in pastures in the west of Scotland. *Applied Soil*

- 573 *Ecology*, **2**, 203–213.
- 574 McGuinness, K.A. (1984) Species-area curves. *Biological Reviews*, **59**, 423–440.
- 575 Menz, M.H.M., Dixon, K.W. & Hobbs, R.J. (2013) Hurdles and Opportunities for Landscape-
576 Scale Restoration. *Science*, **339**, 526–527.
- 577 Merritt, R.W. & Lawson, D.L. (1981) Adult Emergence Patterns and Species Distribution and
578 Abundance of Tipulidae in Three Woodland Floodplains. *Environmental Entomology*,
579 **10**, 915 LP-921.
- 580 Meyer, B., Jauker, F. & Steffan-Dewenter, I. (2009) Contrasting resource-dependent
581 responses of hoverfly richness and density to landscape structure. *Basic and Applied*
582 *Ecology*, **10**, 178–186.
- 583 Millennium Ecosystem Assessment. (2005) *Ecosystems and Human Well-Being: Biodiversity*
584 *Synthesis*. Washington D.C.
- 585 Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R. &
586 Simpson, I.C. (2011) *Final Report for LCM2007 - the New UK Land Cover Map*.
- 587 Quin, A., Sarthou, J.-P., Bouyjou, B., Deconchat, M., Lacombe, J.-P. & Monteil, C. (2006)
588 The species-area relationship in the hoverfly (Diptera, Syrphidae) communities of forest
589 fragments in southern France. *Ecography*, **29**, 183–190.
- 590 Quine, C.P. & Watts, K. (2009) Successful de-fragmentation of woodland by planting in an
591 agricultural landscape? An assessment based on landscape indicators. *Journal of*
592 *Environmental Management*, **90**, 251–259.
- 593 R Core Team. (2016) R: A language and environment for statistical computing.
- 594 Reay, S.D. & Norton, D.A. (1999) Assessing the Success of Restoration Plantings in a
595 Temperate New Zealand Forest. *Restoration Ecology*, **7**, 298–308.
- 596 Service, M.W. (1973) Spatial and Temporal Distributions of Aerial Populations of Woodland
597 Tipulids (Diptera). *Journal of Animal Ecology*, **42**, 295–303.

- 598 Sjödin, N.E., Bengtsson, J. & Ekblom, B. (2007) The influence of grazing intensity and
599 landscape composition on the diversity and abundance of flower-visiting insects.
600 *Journal of Applied Ecology*, **45**, 763–772.
- 601 Stubbs, A.E. (1992) *Provisional Atlas of the Long-Palped Craneflies (Diptera: Tipulinae) of*
602 *Great Britain and Ireland*. Biological Records Centre Institute of Terrestrial Ecology,
603 Huntingdon, UK.
- 604 Stubbs, A.E. & Falk, S.J. (2002) *British Hoverflies*. British Entomological and Natural History
605 Society, Reading, UK.
- 606 Stubbs, A.E. & Kramer, J. (2016) Keys to British crane fly families and species,
607 <http://ccw.naturalis.nl/literature.php>
- 608 Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the
609 extinction debt. *Nature*, **371**, 65–66.
- 610 United Nations. (2012) Rio+20 Dialogues, <http://vote.riodialogues.org/>
- 611 Venables, W.N. & Ripley, B.D. (2003) *Modern Applied Statistics With S*, Four. Springer, New
612 York.
- 613 Vesik, P.A., Nolan, R., Thomson, J.R., Dorrough, J.W. & Nally, R. Mac. (2008) Time lags in
614 provision of habitat resources through revegetation. *Biological Conservation*, **141**, 174–
615 186.
- 616 Villard, M.A. & Metzger, J.P. (2014) Beyond the fragmentation debate: A conceptual model
617 to predict when habitat configuration really matters ed S. Saura. *Journal of Applied*
618 *Ecology*, **51**, 309–318.
- 619 Watts, K., Fuentes-Montemayor, E., Macgregor, N.A., Peredo-Alvarez, V., Ferryman, M.,
620 Bellamy, C., Brown, N. & Park, K.J. (2016) Using historical woodland creation to
621 construct a long-term, large-scale natural experiment: The WrEN project. *Ecology and*
622 *Evolution*, **6**, 3012–25.

- 623 Webb, J. (2014) PANTHEON (version 3), www.brc.ac.uk/pantheon
- 624 Whytock, R.C., Fuentes-Montemayor, E., Watts, K., Barbosa de Andrade, P., Whytock, R.,
625 French, P., Macgregor, N.A. & Park, K.J. Bird community response to habitat creation
626 revealed by a large-scale natural experiment. *In review*.
- 627 Wolton, R.J., Bentley, H., Chandler, P.J., Drake, C.M., Kramer, J., Plant, A.R. & Stubbs, A.E.
628 (2014) The diversity of Diptera associated with a British hedge. *Dipterists Digest*, **21**, 1–
629 36.
- 630 Worboys, G.L., Francis, W.L. & Lockwood, M. (2010) *Connectivity Conservation*
631 *Management: A Global Guide*. Earthscan.
- 632 Zuur, A.F. & Ieno, E.N. (2016) A protocol for conducting and presenting results of
633 regression-type analyses ed R. Freckleton. *Methods in Ecology and Evolution*, **7**, 636–
634 645.
- 635

636

637 **Table 1.** Local and landscape-scale environmental variables and their corresponding ecological network component

Variable scale	Environmental variable	Ecological network component
Local	Patch area (ha)	Habitat area
	Patch age	Habitat quality
	Understory cover	
	Litter/ woody debris	
	Tree density	
	Tree DBH standard deviation	
	Tree species richness	
	Angiosperm richness*	
	Angiosperm abundance*	
Landscape	All woodland proportion cover	Habitat amount (proportion of cover within buffer)
	Semi-natural habitat proportion cover	
	Farmland proportion cover	
	Broadleaf woodland connectivity	Habitat connectivity (connectivity within buffer)

638 *Hoverflies only

639

640

641 **Table 2.** Total abundance, mean and range of hoverflies and craneflies in each study region

		Hoverflies		Craneflies	
		England	Scotland	England	Scotland
Woodland species abundance	Total	77	55	585	2208
	Mean (range)	2 (0 - 14)	1 (0 - 7)	18 (2 - 63)	49 (5 - 186)
Woodland species richness	Total	20	15	40	60
	Mean (range)	2 (0 - 9)	1 (0 - 6)	6 (2 - 14)	11 (3 - 21)
Non-woodland abundance	Total	725	441	151	1663
	Mean (range)	24 (0 - 144)	11 (0 - 39)	22 (4 - 65)	86 (16 - 285)
Non-woodland species richness	Total	30	26	10	35
	Mean (range)	6 (0 - 22)	4 (0 - 15)	8 (3 - 16)	17 (6 - 29)

642

643

644

645

646

647

648

649

650

651

652

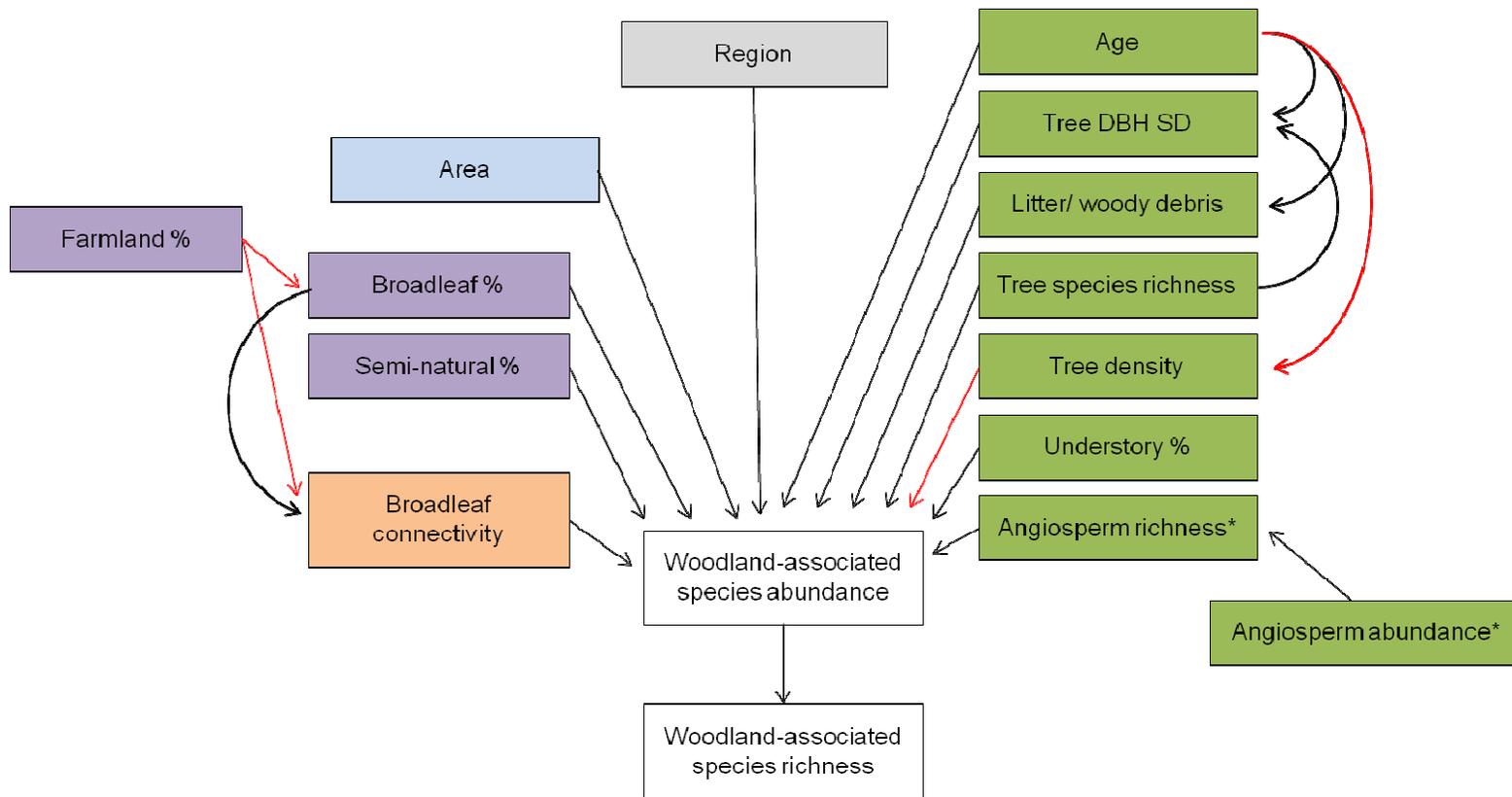
653 **Table 3.** Full piecewise structural equation model (SEM) for woodland-associated hoverfly species richness. The hypothesised beta sign shows
 654 the expected a-priori relationship between pairs of variables. Pairs of variables with correlated errors (i.e. those not considered causative but
 655 which had a significant correlation) are represented as ~. * P< 0.05; ** P<0.01; ***P<0.001.

Response	Predictor	Hypothesised Beta	Observed Beta (SE)
Species richness	Abundance	+	0.48 (0.04)***
Abundance	Understory	+	0.39 (0.14)*
Abundance	Age	+	-0.56 (0.21)*
Abundance	Litter/ woody debris	+	-0.35 (0.15)*
Abundance	Tree DBH SD	+	0.44 (0.2)*
Abundance	Tree density	-	-0.29 (0.17)
Abundance	Tree species richness	+	-0.21 (0.15)
Abundance	Log (area)	+	0.19 (0.17)
Abundance	Region		0.44 (0.48)
Abundance	Proportion cover broadleaf (2000m)	+	-0.19 (0.27)
Abundance	Proportion cover semi-natural (1000m)	+	-0.1 (0.15)
Abundance	Angiosperm richness	+	0.08 (0.15)
Abundance	Interconnectivity broadleaf (2000m)	+	-0.05 (0.27)
Tree density	Age	-	-0.51 (0.07)***
Tree DBH SD	Age	+	4.74 (0.62)***
Tree DBH SD	Tree species richness	+	1.82 (0.62)**
Litter/ woody debris	Age	+	0.2 (0.07)**
Angiosperm richness	Angiosperm abundance	+	0.18 (0.04)***
Interconnectivity broadleaf (2000m)	Proportion cover broadleaf (2000m)	+	0.61 (0.05)***
Interconnectivity broadleaf (2000m)	Proportion cover farmland (2000m)	-	-0.31 (0.05)***
Proportion cover broadleaf (2000m)	Proportion cover farmland (2000m)	-	-0.13 (0.5)
~~Tree density	~~Log (area)	NA	0.21 (0.07)**
~~Tree density	~~Tree DBH SD	NA	-0.31 (0.08)***

656 **Table 4.** Full piecewise structural equation model (SEM) for woodland-associated crane-fly species richness. The hypothesised beta sign shows
 657 the expected a-priori relationship between pairs of variables. Pairs of variables with correlated errors (i.e. those not considered causative but
 658 which had a significant correlation) are represented as ~. * P< 0.05; ** P<0.01; ***P<0.001.

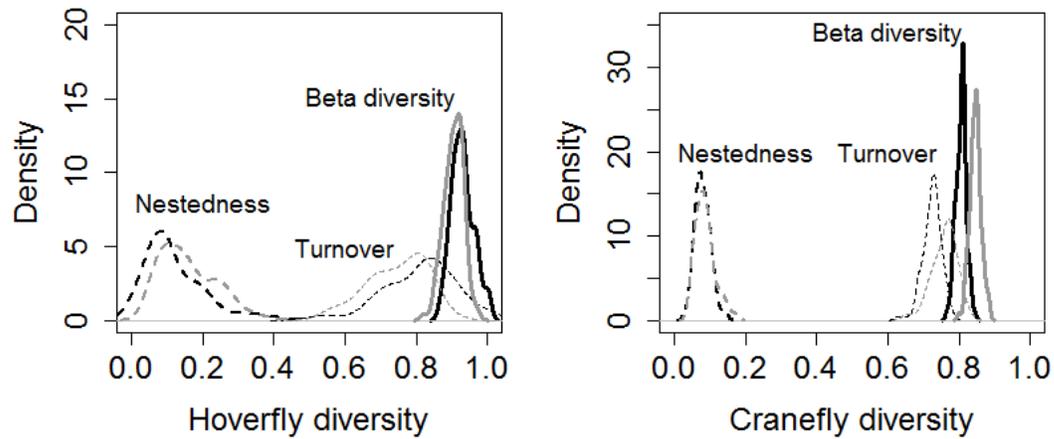
Response	Predictor	Hypothesised Beta	Observed Beta (SE)
Species richness	Crane-fly abundance	+	0.68 (0.08)***
Species richness	Region	Missing path	0.38 (0.17)*
Abundance	Region	+	1.31 (0.3)***
Abundance	Age	+	-0.24 (0.12)*
Abundance	Tree DBH SD	+	0.15 (0.12)
Abundance	Litter/ woody debris	-	0.1 (0.1)
Abundance	Understory	+	0.1 (0.1)
Abundance	Log (area)	+	0.11 (0.12)
Abundance	Tree density		-0.09 (0.11)
Abundance	Proportion cover broadleaf (500m)	+	-0.12 (0.18)
Abundance	Proportion cover semi-natural (2000m)	+	-0.05 (0.1)
Abundance	Interconnectivity broadleaf (500m)	+	0.09 (0.18)
Tree density	Age	-	-0.51 (0.07)***
Tree DBH SD	Age	+	0.64 (0.08)***
Tree DBH SD	Tree species richness	+	0.25 (0.08)**
Litter/ woody debris	Age	+	0.33 (0.11)**
Interconnectivity broadleaf (500m)	Proportion cover broadleaf (500m)	+	0.86 (0.06)***
Interconnectivity broadleaf (500m)	Proportion cover farmland (500m)	+	0.08 (0.06)
Proportion cover broadleaf (500m)	Proportion cover farmland (500m)	-	0.03 (0.5)
~~Tree density	~~Log (area)	NA	0.21 (0.07)**
~~Tree density	~~Tree DBH SD	NA	-0.31 (0.08)***

659



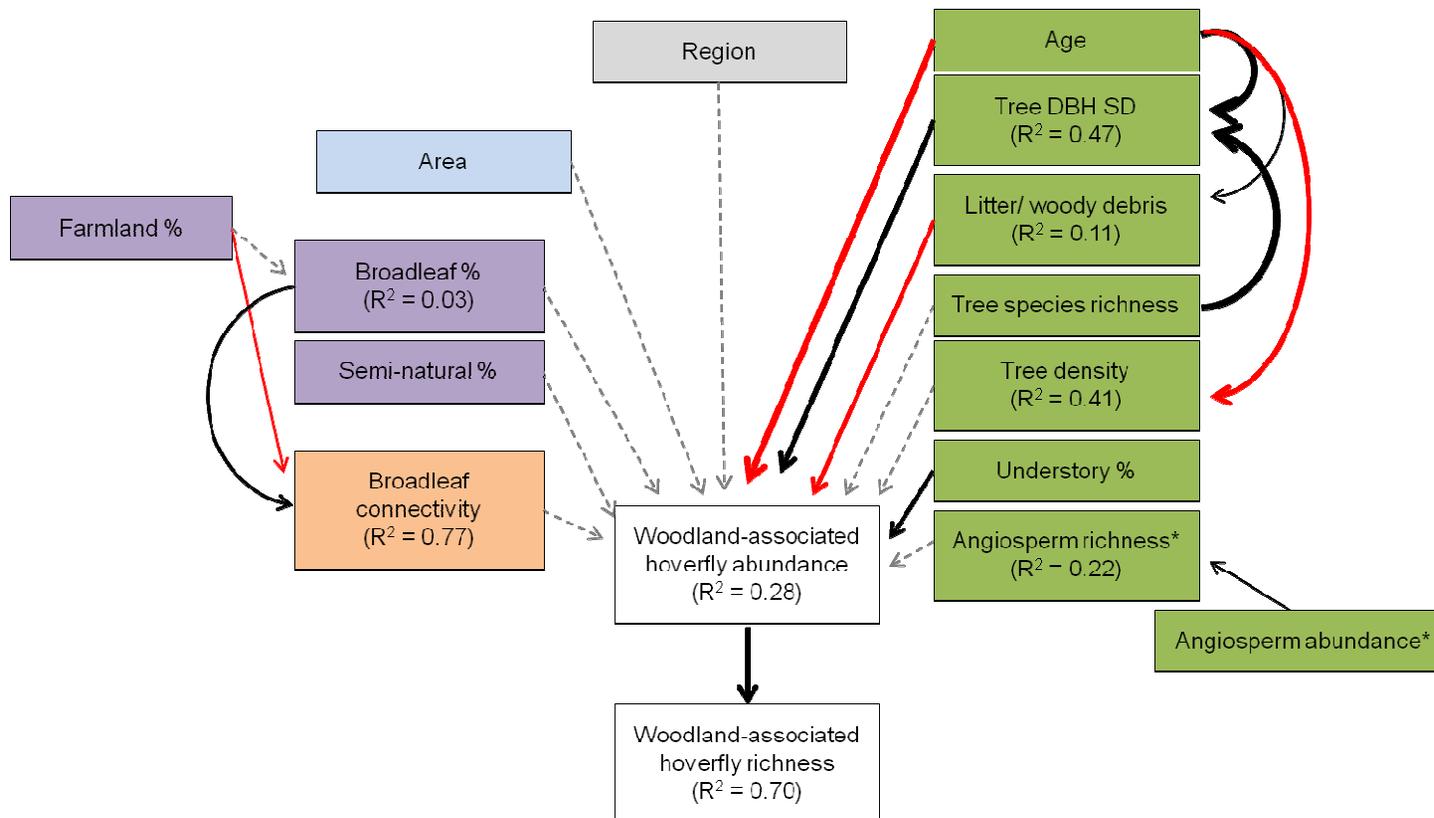
660

661 **Figure 1.** Global conceptual model used to guide SEM construction illustrating hypothesised direct and indirect relationships between response
 662 variables (woodland-associated hoverfly/ crane fly abundance, woodland-associated hoverfly/ crane fly species richness; white boxes)
 663 and metrics of patch geometry (blue box), vegetation structure (green boxes), landscape composition (purple boxes), landscape configuration
 664 (orange box) and study region (grey box). Black arrows indicate hypothesised positive effects and red arrows negative effects.



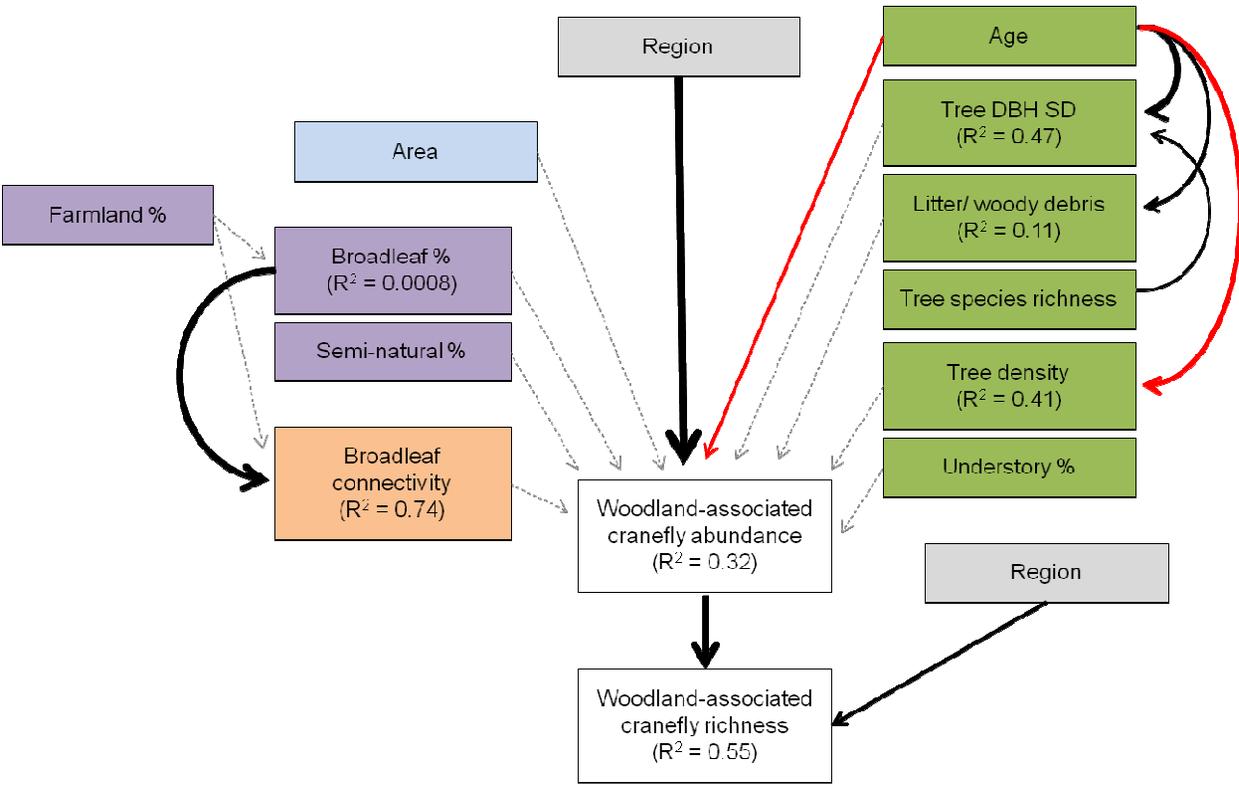
665

666 **Figure 2.** Multiple site dissimilarity values for nestedness (subsets of species communities
 667 between sites), turnover (replacement of species between sites) and beta diversity
 668 (differences in species between sites) of woodland-associated hoverfly and crane fly species
 669 in England (grey) and Scotland (black). Diversity values are displayed along the x-axis for
 670 each species group and the number of sites from 20 subsets of sites resampled 100 times
 671 are displayed along the y-axis.



672

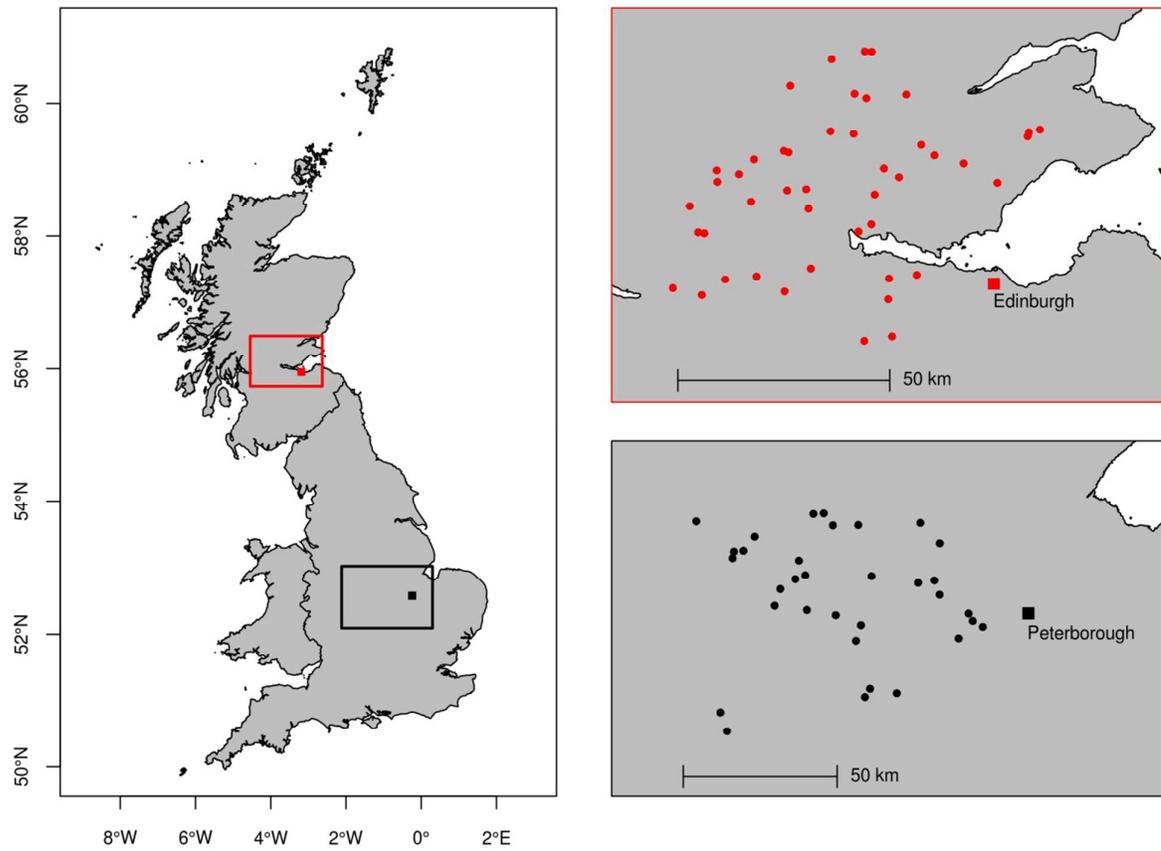
673 **Figure 3.** Individual SEM path diagrams for woodland-associated hoverfly species richness/ abundance. Arrows show observed positive (black)
 674 and negative (red) relationships between response variables (relative abundance, species richness; white boxes) and metrics of patch
 675 geometry (blue box), vegetation structure (green boxes), landscape composition (purple boxes), landscape configuration (orange box) and
 676 study region (grey box). Dashed grey arrows indicate non-significant relationships that were included in the a-priori model. Arrow thickness is
 677 proportional to its effect size and coefficients of determination (R^2) are shown for all response variables.



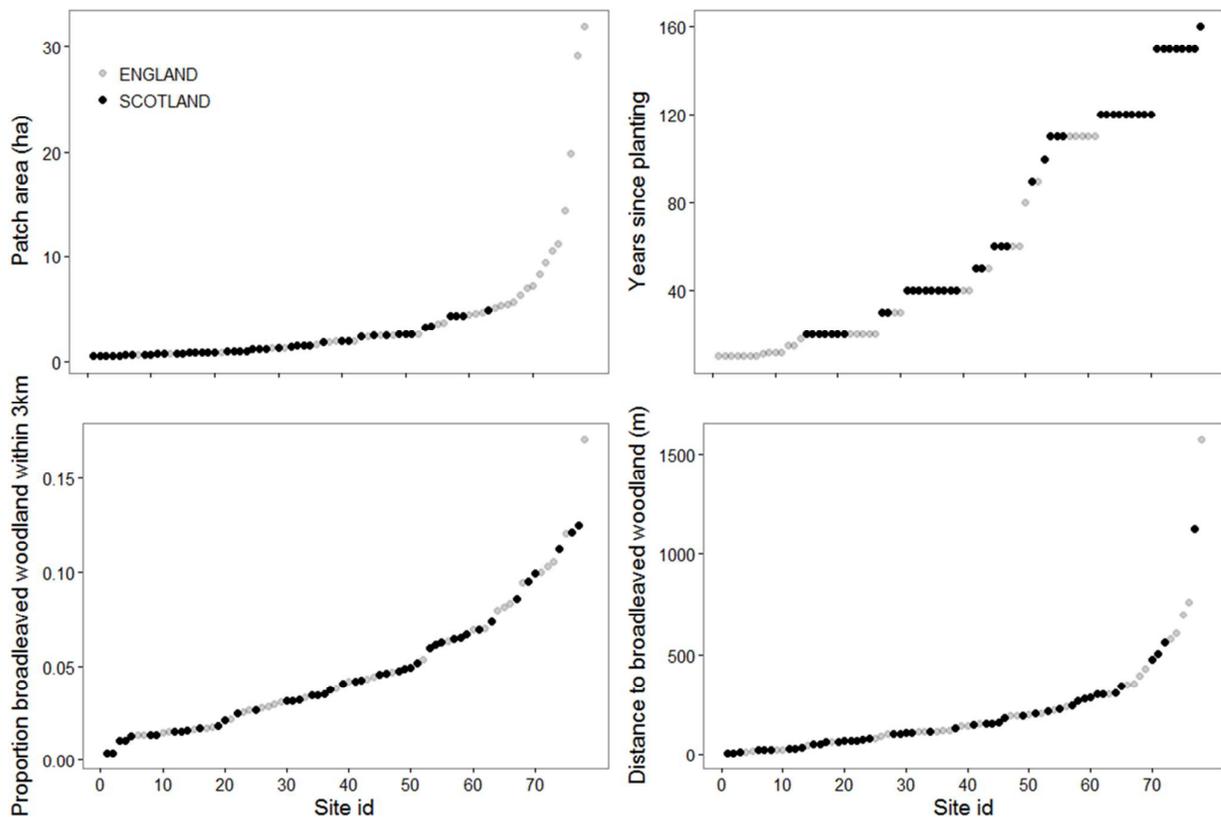
678

679 **Figure 4.** Individual SEM path diagrams for woodland-associated crane fly species richness/ abundance. Arrows show observed positive (black)
 680 and negative (red) relationships between response variables (relative abundance, species richness; white boxes) and metrics of patch
 681 geometry (blue box), vegetation structure (green boxes), landscape composition (purple boxes), landscape configuration (orange box) and
 682 study region (grey box). Dashed grey arrows indicate non-significant relationships that were included in the a-priori model. Arrow thickness is
 683 proportional to its effect size and coefficients of determination (R^2) are shown for all response variables.

Appendix S1. Map of study sites located across central England and central Scotland in the UK



Appendix S2. Distribution of study sites across the four site selection variables in England and Scotland



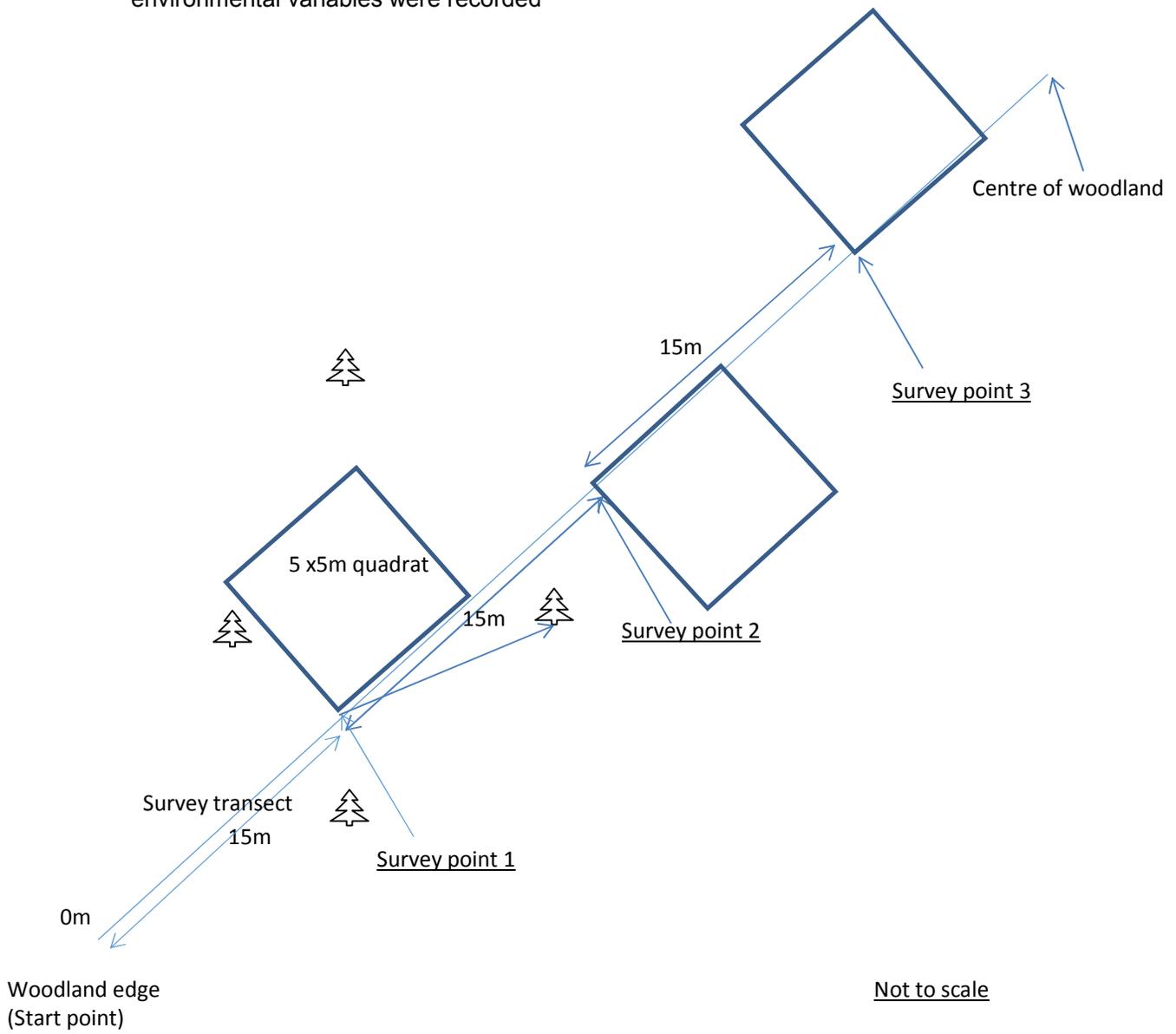
Appendix S3. Tree, vegetation and deadwood cover survey method

Surveys were conducted in alternate positions (survey points) along a transect extending from the edge of the woodland to the centre of the woodland (Figure 1). Transects varied in length depending on the woodland size. A minimum of five survey points per transect starting at 15m from the edge were used in the smallest woodland and this number increased successively in larger woods. Survey points were placed on alternate sides of the survey transect. The transect was placed through habitat which was representative of the woodland.

Survey points were established every 15m along the survey transect to serve as the corner of a 5 m x 5 m quadrat within which understory (trees and shrubs < 7 cm DBH and/or \leq 3 m in height) percentage cover was assessed using the Domin scale and the presence of litter/woody debris (CWD) on the ground was quantified using an indicator scale of 1 – 3: 1 = leaf litter & twigs (\leq 1 cm), 2 = large branches (<10 cm) and 3 = coarse woody debris (\geq 10 cm diameter) (see Appendix S3 in Supporting Information for more detailed descriptions).

At each survey point, the point-centred quarter method was used to select the four closest trees (\geq 7 cm DBH). The distance from the survey point to each tree was measured, the tree species was recorded, and the DBH (Diameter at Breast Height 1.3m from the ground) of each tree was measured.

Figure 1. Graphical representation of the survey transect and positions of quadrats where environmental variables were recorded



Appendix S4. Details of calculations of inter-patch connectivity indices (modified from Watts & Handley 2010).

The calculation of inter-patch connectivity was based on the connectivity measure within the incidence function model (IFM) (Hanski 1994; Moilanen & Hanski 2001; Moilanen & Nieminen 2002):

$$S_i = \sum_{j \neq i} A_j e^{-\alpha D_{ij}}$$

Where S_i is the sum of the contribution from all surrounding woodland patches (j) to the target woodland patch (i). A_j is the area of a surrounding woodland patch j , as a surrogate for population size, and e is the natural exponent. A value α describes the rate at which individuals move between patches, based on a percentage of dispersers reaching a specific distance (i.e. 250, 500, 1000 and 2000 m; see Methods section in main manuscript for a justification of spatial scales used). D_{ij} is the Euclidean distance between the target woodland patch i and the surrounding woodland patches j . Therefore, the contribution from patch j to patch i will decline along a negative exponential dispersal function.

Literature cited:

- Hanski, I. (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**, 151-162.
- Moilanen, A. & Hanski, I. (2001) On the use of connectivity measures in spatial ecology. *Oikos*, **95**, 147-151.
- Moilanen, A. & Nieminen, M. (2002) Simple connectivity measures in spatial ecology. *Ecology*, **83**, 1131-1145.
- Watts, K. & Handley, P. (2010) Developing a functional connectivity indicator to detect change in fragmented landscapes. *Ecological Indicators*, **10**, 552–557.

Appendix S5. Correlation matrix of local-scale habitat variables included in the SEM models. Not all variables were included in each model; please refer to the main paper for an explanation of which variables were included in each model.

	Patch age	Area	Tree species richness	Tree density	Tree DBH SD	Understory cover	CWD	Angiosperm abundance	Angiosperm richness
Patch age		-0.29	-0.01	-0.51	0.64	-0.07	0.33	0.35	0.23
Area	-0.29		-0.06	0.43	-0.35	0.25	-0.35	-0.30	-0.24
Tree species richness	-0.01	-0.06		-0.14	0.24	0.00	0.12	0.04	0.06
Tree density	-0.51	0.43	-0.14		-0.51	0.07	-0.30	-0.26	-0.28
Tree DBH SD	0.64	-0.35	0.24	-0.51		-0.02	0.39	0.33	0.26
Understory cover	-0.07	0.25	0.00	0.07	-0.02		-0.15	-0.46	-0.25
CWD	0.33	-0.35	0.12	-0.30	0.39	-0.15		0.26	0.26
Angiosperm abundance	0.35	-0.30	0.04	-0.26	0.33	-0.46	0.26		0.45
Angiosperm richness	0.23	-0.24	0.06	-0.28	0.26	-0.25	0.26	0.45	

Appendix S6. SEM hypotheses, global conceptual model and results for non-woodland associated hoverfly and crane fly species

Hypotheses

The effect of local and landscape-scale variables on non-woodland species abundance and richness was tested using piecewise structural equation models (SEM) in the piecewiseSEM package (Lefcheck, 2015). A global conceptual model based on underlying theory and evidence was used to guide the construction of hypotheses for species abundance and species richness (Figure 1). Preliminary analysis showed that abundance and species richness were highly correlated (non-woodland hoverflies: Pearson's $r = 0.75$, $P < 0.001$; non-woodland crane flies: Pearson's $r = 0.61$, $P < 0.001$), suggesting that both response variables were likely to exhibit similar relationships with environmental variables. Species richness is known to increase with abundance (Gotelli and Colwell, 2001) and we hypothesised that local and landscape-scale variables indirectly affect species richness through direct effects on abundance. Species abundance is directly linked to the area of suitable habitat (species-area relationship: MacArthur and Wilson, 1967; McGuinness, 1984) so we expected non-woodland species to show a negative relationship with woodland patch size. Angiosperms (flowering plants) are an important resource for adult hoverflies; species which flower at different times of the year increase resource provision of nectar and pollen and some hoverfly species show preferences for particular plant species. Therefore the species richness and abundance of angiosperms were expected to have a positive effect on non-woodland associated hoverflies. However, we expected angiosperm richness and abundance to be highly correlated and included this relationship in the model by testing for an indirect effect of angiosperm abundance mediated through a direct effect of angiosperm richness. We expected a negative relationship of patch age, understory cover and tree density with non-woodland species as they are adapted to open habitats with lower vegetation density and complexity. In turn, tree density was expected to be negatively affected by patch age, as older woodlands have trees that have died, creating gaps where they have fallen.

Broadleaf cover and connectivity were expected to have indirect negative relationships with non-woodland species through the reduction in cover of agricultural habitats. Both semi-natural habitat and agricultural land cover were expected to directly positively affect non-woodland species by providing prey for hoverfly larvae and nectar and pollen for adult hoverflies (Meyer et al., 2009). Non-woodland crane flies were also expected to be positively affected by these two habitat types as they prefer grassland and agricultural habitats where the larvae feed on the roots of plants and crops (Stubbs, 1992).

Results

The initial model of hypothesised direct and indirect effects of local and landscape-scale variables on non-woodland hoverflies was not significantly different from the observed data (Fisher C = 84.43, df = 72, P = 0.15). No additional missing paths were identified, although tree density was correlated with log area (Table 1). None of the landscape-scale variables directly or indirectly influenced non-woodland hoverfly abundance and species richness (Figure 2). There was a direct negative effect of tree density on hoverfly abundance, which was equivalent to a 3.5% reduction in abundance per 10% increase in density. In turn, tree density was negative affected by patch age (Table 1). Therefore, patch age could help to mitigate the negative effects of tree density and make woodlands more open and accessible to non-woodland hoverfly species.

The model specified for non-woodland craneflies was not significantly different from the observed data (Fisher C = 58.13, df = 42, P = 0.05) after a missing path of a direct effect of region on cranefly species richness and the correlation between tree density and log area were incorporated into the model (Table 2). Cranefly abundance and species richness was strongly influenced by region, with higher numbers in Scotland than England. The size of woodland patches had a negative influence on non-woodland cranefly abundance. The effect of this variable was equivalent to a 4.2% reduction in abundance per 10% increase in patch size. The amount of farmland within a 2000m radius had a negative effect, which was equivalent to a 3.2% decrease in abundance per 10% increase in the amount of farmland.

Table 1. Full piecewise structural equation model (SEM) for non-woodland hoverfly species richness. The hypothesised beta sign shows the expected a-priori relationship between pairs of variables. Pairs of variables with correlated errors (i.e. those not considered causative but which had a significant correlation) are represented as $\sim\sim$. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Response	Predictor	Hypothesised Beta	Observed Beta (SE)
Species richness	Abundance	+	0.75 (0.08)***
Abundance	Tree density	-	-0.35 (0.14)*
Abundance	Angiosperm richness	+	0.22 (0.12)
Abundance	Age	-	-0.22 (0.14)
Abundance	Understory cover	-	0.17 (0.13)
Abundance	Proportion cover semi-natural (1000m)	+	-0.17 (0.15)
Abundance	Log (area)	-	0.16 (0.14)
Abundance	Proportion cover farmland (2000m)	+	0.17 (0.18)
Abundance	Region	-	-0.18 (0.42)
Tree density	Age	-	-0.51 (0.07)***
Angiosperm richness	Angiosperm abundance	+	0.18 (0.04)***
Proportion cover farmland (2000m)	Interconnectivity broadleaf (2000m)	-	-0.83 (0.46)
Proportion cover farmland (2000m)	Proportion cover broadleaf (2000m)	-	0.5 (0.44)
$\sim\sim$ Tree density	$\sim\sim$ Log (area)	NA	-0.21 (0.07)**

Table 2. Full piecewise structural equation model (SEM) for non-woodland crane-fly species richness. The hypothesised beta sign shows the expected a-priori relationship between pairs of variables. Pairs of variables with correlated errors (i.e. those not considered causative but which had a significant correlation) are represented as $\sim\sim$. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Response	Predictor	Hypothesised Beta	Observed Beta (SE)
Species richness	Region	Missing path	1.18 (0.17)***
Species richness	Abundance	+	0.01 (0)***
Abundance	Region		1.89 (0.38)***
Abundance	Log (area)	-	-0.42 (0.14)**
Abundance	Proportion cover farmland (2000m)	+	-0.32 (0.14)*
Abundance	Proportion cover semi-natural (250m)	+	0.11 (0.11)
Abundance	Understory	-	-0.11 (0.12)
Abundance	Tree density	-	-0.04 (0.14)
Abundance	Age	-	0 (0.12)
Tree density	Age	-	-0.51 (0.07)***
Proportion cover farmland (2000m)	Interconnectivity broadleaf (2000m)	-	-0.83 (0.46)
Proportion cover farmland (2000m)	Proportion cover broadleaf (2000m)	-	0.5 (0.44)
$\sim\sim$ Tree density	$\sim\sim$ Log (area)	NA	-0.21 (0.07)**

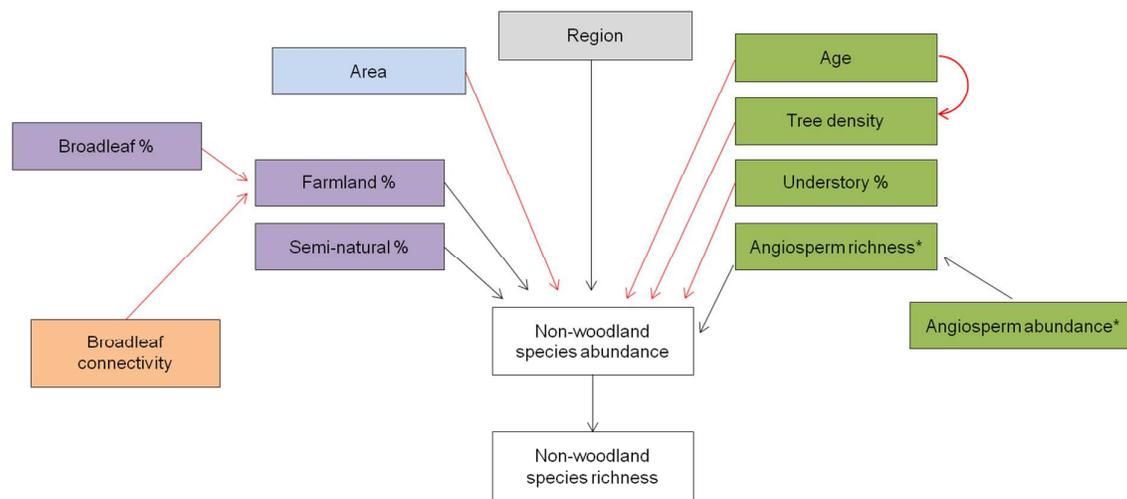


Figure 1. Global conceptual model used to guide SEM construction illustrating hypothesised direct and indirect relationships between response variables (non-woodland hoverfly/cranefly abundance, non-woodland hoverfly/cranefly species richness; white boxes) and metrics of patch geometry (blue box), vegetation structure (green boxes), landscape composition (purple boxes) and landscape configuration (orange box). Black arrows indicate hypothesised positive effects and red arrows negative effects.

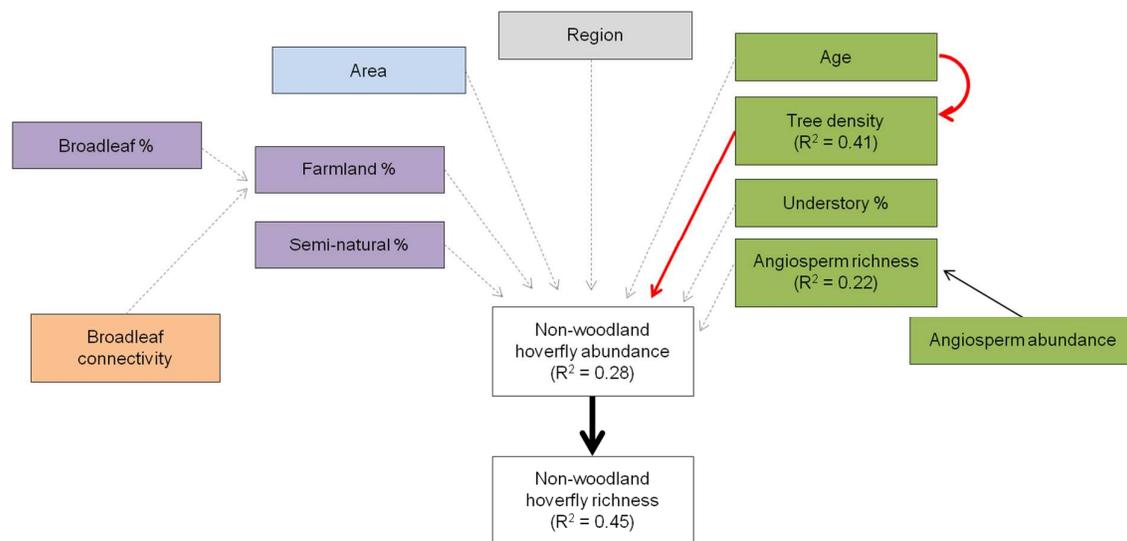


Figure 2. Individual SEM path diagrams for non-woodland hoverfly species richness/abundance. Arrows show observed positive (black) and negative (red) relationships between response variables (relative abundance, species richness; white boxes) and metrics of patch geometry (blue box), vegetation structure (green boxes), landscape composition (purple boxes), landscape configuration (orange box) and study region (grey box). Dashed grey arrows indicate non-significant relationships that were included in the a-priori model. Arrow

thickness is proportional to its effect size and coefficients of determination (R^2) are shown for all response variables.

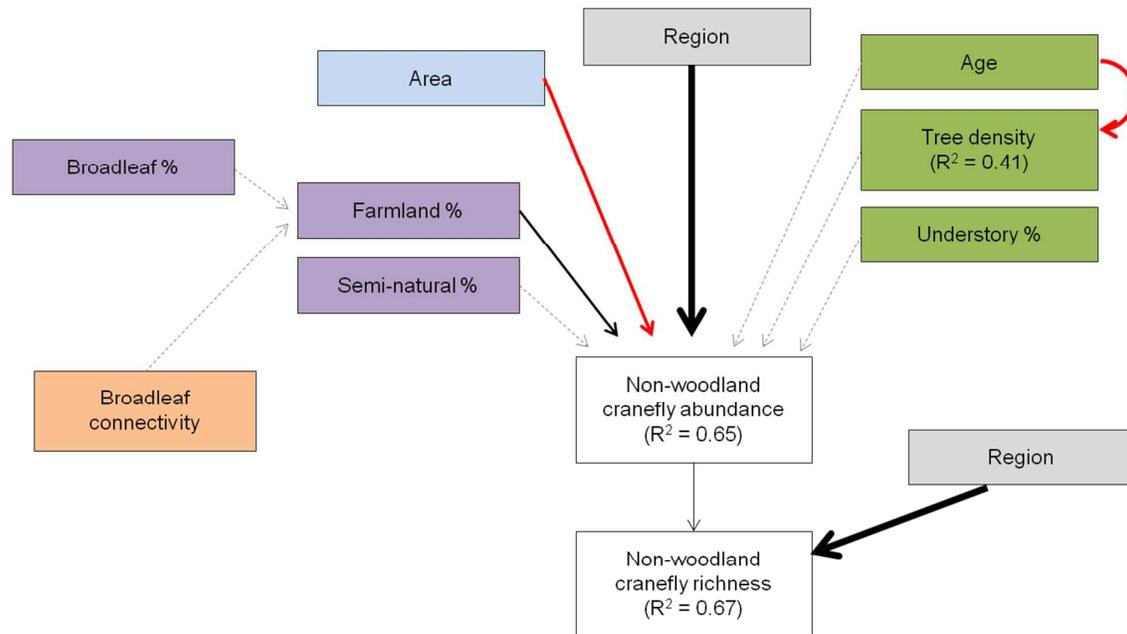


Figure 3. Individual SEM path diagrams for non-woodland cranefly species richness/abundance. Arrows show observed positive (black) and negative (red) relationships between response variables (relative abundance, species richness; white boxes) and metrics of patch geometry (blue box), vegetation structure (green boxes), landscape composition (purple boxes), landscape configuration (orange box) and study region (grey box). Dashed grey arrows indicate non-significant relationships that were included in the a-priori model. Arrow thickness is proportional to its effect size and coefficients of determination (R^2) are shown for all response variables.

References

- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
- Lefcheck, J.S., 2015. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573–579.
- MacArthur, R.H., Wilson, E.O., 1967. *The theory of island biogeography*. Princeton University Press, New Jersey.
- McGuinness, K.A., 1984. Species-area curves. *Biol. Rev.* 59, 423–440. doi:10.1111/j.1469-185X.1984.tb00711.x

- Meyer, B., Jauker, F., Steffan-Dewenter, I., 2009. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic Appl. Ecol.* 10, 178–186. doi:10.1016/j.baae.2008.01.001
- Stubbs, A.E., 1992. Provisional atlas of the long-palped crane-flies (Diptera: Tipulinae) of Great Britain and Ireland. Biological Records Centre Institute of Terrestrial Ecology, Huntingdon, UK.