

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

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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.

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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](http://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, crane flies (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 crane fly 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 crane flies, 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 crane fly  
134 diversity, but also that woodland specialist crane flies 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 crane flies.

138 In this study, hoverflies and crane flies 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 crane fly 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 crane fly 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 crane flies would be more influenced by woodland connectivity when compared to

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

## Methods

### *Site selection*

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

### *Insect sampling*

One Malaise net trap was placed in a suitable location as close to the centre of the woodland as possible. A suitable location was defined as a clearing which received sun exposure for the majority of the day. The collecting bottle was oriented south and filled with 100% ethanol to kill and preserve the insects. The trap was left in place for a sampling period of seven days each in June, July and August. In each week of sampling between 19 and 23 sites were sampled at the same time and the traps were rotated around the sites over a three week period. This was repeated three times, totalling 21 days of sampling at each site across the summer period. A second trap was also placed at least 100m from the first Malaise trap in each site for one sampling period of seven days to capture variation across the site. The second trap was located in the same environmental conditions as the first trap, i.e. same amount of vegetation and canopy cover. Hoverflies and crane flies were extracted from the samples and identified to species level using Stubbs & Falk (2002) and Stubbs & 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 ( $\leq 1$  cm), 2 = large branches ( $< 10$  cm) and 3 = coarse woody  
 196 debris ( $\geq 10$  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).

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

### *Data analysis*

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

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

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

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

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

Preliminary analysis showed that abundance and species richness were highly correlated (woodland-associated hoverflies: Pearson's  $r = 0.96$ ,  $P < 0.001$ ; woodland-associated crane flies: Pearson's  $r = 0.76$ ,  $P < 0.001$ ), suggesting that both response variables were likely to exhibit similar relationships with environmental variables. Species richness is known to increase with abundance (Gotelli & Colwell 2001) and we hypothesised that local and landscape-scale variables indirectly affect species richness through direct effects on abundance. Species abundance typically increases with the area of suitable habitat (species-area relationship: MacArthur and Wilson, 1967; McGuinness, 1984) so we expected woodland species richness to increase with woodland patch size. We expected patch age to directly positively affect the abundance of woodland-associated species 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  $\leq 7$  cm DBH and/or  $\leq 3$  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.

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

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

## Results

### *Value of woodland creation sites*

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

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

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

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

#### *Effects of local and landscape scale variables*

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

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

**Discussion**

*Value of woodland creation sites*

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

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

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

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

#### *Relative and combined effects of ecological network variables*

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

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

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

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

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

## **Synthesis and applications**

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

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

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

**Authors' Contributions**

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

**Data accessibility**

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

## 474 **Acknowledgements**

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634 645.
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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

**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)

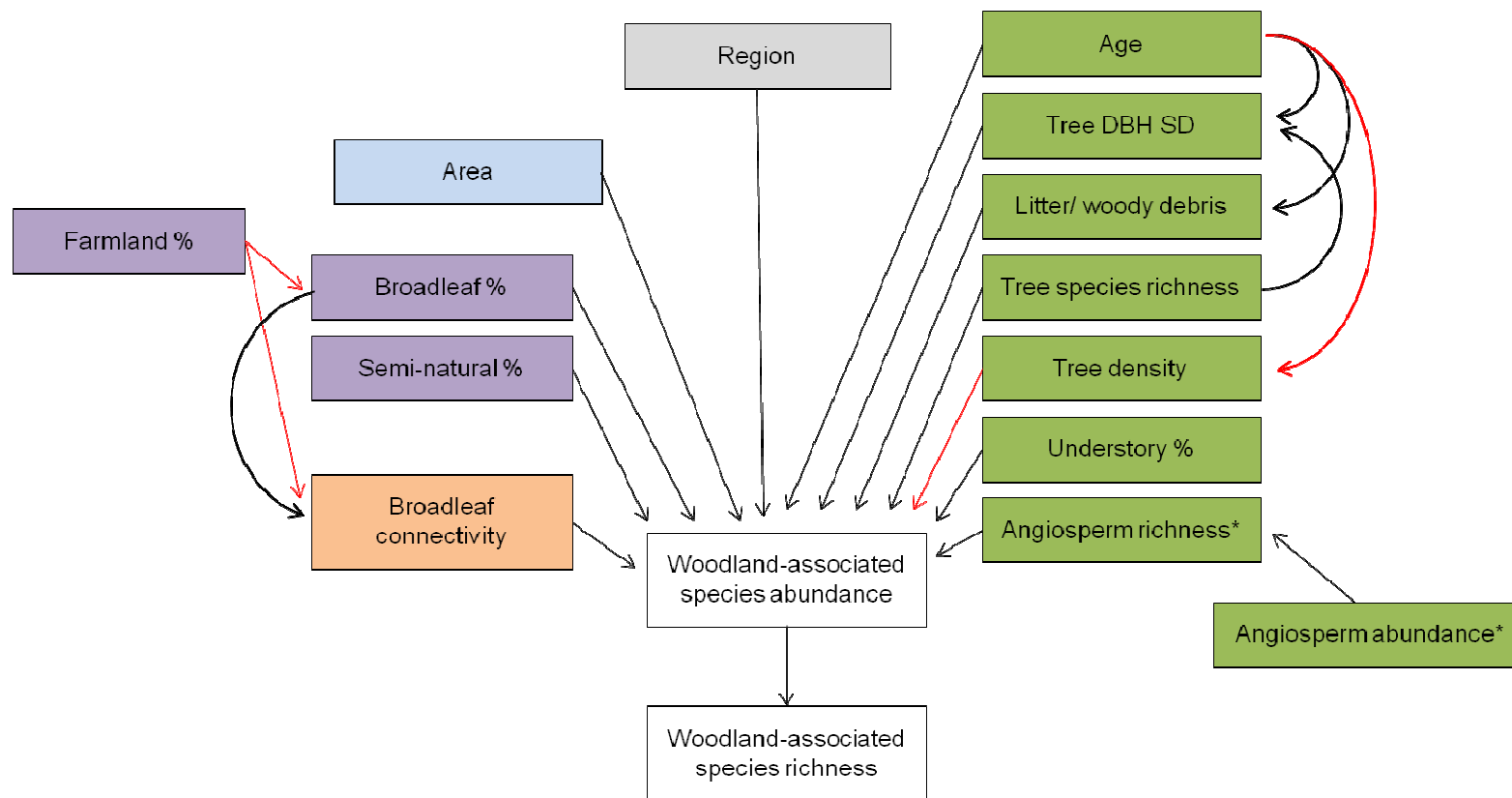
653 **Table 3.** Full piecewise structural equation model (SEM) for woodland-associated hoverfly species richness. The hypothesised beta sign shows  
 654 the expected a-priori relationship between pairs of variables. Pairs of variables with correlated errors (i.e. those not considered causative but  
 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.

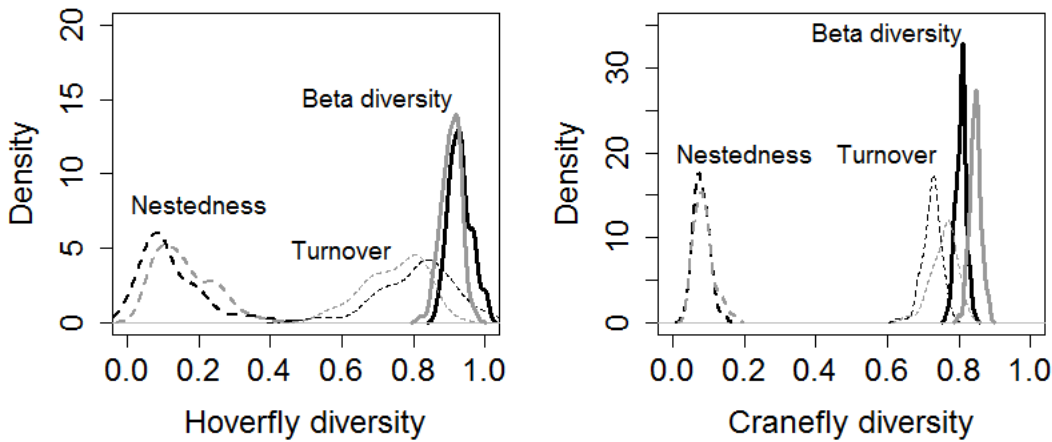
Response	Predictor	Hypothesised Beta	Observed Beta (SE)
Species richness	Crane-fly abundance	+	0.68 (0.08)***
Species richness	Region	Missing path	0.38 (0.17)*
Abundance	Region	+	1.31 (0.3)***
Abundance	Age	+	-0.24 (0.12)*
Abundance	Tree DBH SD	+	0.15 (0.12)
Abundance	Litter/ woody debris	-	0.1 (0.1)
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

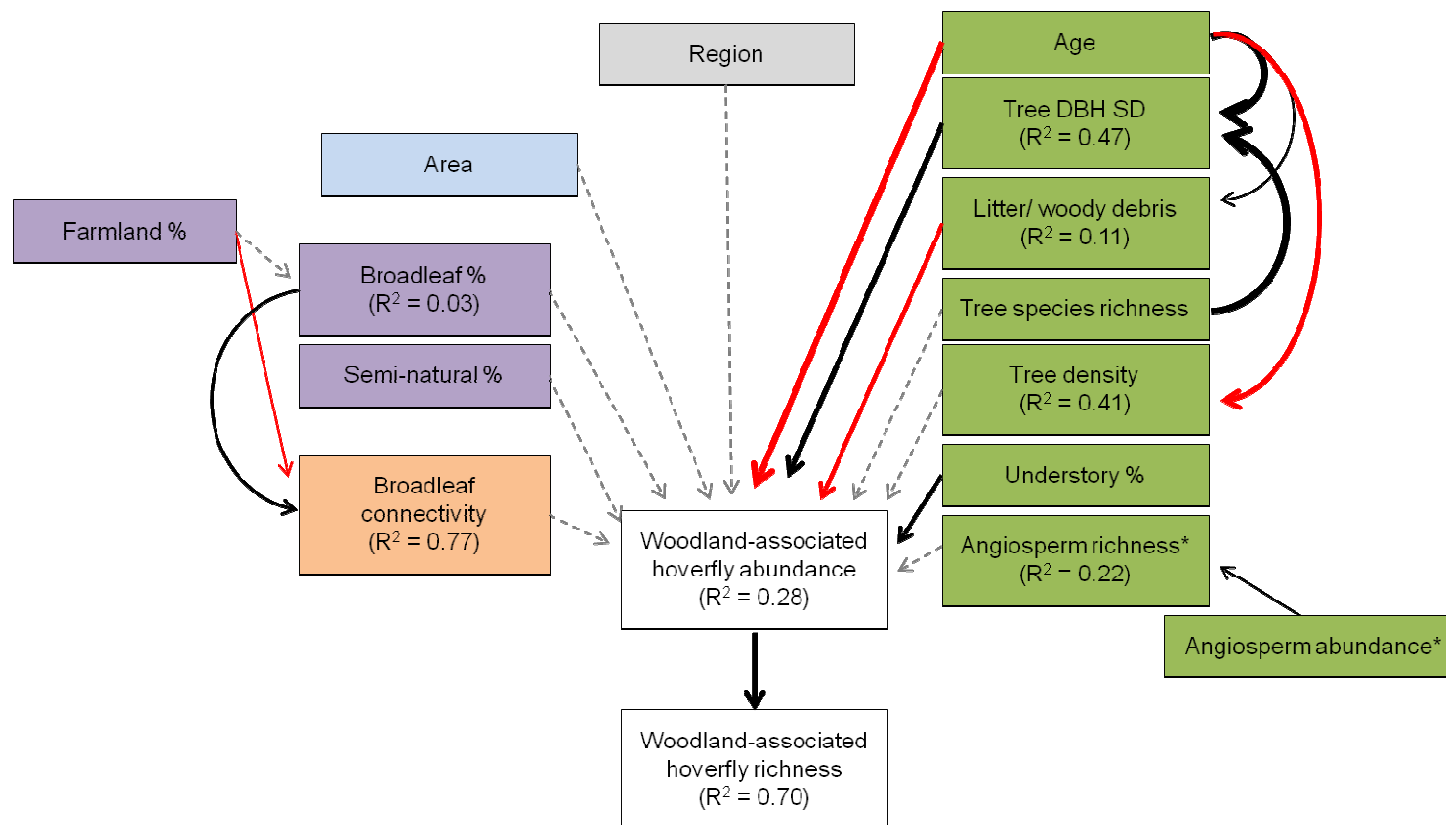


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661 **Figure 1.** Global conceptual model used to guide SEM construction illustrating hypothesised direct and indirect relationships between response  
 662 variables (woodland-associated hoverfly/ crane fly abundance, woodland-associated hoverfly/ 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.

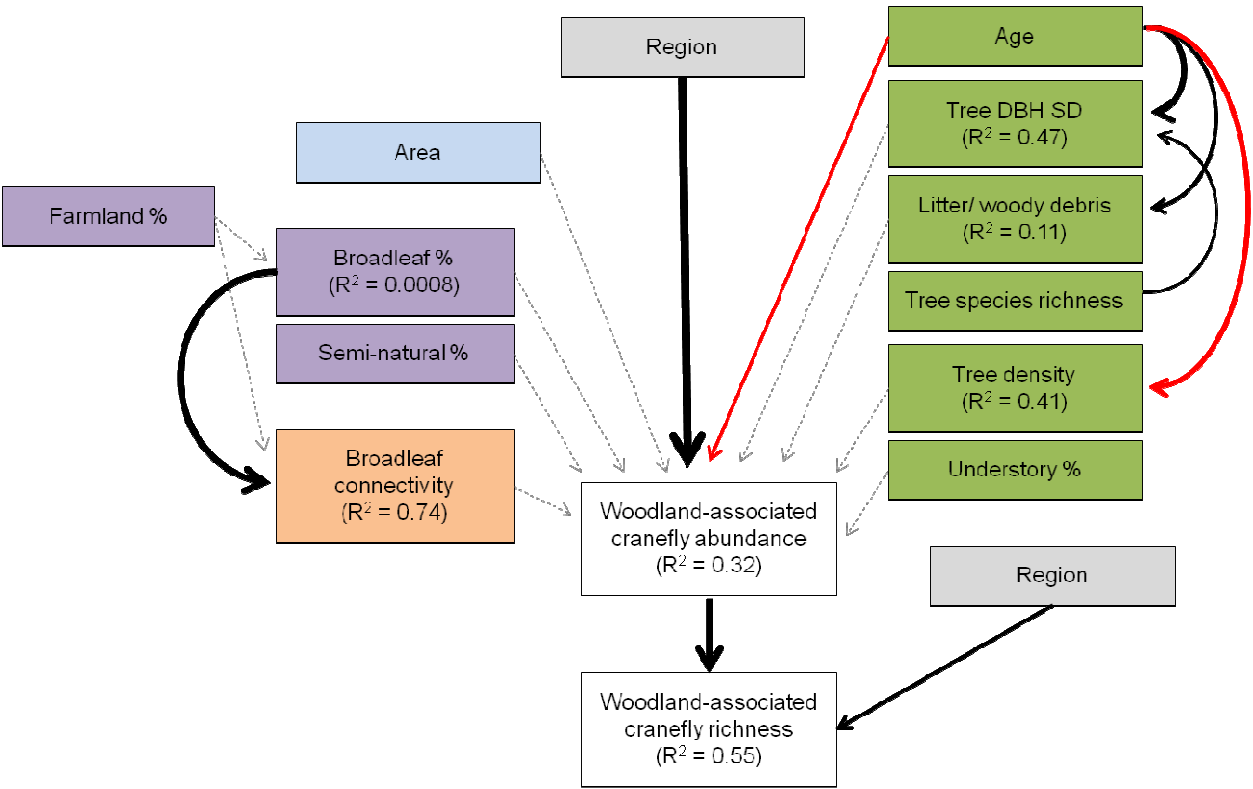


**Figure 2.** Multiple site dissimilarity values for nestedness (subsets of species communities between sites), turnover (replacement of species between sites) and beta diversity (differences in species between sites) of woodland-associated hoverfly and crane fly species in England (grey) and Scotland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



672

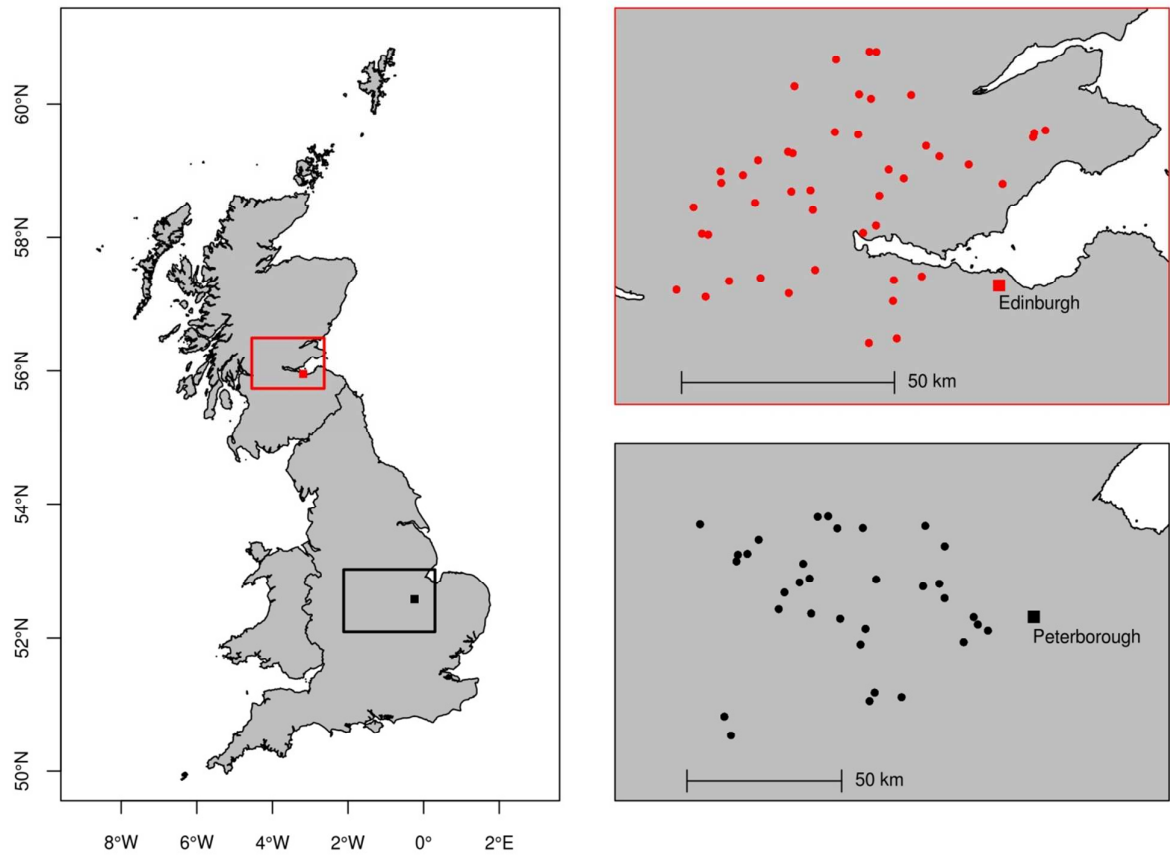
673 **Figure 3.** Individual SEM path diagrams for woodland-associated hoverfly species richness/ abundance. Arrows show observed positive (black)  
 674 and negative (red) relationships between response variables (relative abundance, species richness; white boxes) and metrics of patch  
 675 geometry (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.



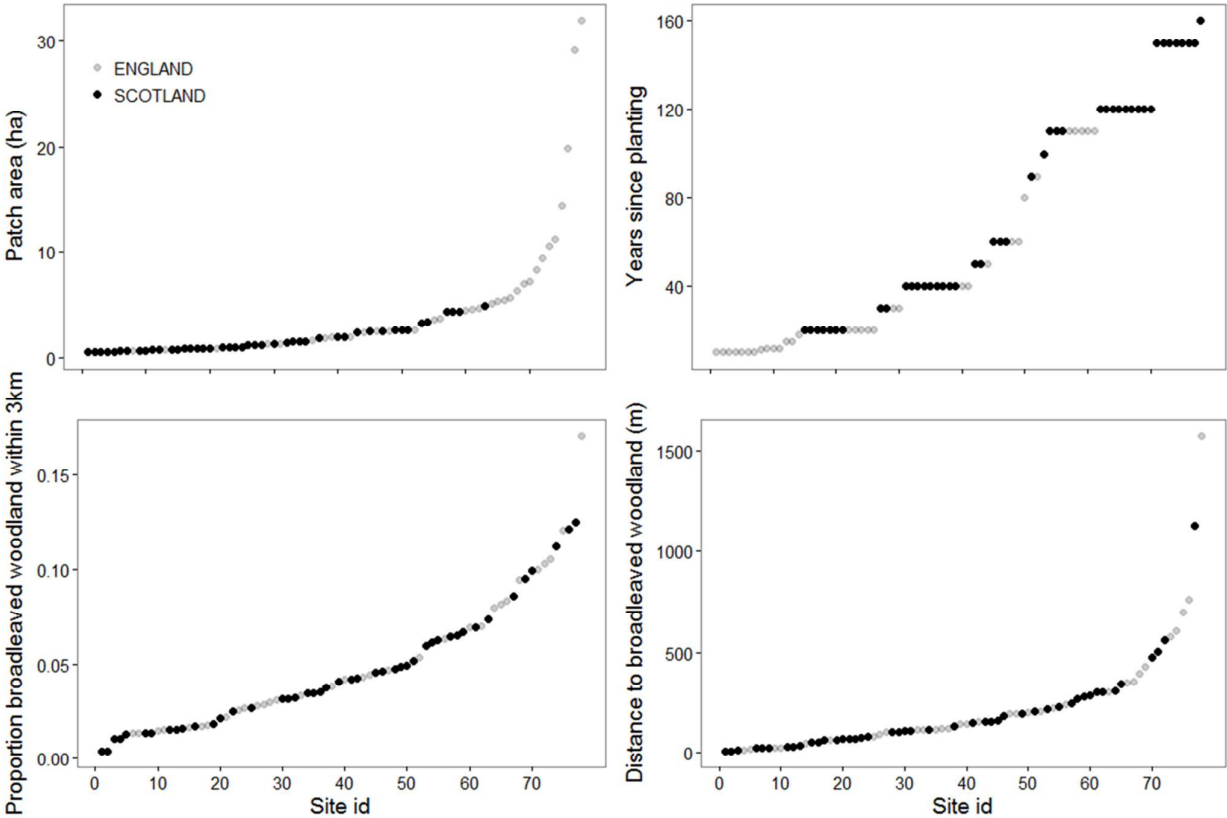
678

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



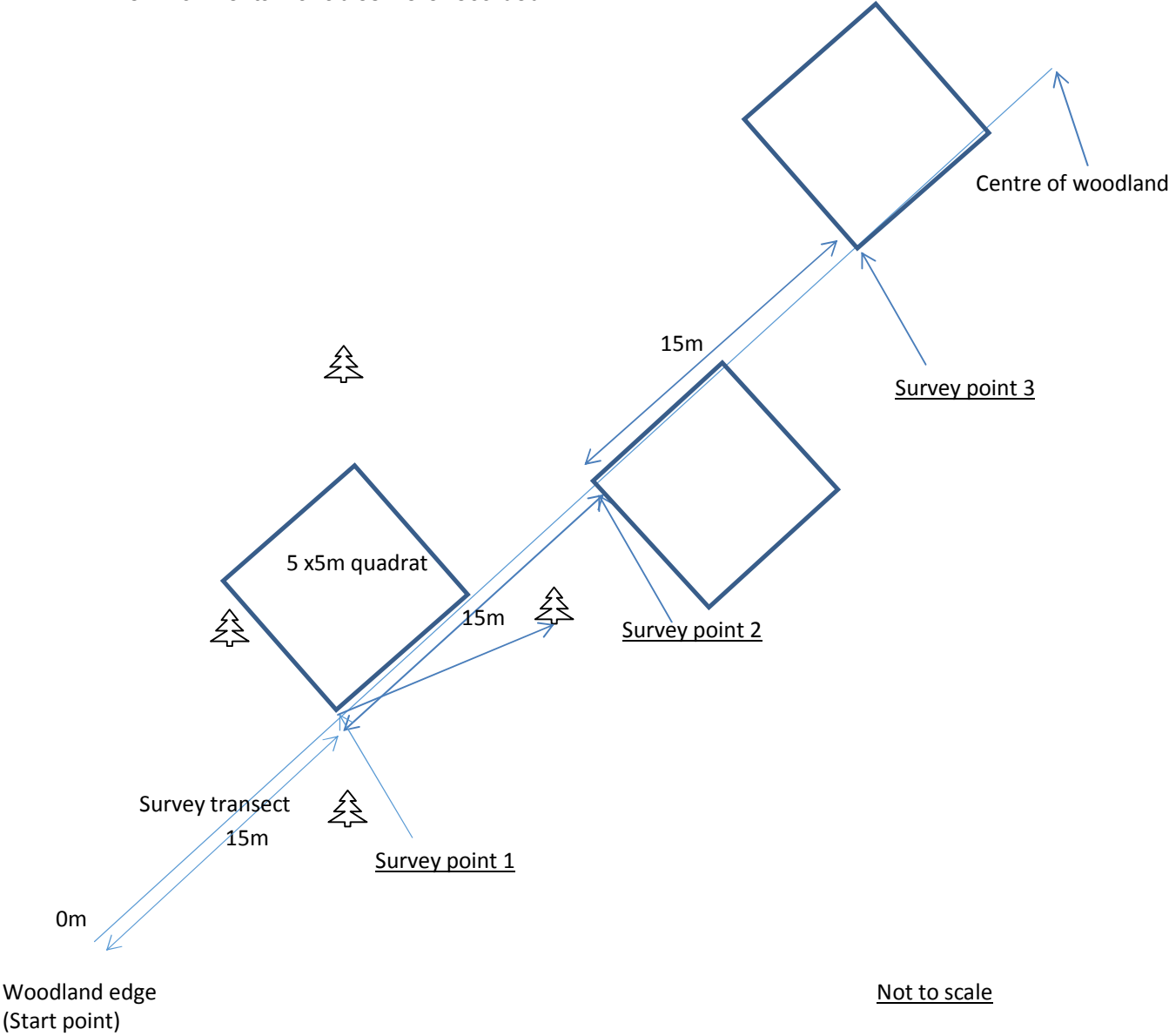
**Appendix S3. Tree, vegetation and deadwood cover survey method**

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  $\alpha$  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:**

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**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 crane flies 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 crane fly species richness and the correlation between tree density and log area were incorporated into the model (Table 2). Crane fly 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 crane fly 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 ~~. \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\* $P < 0.001$ .

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)
~~Tree density	~~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 ~. \* 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)
~~Tree density	~~Log (area)	NA	-0.21 (0.07)**

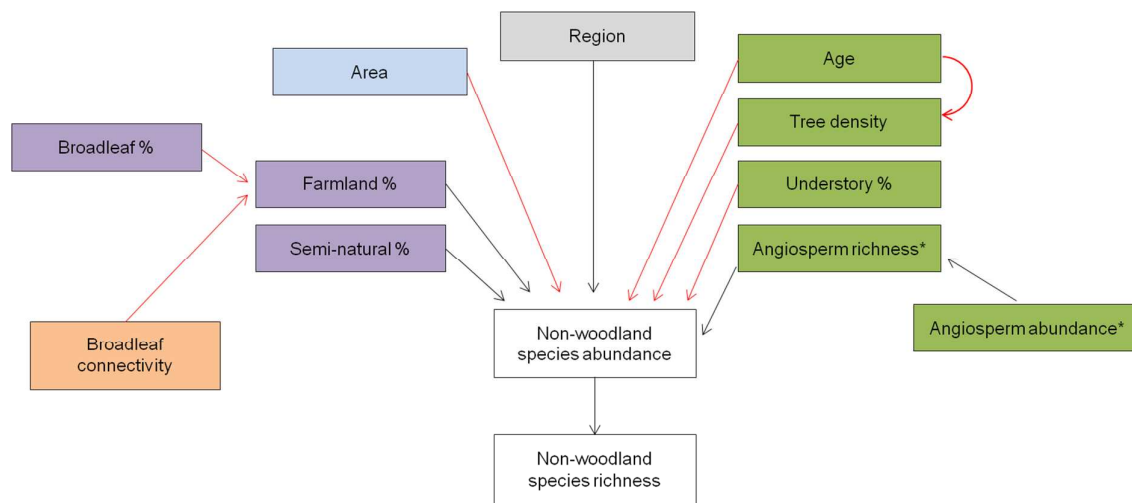


Figure 1. Global conceptual model used to guide SEM construction illustrating hypothesised direct and indirect relationships between response variables (non-woodland hoverfly/cranefly abundance, non-woodland hoverfly/cranefly species richness; white boxes) and metrics of patch geometry (blue box), vegetation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

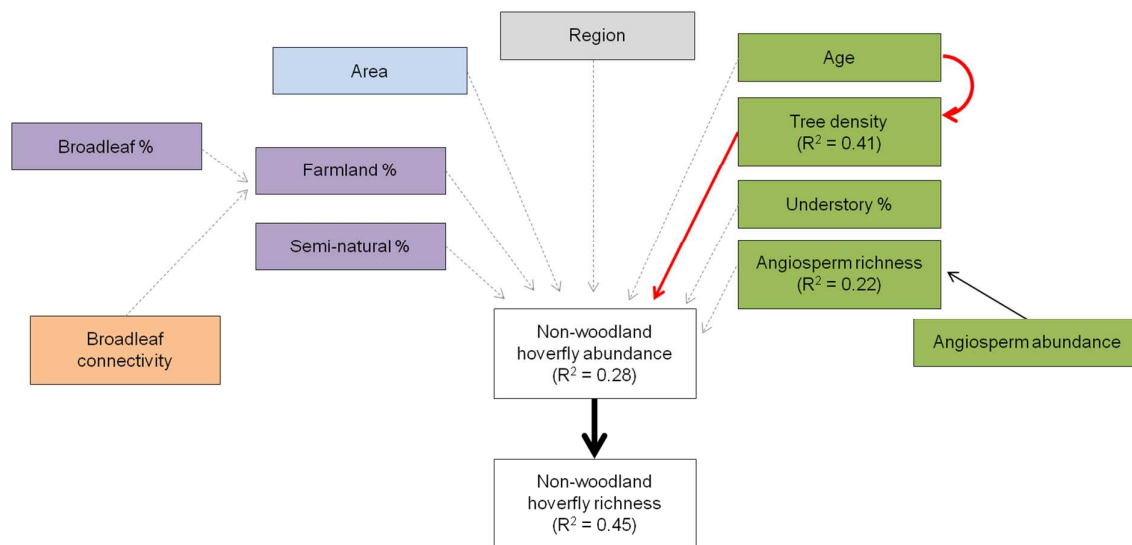


Figure 2. Individual SEM path diagrams for non-woodland hoverfly species richness/abundance. Arrows show observed positive (black) and negative (red) relationships between response variables (relative abundance, species richness; white boxes) and metrics of patch geometry (blue box), vegetation structure (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.

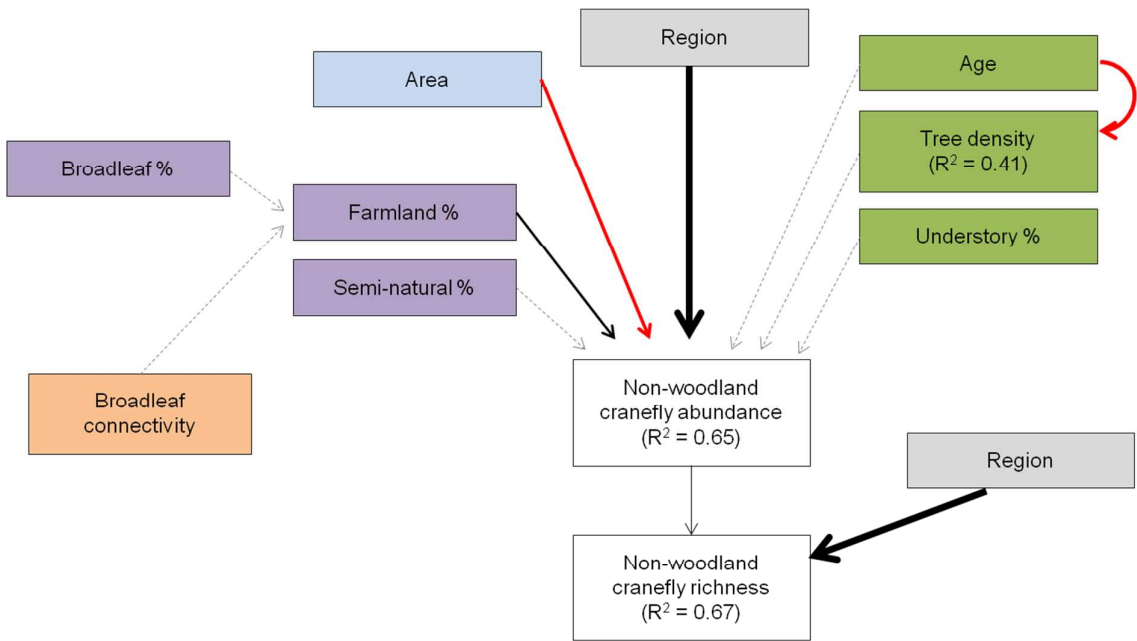


Figure 3. Individual SEM path diagrams for non-woodland cranefly species richness/abundance. Arrows show observed positive (black) and negative (red) relationships between response variables (relative abundance, species richness; white boxes) and metrics of patch geometry (blue box), vegetation structure (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.

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