

1 **Forest edges and other semi-natural habitat edges increase wild bee species richness and**
2 **habitat connectivity in intensively managed temperate landscapes.**

3 **Article impact statement:**

4 We show that seminatural habitat edges contribute to local bee diversity and as dispersal
5 corridors between bee habitats.

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43 **Data archiving statement**

44 Data and R code associated with this paper will be deposited on Dryad if the manuscript is
45 accepted for publication.

46 **Conflict of interest statement**

47 The authors declare no conflicts of interest.

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52 **Abstract**

53 Pollinator conservation schemes are typically focused on conserving existing-, restoring
54 degraded- or establishing new wild bee habitats. The effectiveness of such conservation
55 schemes depends on the presence of dispersal corridors that allow habitat colonization by bees.
56 Nonetheless, we lack an understanding of the role of semi-natural habitats edges on the
57 connectivity of pollinator communities across intensively managed landscapes. Here, we use
58 data from wild bee communities comprising 953 occurrences from 79 species of non-parasitic
59 bees, sampled at 68 locations distributed across a Norwegian and a Danish landscape to show
60 that the proportion of semi-natural habitat edges is positively correlated to bee species richness
61 and habitat connectivity. Specifically, we found that wild bee species richness sampled along
62 roadsides increased with the proportion of semi-natural habitat edges within 1.5 km of the study
63 sites and with local plant species richness. We combined maps showing the proportion of
64 seminatural habitat edges with least cost path analysis to find the most likely dispersal route
65 between our bee communities. We find that these least cost path lengths provide better models
66 of bee species compositional similarity than geographic distance ($|\Delta AICc| > 2$), suggesting that
67 seminatural habitat edges act as dispersal corridors in intensively managed landscapes.
68 However, we also find that compositional similarity between communities depend on site-
69 specific plant species richness stressing the importance of improving the habitat quality of edge
70 habitats if they are to function as dispersal corridors. We discuss potential management options
71 for improving wild bee habitat conditions along seminatural habitat edges and illustrate how
72 maps of least cost paths can be used to identify dispersal corridors between pollinator habitats
73 of conservation priority. Maps of dispersal corridors can be used to direct wild bee habitat
74 management actions along seminatural habitat edges to facilitate the dispersal of bees between
75 larger grassland habitats.

76 **Introduction**

77 Land use intensity and the associated loss of semi-natural habitats is a main driver of pollinator
78 declines and threatens ecosystem functioning in the cultural landscape (Dicks et al., 2021).
79 Pollinator diversity increases with habitat size (Steffan-Dewenter et al., 2006) and quality
80 (Rollin et al., 2019) and conserving or restoring habitats is a central component of many
81 pollinator conservation schemes (Senapathi et al., 2017). However, the species composition
82 within habitats is dynamic (Leibold et al., 2004); species disperse across the landscape and
83 colonize suitable patches of habitats (Franzén & Nilsson 2010) where they may remain or
84 eventually drift to local extinction before the patch is potentially colonized again (Vellend,
85 2010; Hanski, 1998). Indeed, wild bee meta-population dynamics can be highly dynamic in
86 terms of extinction and colonization events (Franzén & Nilsson 2010). The species diversity
87 and functioning of pollinator communities within habitats therefore depends on habitat-specific
88 environmental conditions that determine the number of individuals and species richness that a
89 habitat can sustain (Krauss et al., 2009). Furthermore, spatial (Beduschi et al., 2018) and
90 temporal (Griffin et al., 2017) connectedness to other habitat patches determine the species
91 composition in habitats (Taylor et al., 1993). Mitigating insect declines and preserving
92 ecological functions such as pollination therefore requires an understanding of how land use
93 management affects the connectedness of pollinator communities and plant-pollinator
94 interactions across landscapes (Cranmer et al., 2012). While it is well established that semi-
95 natural habitat patches, often in the form of edges along land use types, provide important
96 resources for pollinators in intensively managed landscapes (Eldegard et al., 2015; von
97 Königslöw, 2021; Johansen et al., 2022) it is less well known how semi-natural edge habitats
98 affect dispersal rates and thereby the connectivity of pollinator communities across intensively
99 managed landscapes.

100 Pollinators can forage or nest in forest-field edges (Kells & Goulson 2003; Sydenham et al.,
101 2014; Söber et al., 2020), forest-shrubland edges (Glenny et al., 2023), grassland edges (Cole
102 et al., 2015), road verges (Hopwood, 2008), and edges around sparsely vegetated areas such as
103 quarries and other low productive areas (Heneberg & Bogusch 2020). Moreover, improving or
104 introducing edge habitats in the form of flower strips (Haaland et al., 2011; von Königslöw et
105 al., 2021) or hedgerows (Morandin & Kremen 2013) can provide pollinators with resources that
106 are otherwise limiting in the landscape. By providing pollinators with nesting sites (Kells &
107 Goulson 2003; Osborne et al., 2008; Morandin & Kremen 2013) and by guiding the flight
108 direction of pollinators (Cranmer et al., 2012) the presence of semi-natural edge habitats may
109 function as corridors and increase the dispersal rate of species through the landscape. Indeed,
110 colonization of open habitats in a forested landscape by the solitary bee *Megachile rotundata*
111 increases in the presence of open linear corridors between habitats (Griffin & Haddad 2021).

112 A lack of dispersal corridors among habitat patches can reduce species flow across the
113 landscape, making local populations more vulnerable to stochastic fluctuations in population
114 growth rates (Vellend 2010). Land use change can impact landscape connectivity if availability
115 of semi-natural habitat patches is reduced along dispersal corridors of species. Hence, a
116 reduction in semi-natural habitat in the wider landscape may result in dispersal barriers,
117 increasing the rate of wild bee species turnover with geographic distance between habitat
118 patches (Beduschi et al., 2018). For wild bees in power line clearings the likelihood of occurring
119 within a site has also been shown to decrease with the distance to the nearest site where the
120 species occurs (Sydenham et al., 2017). The similarity of bee communities can therefore be
121 indicative of their connectedness. Least-cost-path analysis provides a useful framework for
122 identifying the shortest route between two communities that minimizes the cost of travelling
123 across the landscape and thereby reflects the most likely dispersal route between communities
124 (Adriaensen et al., 2003). In least-cost-path analysis, the landscape is viewed as a resistance

125 surface, where local environmental conditions can either increase or decrease the rate, or ‘cost’,
126 of movement depending on the availability of habitats (Etherington, 2016). Least-cost-path
127 analysis is frequently applied in landscape-genetics and in movement ecology to estimate
128 effects from land use on the dispersal of species (Zeller et al., 2012). Least cost path analysis
129 has also proven useful when studying patterns of species compositional similarity, where the
130 accumulated habitat availability, or its inverse – the cost of movement, has been shown to be a
131 better predictor of ant species turnover than geographic distance (Liu et al., 2018). Longer least
132 cost path distances reduce the rate of patch colonization. As a result, colonization events cannot
133 counter the effects of local extinctions and the species compositional similarity between
134 communities drifts apart (Vellend, 2010). For pollinators, such as wild bees, the presence of
135 semi-natural edge habitats could be expected to reduce the resistance of the landscape to
136 movement because dispersing individuals can find nesting and foraging habitats within edge
137 habitats (Kells & Goulson 2003). Edge habitats may therefore act as steppingstones along
138 dispersal corridors between larger habitats (Menz et al., 2011) and thereby contribute to
139 preserving metapopulation dynamics (Saura et al., 2014; Hanski 1998). However, to our
140 knowledge, the potential contribution of habitat edges to wild bee habitat connectivity in
141 intensively managed landscapes has not yet been formally investigated.

142 We use data from 68 wild bee communities sampled across a Norwegian and a Danish landscape
143 to test whether semi-natural edge habitats increase the connectedness of wild bee communities
144 and to illustrate how least cost path analyses can be used to identify important dispersal
145 corridors for wild bees in intensively managed landscapes. We hypothesize that:

146 (1) Semi-natural habitat edges provide habitat resources for wild bees in managed landscapes.
147 We test if wild bee species richness in semi-natural plant communities increases with the
148 amount of semi-natural habitat edges within typical wild bee foraging ranges. Specifically, we
149 test if wild bee species richness increased with the amount of (i) semi-natural habitat edges

150 including forest edges, (ii) forest edges alone, (iii) or semi-natural habitat edges excluding forest
151 edges. We define semi-natural edge habitats as edges around forest, grassland, shrubland,
152 wetlands, and sparsely vegetated areas.

153 (2) Semi-natural habitat edges increase the connectivity of bee communities across the
154 landscape. We test if the species compositional similarity and the number of shared species
155 between pairs of sites decreases with the length and cost of least cost paths, where least cost
156 paths are estimated from maps showing the proportion of seminatural habitat edges in the
157 landscape. We compare the relationships between compositional similarity and least cost path
158 lengths to that of geographic distances, the latter acts as a null model by assuming that species
159 can disperse freely across the landscape. We estimate least cost paths between site-pairs using
160 maps of the proportion of 10m pixels classified as semi-natural habitat edges (forest, grassland,
161 shrubland, wetlands, and sparsely vegetated areas) or only forest edges, to define the resistance
162 of pixels to movement.

163 **Methods**

164 *Sampling*

165 We sampled plant-bee interactions in 68 semi-natural, forb-dominated, plant communities (Fig.
166 1). We focused on wild bees because (1) they are considered central pollinators for many plant
167 species (Willmer et al., 2017), (2) bees are central place foragers with restricted home ranges,
168 and (3) even large bees often show limited movement between habitat patches (Franzén et al.,
169 2010), making them ideal for studying impacts of land use on habitat connectivity. We used
170 linear open landscape features such as roadsides as a model system and established one 50×2m
171 transect for our surveys in each site. To cover the main flowering period, we sampled flower
172 visiting bees once in May, June and July at each site. To standardize sampling times across sites
173 and countries, timing of the first sampling was determined by the peak flowering of dandelions

174 (*Taraxacum officinale*). All flower-visiting bees were collected from flowers and stored in 96%
175 EtOH prior to identification. Species within the *Bombus sensu stricto* subgenus are cryptic and
176 cannot be reliably identified manually. Specimens within the *B. sensu stricto* subgenus were
177 treated as one morpho-species. Each transect observation lasted 30 minutes, adding 30 seconds
178 per collected specimen, to account for handling time. To sample all target species when they
179 were active, sampling only took place on days with temperatures > 15°C, local wind speed < 5
180 m/s, with little to no cloud cover and no rain. At each site we conducted a vegetation survey in
181 July and recorded the occurrence of herbaceous plants in ten 1m² vegetation survey plots placed
182 regularly along the transect. As an indicator of local plant species richness we tallied the number
183 of plant species within a site for which we had observed at least one interaction with wild bees
184 across the 68 sites.

185 *Mapping edge habitats*

186 We derived three habitat edge maps at a 10m resolution with maps showing (1) all semi-natural
187 habitat edges, (2) forest edges only, and (3) all non-forest semi-natural edges. We used the
188 CLC+ back bone land cover map from the European Environment Agency (© European Union,
189 Copernicus Land Monitoring Service, 2022, European Environment Agency (EEA)). The
190 CLC+ is a 10m resolution land cover map with pixels classified according into 11 land use
191 classes: (1) Sealed; (2) Woody – needle leaved trees; (3) Woody – Broadleaved deciduous trees;
192 (4) Woody – Broadleaved evergreen trees; (5) Low-growing woody plants (bushes, shrubs); (6)
193 Permanent herbaceous; (7) Periodically herbaceous; (8) Lichens and mosses; (9) Non- and
194 sparsely-vegetated; (10) Water; and (11) Snow and ice. We identified semi-natural edge habitats
195 by using the `as.lines`, `as.polygons`, and `rasterize` functions from the `terra` package in R (Hijmans,
196 2023) to first polygonise all pixels classified as forest (CLC+ classes 2 and 3); low-growing
197 woody plants (class 5); grassland (class 6); and non- and sparsely-vegetated (class 9), and then
198 converting these polygons into lines which we rasterized to produce a raster of semi-natural

199 habitat edges. We followed the same procedure to produce a raster map that included only forest
200 edges (CLC+ classes 2 and 3), and one that included non-forest semi-natural habitat edges, i.e.
201 by subtracting forest edges from the semi-natural habitat edge map prior to calculating the
202 proportion of edge habitats.

203 *Statistical analyses*

204 To test if semi-natural edges provide habitat for wild bees, we used a Poisson GLM and test if
205 wild bee species richness increased with the proportion of semi-natural habitat edges, forest
206 edges, or non-forest semi-natural edges within the surrounding landscape in R (R Core Team,
207 2023). We calculated the proportion of the area within circular buffers around each sampling
208 location classified as habitat edges. To identify the spatial scale where the proportion of edge
209 habitats had the strongest effect on bee species richness, we compared models where the
210 proportion of edge habitats was calculated within buffers of 250m, 500m, 750m, 1000m, 1250,
211 and 1500m and selected the model that best fitted the data, indicated by having the lowest AICc
212 value. We ran models with the proportion of all semi-natural edge habitat, or as edge habitats
213 defined by only including forest edges. For all models we included the species richness of
214 flowering plants to control for site-specific differences in habitat quality. We used AICc to
215 compare the best semi-natural edge habitat model against the forest edge habitat model and a
216 model that only contained local plant species richness. We used DHARMA residuals (Hartig,
217 2022) to test for overdispersion and assess residual distributions from the models with the
218 lowest AICc and likelihood ratio test statistics to assess the statistical significance of edge
219 habitat variables.

220 We calculated the wild bee species compositional similarity between study sites as 1-BC where
221 BC was the Bray-Curtis dissimilarity calculated using the 'vegdist' function in Vegan (Oksanen
222 et al., 2022). We excluded parasitic bees because their distributions are indirectly related to the
223 environmental conditions that determine the distribution of their hosts. All BC dissimilarities

224 were calculated on binary, presence-absence matrices. We assembled a data frame with one
225 column defining the identity of the i th site, and another column defining the identity of the j th
226 site. For each combination of the i th and j th sites we appended the wild bee species
227 compositional similarity, in addition to the number of bee species shared between the two sites.
228 For each i th and j th site-pair we appended the geographic distance, and the least cost path
229 lengths between sites using the maps of semi-natural edge habitats and forest edges. We
230 calculated the geographic distance between all site pairs using the ‘distance’ function in terra
231 (Hijmans, 2023) in R. To estimate least cost paths between site pairs, we used the ‘create_cs’
232 function with neighbors set to 8 in the leastcostpath (Lewis 2023) package to create a
233 conductance surface from the 100m semi-natural habitat edge raster and from the 100m forest
234 edge map, where we interpreted increasing proportions of semi-natural habitat edges and forest
235 edges as increasing the permeability of the landscape to movement.

236 We adapted the function ‘create_lcp’ in leastcostpath (Lewis, 2023) to identify the least cost
237 paths between all pairs of sites based on cost surface. We used the igraph package in R (Csárdi
238 & Nepusz 2006; Csárdi et al., 2024) to identify least cost paths. We used the
239 graph_from_adjacency_matrix function with mode = ‘min’ and weighted = ‘TRUE’ to create a
240 weighted graph from the conductance matrix between all cells in the cost surface. As in the
241 ‘create_lcp’ function (Lewis, 2023) we $1/x$ transformed the weights to convert the edge weights
242 from the conductance values into costs, with costs increasing exponentially as the proportion
243 of edge habitats decreased. For each study site to all other study sites within the same country
244 (Norway and Denmark) we then used the ‘shortest_paths’ function in igraph to identify all raster
245 cells connecting site pairs along the shortest path and converted the coordinates of these cells
246 into a spatial lines object (spatvector) and used the ‘perim’ function from terra (Hijmans, 2023)
247 to calculate the length of the resulting lines (i.e. least cost paths). Least cost path lengths may
248 not equate the cost of movement across the landscape (Etherington & Holland 2013). We

249 therefore 1-x transformed the 100m habitat edge raster maps and extracted the resulting pixel
250 values along each least cost path which we summed to obtain estimates of the total cost of
251 movement along a path. Because we were interested in how land use conditions affect habitat
252 connectivity we restricted our analyses to site-pair comparisons within the same country.

253 We used zero-inflated Beta GLMMs from the `glmmTMB` package (Mollie et al., 2017) to model
254 the bee species compositional turnover with the site identity of the i_{th} and j_{th} sites as random
255 intercept terms. Species compositional similarity showed a unomial response to the distance
256 between sites which ranged from within one km up to 105 km (mean = 41.8 ± 24.4). To limit
257 our analyses to the data where species compositional similarity decreased with distance, we
258 conducted a sensitivity analysis to identify the geographic distance from which species
259 compositional similarity increased with distance. We created a sequence of numbers from 10 to
260 105 with increments of 5 to create 20 subsets of our data where the uppermost distance between
261 sites was restricted to within 5km increments from 10km to 105km. For each subset of the data,
262 we used a zero-inflated Beta GLMM to model the species compositional similarity as a function
263 of either the untransformed geographic distance between sites or as a function that included a
264 second order polynomial transformation of geographic distance and calculated the difference in
265 AICc values (Fig. S1). We then selected the largest distance (60km) where the polynomial and
266 the untransformed models performed equally well ($|\Delta AICc| < 2$), to include as much data as
267 possible in subsequent tests. For site-pairs located less than 60km apart, the corresponding least
268 cost paths when considering all semi-natural habitat edges (mean = 84km, min = 75km, max =
269 97km) and when considering only forest edges (mean = 85km, min = 76km, max = 104km)
270 were considerably longer than the geographic distances. For all site-pairs within 60km of each
271 other we used zero-inflated Beta GLMMs to model species compositional similarity and
272 Generalized Poisson GLMMs to model the number of shared species. For all models, we
273 included an interaction term between the plant species richness in the i_{th} and j_{th} to control for

274 site-specific differences in plant diversity and its potentially confounding effect on species
275 compositional similarity and the number of shared species. For both compositional similarity
276 and the number of shared species, we used AICc to compare the goodness of fit of models with
277 the least cost path length and path cost estimated from the proportion semi-natural habitat edges
278 or from forest edges as fixed effects against models using geographic distance as fixed effect.

279 To illustrate how maps of least cost paths can aide in identifying important dispersal corridors
280 between seminatural grasslands, we used georeferenced data on the location of 125 seminatural
281 hay-meadows (EUNIS Annex I code: EUNIS R22) of high (“Klasse A”) or good (“Klasse B”)
282 quality from within the extent of our Norwegian study sites. For the Danish case, we considered
283 314 georeferenced meadows within the spatial extent of our study sites, focusing on meadows
284 that are included in the proposed Natura2000 action plan areas for 2022-2027 (The Danish
285 Environmental Protection Agency 2023): 13 Xeric sand calcareous grasslands (EUNIS Annex
286 I code: 6120);102 Semi-natural dry grasslands and scrubland facies on calcareous substrates
287 (Festuco-Brometalia) [EUNIS Annex I code: 6210]; 212 Species-rich *Nardus* grasslands, on
288 silicious substrates in mountain areas (and submountain areas in Continental Europe) [EUNIS
289 Annex I code: 6230]; and 47 *Molinia* meadows on calcareous, peaty or clayey-silt-laden soils
290 (*Molinion caeruleae*) [Annex I code: 6410). To focus on meadows that would be of likely high
291 value for wild bees, we restricted the analyses to meadows of high (“I. Høj tilstand”) or good
292 (“II. God tilstand”) condition and which were at least two hectares large, resulting in 23 EUNIS
293 Annex I code 6210 grasslands and 54 EUNIS Annex I code 6230 grasslands. For the meadows
294 within each region, we used the centroid location of each meadow to estimate least cost paths
295 between all pairs of meadows based on proportion of seminatural habitat edges within 100m
296 raster pixels.

297 **Results**

298 We sampled a total of 953 occurrences of 79 species of non-parasitic wild bees distributed
299 across 68 wild bee communities located in two regions, one in Denmark and one in Norway
300 (Fig. 1). The sampled bees belonged to 21 genera within six the families: Melittidae;
301 Andrenidae; Colletidae; Halictidae; Megachilidae; and Apidae. Bee species richness within
302 sites ranged from two to 18 (mean = 9.34, standard deviation = 4.05). The species compositional
303 similarity, or the proportion of species co-occurring in two sites, ranged from zero to 0.89 (mean
304 = 0.35, s.d. = 0.15), while the number of shared species ranged from zero to 11 (mean = 3.49,
305 s.d. = 1.95), when considering all site-pairs within each country. Values were similar when
306 considering the 873 site-pairs located within 60km of each other: species compositional
307 similarity ranging from zero to 0.89 (mean = 0.36, s.d. = 0.15), and the number of shared species
308 ranging from zero to 11 (mean = 3.30, s.d. = 1.83).

309 Wild bee species richness increased with plant species richness and with the proportion of semi-
310 natural habitat edges in the surrounding landscape (Table 1, Fig. 2). The goodness of fit of the
311 Poisson GLMs with the proportion of all semi-natural habitat edges improved gradually with
312 the size of the buffer within which edge habitat was estimated. The lowest AICc value was
313 obtained from the model with a 1500m buffer (Table 1). Forest edges were an important
314 contributor to the value of seminatural habitat edges as bee habitat. Indeed, considering only
315 forest edges yielded models of bee species richness that were comparable to the models that
316 included all edge habitats ($|\Delta AICc| = 1.2$) but better than the null model that included only plant
317 species richness ($|\Delta AICc| < 2$). By contrast, excluding forest edges reduced the goodness of fit
318 compared to models that included all semi-natural habitat edges ($|\Delta AICc| = 3$) or only forest
319 edges ($|\Delta AICc| = 4.3$).

320 Wild bee species compositional similarity decreased with the length of least cost paths (Table
321 S1) identified from the semi-natural habitat edge map (Fig. 3A, d.f. = 1, $\chi^2 = 33.9$, $p < 0.001$)
322 which provided a slightly better fit ($|\Delta AICc| = 1.3$, Table S2) than that of the least cost path

323 lengths when considering only forest edges (d.f. = 1, $\chi^2 = 32.6$, $p < 0.001$). Both zero-inflated
324 GLMMs with least cost path lengths provided better models ($|\Delta AICc| > 3.9$, Table S2) of wild
325 bee species compositional similarity than the model that included geographic distance (d.f. =
326 1, $\chi^2 = 28.7$, $p < 0.001$). Contrary to our expectations, models of bee compositional similarity
327 as functions of the least cost path costs did not perform better than the geographic distance
328 model ($|\Delta AICc| < 2$, Table S2). Bee species compositional similarity was highest between
329 site-pairs that both had a high plant species richness and lowest when comparing a plant
330 species rich site to a plant species poor site (Fig. 3B, plant richness site $i \times$ plant richness site j
331 interaction term: d.f. = 1, $\chi^2 = 17.21$, $p < 0.001$). Results were broadly similar when assessing
332 connectivity as the number of shared species between site-pairs with the least cost path length
333 models outperforming ($|\Delta AICc| > 2.7$, Table S2) and least cost path cost models performing
334 similarly or even slightly worse ($|\Delta AICc| = 2.1$) to the geographic distance model. The
335 decrease in shared species was modelled equally well ($|\Delta AICc| = 1$, Table S2) by the
336 seminatural edge habitat least cost path model (d.f. = 1, $\chi^2 = 27.0$, $p < 0.001$) and the forest
337 edge least cost path model (d.f. = 1, $\chi^2 = 26.1$, $p < 0.001$). As for species compositional
338 similarity, the number of shared species between site-pairs depended on the plant species
339 richness of the two sites (Fig. 3D, plant richness site $i \times$ plant richness site j interaction term:
340 d.f. = 1, $\chi^2 = 19.63$, $p < 0.001$). See Table S1 for full zero-inflated Beta GLMM and
341 generalized Poisson GLMM model summary statistics.

342 We used the map of our study region (Fig. 4A) with the proportion of seminatural grasslands
343 (Fig. 4B) to identify least cost paths between seminatural grasslands of conservation priority
344 in Norway (Fig. 4C) and Denmark (Fig. 4D). Mapping the least cost paths revealed how
345 Norwegian seminatural grasslands that for historical reasons are often located in forested
346 areas can be viewed as a network of habitats where connectivity can be improved by targeting
347 habitat improvement schemes to seminatural edges that connect grassland habitats. For the

348 Danish case the prioritized grassland habitats occurred in clusters, defined by the Natura2000
349 target areas for 2022-2027. The least cost paths revealed how corridors between clusters of
350 prioritized habitats are likely to converge along shared paths where habitat improvement
351 schemes are likely to improve the connectivity between multiple habitats.

352 **Discussion**

353 We found that the presence of seminatural habitat edges not only increased species richness
354 within bee communities but also the connectivity of between bee communities. Least cost path
355 lengths between site-pairs provided models with a better fit to the species compositional
356 similarity and to differences in the number of shared species, than models using inter-site
357 geographical distances suggesting that seminatural habitat edges act as dispersal corridors in
358 the landscape. However, least cost paths were substantially longer than the geographical
359 distances, stressing the importance of habitat quality for bee movement across the landscape.

360 Seminatural habitat edges may increase dispersal rates by providing wild bees with foraging
361 and nesting habitats along dispersal routes. Habitat resources are often a limiting factor for bee
362 species diversity in intensively managed agricultural (Le Féon et al., 2010; Steffan-Dewenter
363 et al., 2002) and forested (Winfree et al., 2007) landscapes. In forested landscapes, clear-cuts
364 can provide important floral resources for pollinators (Rubene et al., 2015; Nielsen and Totland
365 2014), however clear-cuts quickly lose their value as habitat due to regrowth and canopy closure
366 (Zitomer et al., 2023). That bee diversity is often lower in forested micro-habitat sites compared
367 to clear-cuts, or forest edges (Mullally et al., 2019), suggests that the edge habitat - and not the
368 forest itself - provides resources for bees. In forested landscapes, seminatural edge habitats
369 occur in the form of sun-exposed forest edges (Sydenham et al. 2014, Proesmans et al. 2019),
370 road verges (Eckerter et al., 2023) and power line clearings (Eldegard et al., 2015, Wagner et
371 al., 2019) which provide important, and persistent, habitat resources for wild bees. Indeed, and

372 in line with our findings, the species richness and abundance of flower-visitors to oilseed rape
373 (Bailey et al. 2014) and coffee (Ricketts 2004) has been shown to decrease with distances to
374 forest edges. However, wild bees require large quantities of pollen to sustain their populations,
375 with many bee species requiring the pollen from more than 30 flowers to rear a single larva
376 (Müller et al., 2006). Because of the high pollen requirements of many species, the short
377 foraging range of wild bees (Zurbuchen et al. 2010), and the limited size of semi-natural habitat
378 edges which restricts the amounts resources they can provide (Johansen et al. 2022), semi-
379 natural habitat edges are unlikely to be able to sustain large bee populations for extended periods
380 of time. Seminatural habitat edges should therefore not be viewed as a substitute for seminatural
381 grassland habitats (Von Königslöw et al. 2021).

382 While seminatural habitat edges may not be able to replace seminatural grasslands (Von
383 Königslöw et al. 2021), they may act as important stepping-stones (Menz et al. 2011),
384 increasing the dispersal rate between seminatural grasslands that are of conservation concern.
385 In forested landscapes, patch colonization experiments have shown that strips of open, non-
386 forested habitat can act as corridors by facilitating colonization (Griffin & Haddad 2021) as has
387 been also shown in urban settings (Balbi et al. 2019, 2021). However, the functioning of semi-
388 natural habitat edges as dispersal corridors for bees likely depends on the floral and nesting
389 resources they provide. Indeed, we found that the bee species richness within sites increased
390 with local plant richness, indicated by bee communities from plant species rich sites
391 sharing more species. In contrast, bee communities on plant species poor sites or on sites that
392 differed in their plant diversity shared fewer bee species. The importance of plant species
393 richness in relation to the habitat quality of edges has also been found for bumblebee and
394 butterfly species richness along Swedish roadsides (Horstmann et al. 2023). Using maps of
395 least-cost paths between new, restored, or existing semi-natural grassland habitats can provide
396 a useful tool for identifying and directing management efforts towards potentially important

397 dispersal corridors. Facilitating the movement of wild bees across landscapes through directed
398 management interventions that improve habitat conditions along forest edges is likely to
399 increase the rate at which species disperse and colonize suitable habitats.

400 Management schemes for improving habitat conditions for wild bees along seminatural habitat
401 edges will differ depending on the type of habitat edge. For roadsides traffic safety restricts the
402 type of management schemes that can be adopted and where they can be implemented. In
403 Norway for instance, vegetation must be repeatedly mowed during the season along curved
404 roads, near road crosses, and near bus stops, for safety reasons to ensure visibility (Pers. Comm.
405 Astrid B. Skrindo). For roadsides along linear road sections management regimes could entail
406 mowing parts of the edge habitat, to prevent them becoming overgrown with grasses, while
407 leaving other parts as refuges (Buri et al. 2014). Allowing for grass tussocks to form along parts
408 of the roadside can improve the nesting conditions for bumblebees where several species nest
409 under thick swards of grass (O'Connor et al. 2017). For the mowed parts, the hay should ideally
410 be removed after mowing (Jakobsson et al., 2018). The timing of mowing should be tailored to
411 the flowering time of the local flora to ensure floral resources are present when bee require
412 them, and that plants are given time to produce and disperse their seeds (Johansen et al., 2019).
413 Altered mowing regimes are however only likely to give immediate effects if plants have
414 already established a seedbank or seedlings. Indeed, the natural establishment of species rich
415 plant communities along roadsides can take several decades (Horstmann et al. 2023). The plant
416 diversity in roadsides without a species rich seedbank can be improved by sowing seeds from
417 pollen and nectar producing plants. Seed-mixes that are often used contain non-native plants
418 which should be avoided because of the potential threat they may pose to the native flora (Valkó
419 et al. 2023). Also, the presence of non-native, and invasive, plants may require the road
420 authorities to intensify mowing regimes (Pers. Comm. Astrid B. Skrindo). An alternative is to
421 use seed-rich hay collected from local seminatural grasslands and spread the hay to allow seeds

422 to establish along roadsides. The ‘hay-method’ has previously been shown to be effective and
423 less costly than using commercial seeds when establishing seminatural grasslands (Rydgren et
424 al. 2010) and comes with the added benefit that it contributes to conserving local plant genetic
425 diversity. In addition to improving plant species richness and bumblebee nesting conditions
426 through altered mowing regimes, nesting sites for ground nesting bees can be introduced in the
427 form of non-vegetated sand pockets (Fortel et al. 2016). Improving pollinator habitat through
428 altered mowing regimes, potentially coupled with the hay-method, and the establishment of
429 nesting sites for ground nesting bees can also be adopted along other edge habitats, such as
430 grassland and forest edges. Along these other types of habitat-edges it is also possible to cater
431 for cavity nesting bees by allowing dead wood to gather (Westerfelt et al. 2015), and by
432 preserving or building stone drywalls (Xie et al., 2020). Implementing these management
433 actions will incur a cost for managers and should be directed to where they will have the desired
434 effect. Maps of least cost paths between pollinator habitats of conservation priority can be used
435 to identify potentially important dispersal corridors along which management actions should be
436 prioritized.

437 We used the compositional similarity and numbers of shared species between sites as measures
438 of connectivity. The compositional similarity between sites is known to depend on the sample
439 size within site-pairs, and under sampling may inflate estimates of (dis-)similarity (Beck et al.
440 2013, Stier et al. 2016). Still, despite that our sampling effort was restricted to three surveys per
441 site, and that of the variability in local plant species richness which was strongly related to bee
442 species richness and compositional similarity, we were still able to detect a statistically
443 significant relationship between least cost path lengths and habitat connectivity between sites.
444 These findings support those of Sydenham et al., (2017) that the species diversity within bee
445 communities can be dispersal limited. That habitat conditions in the landscape can increase the
446 dispersal rate of bees has been shown in agricultural landscapes, where high amounts of

447 seminatural habitat reduces the distance decay in species compositional similarity (Beduschi et
448 al. 2018). However, to our knowledge it has not previously been shown that least cost paths
449 lengths are more strongly related to bee community connectivity than geographic distance.

450 Our results suggest that linear edge habitats contribute to the connectivity among bee
451 communities in intensively managed temperate landscapes. However, the value of such edges
452 as habitat depends on their plant diversity. While implementing management actions such as
453 altered mowing regimes to increase plant diversity seminatural habitat edges is costly least-
454 cost-path analyses can provide an efficient tool for identifying important dispersal corridors
455 along which management actions should be prioritized. Considering dispersal corridors as an
456 integrated part of pollinator conservation planning will allow the establishment of networks of
457 high-quality habitats where the longevity of populations of pollinators can be maintained
458 through dispersal dynamics.

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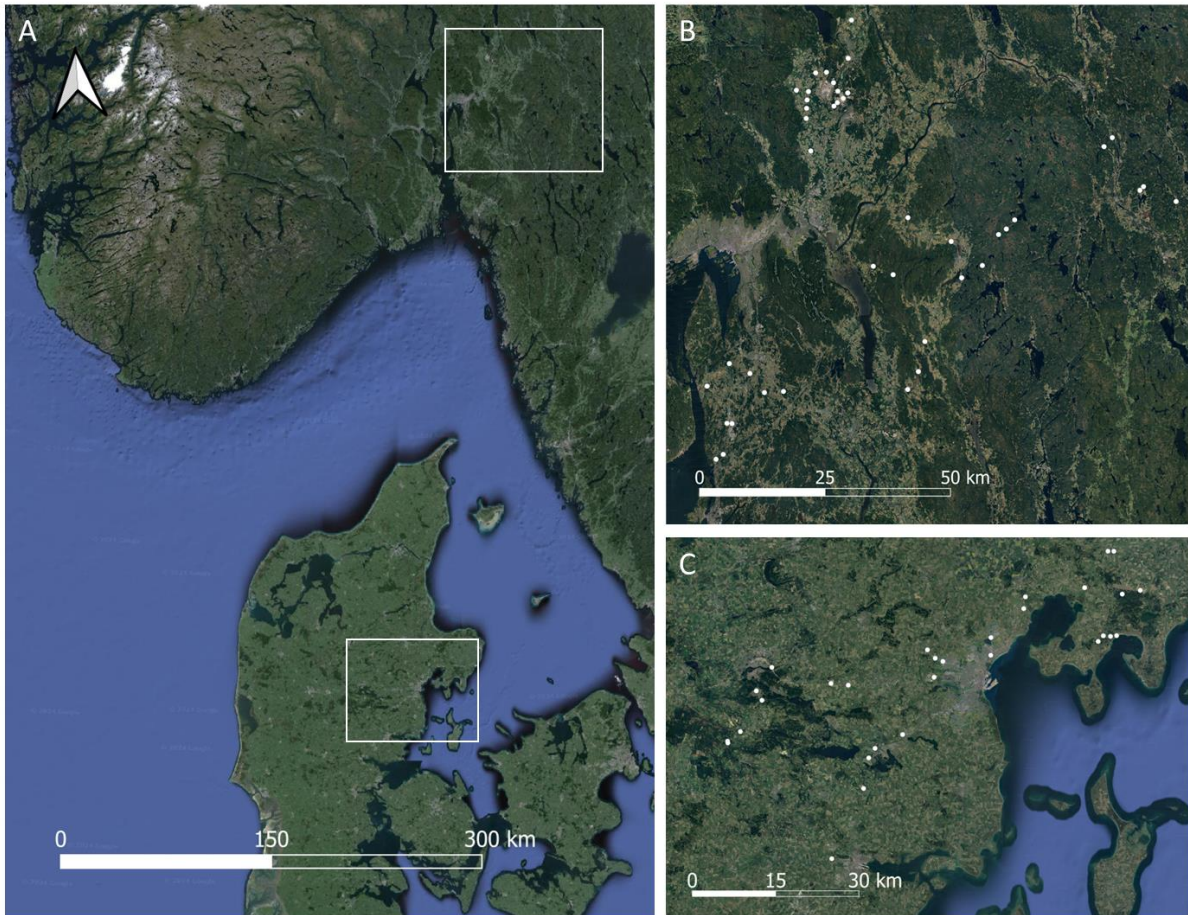
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668 Table 1 Comparisons of Poisson GLMs of wild bee species richness as a function of semi-
 669 natural edge habitats within circular buffers around sites.

Wild bee species richness	AICc _{Semi-natural}	AICc _{Forest}	AICc _{Non-forest}
Edges in 250m radius + plant richness	371.1	371.7	368.1
Edges in 500m radius + plant richness	372.1	371.2	371.0
Edges in 750m radius + plant richness	370.7	368.8	371.9
Edges in 1km radius + plant richness	369.2	367.6	372.0
Edges in 1.25km radius + plant richness	369.3	367.8	372.0
Edges in 1.5km radius + plant richness	368.8	367.6	371.8
Wild bee species richness _{null model}	AICc _{Null model}		
Plant species richness	369.9		

670 **Comparisons were done using AICc values across models where edge habitat was identified*
 671 *using all semi-natural edge habitats (AICc_{Semi-natural}), forest edges only (AICc_{Forest}), or all*
 672 *non-forest edge habitats (AICc_{Non-forest}). Poisson GLMs of wild bee species richness were*
 673 *compared to a null model that only included plant species richness (AICc_{Null model}).*

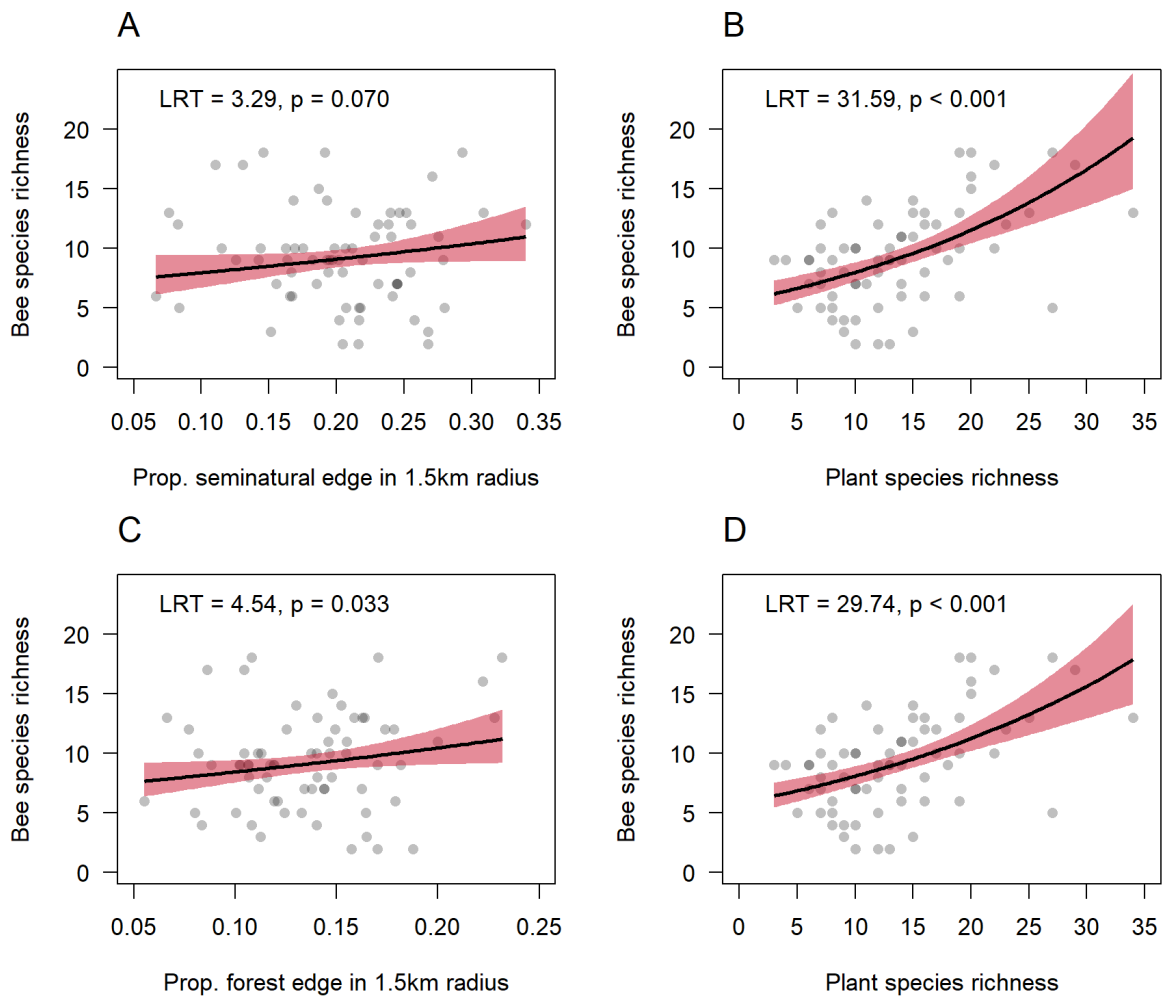


674

675 Figure 1. Wild bee communities were sampled at 68 roadsides and other linear habitats
676 distributed along gradients of agricultural intensity within two landscapes (A) in southeastern
677 Norway (B) and in western Denmark (C). Satellite imagery from Map data ©2024 Google via
678 QGIS 2024

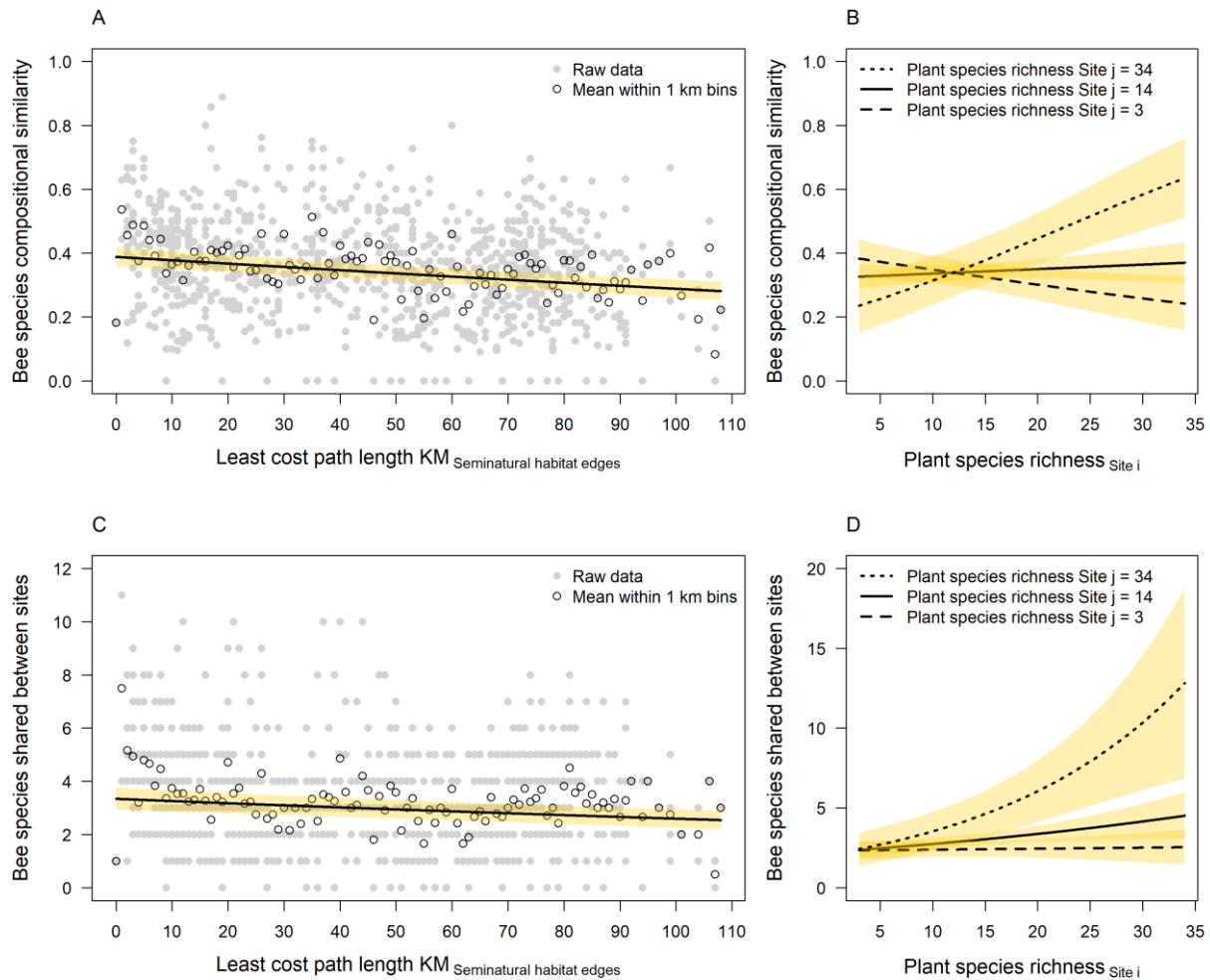
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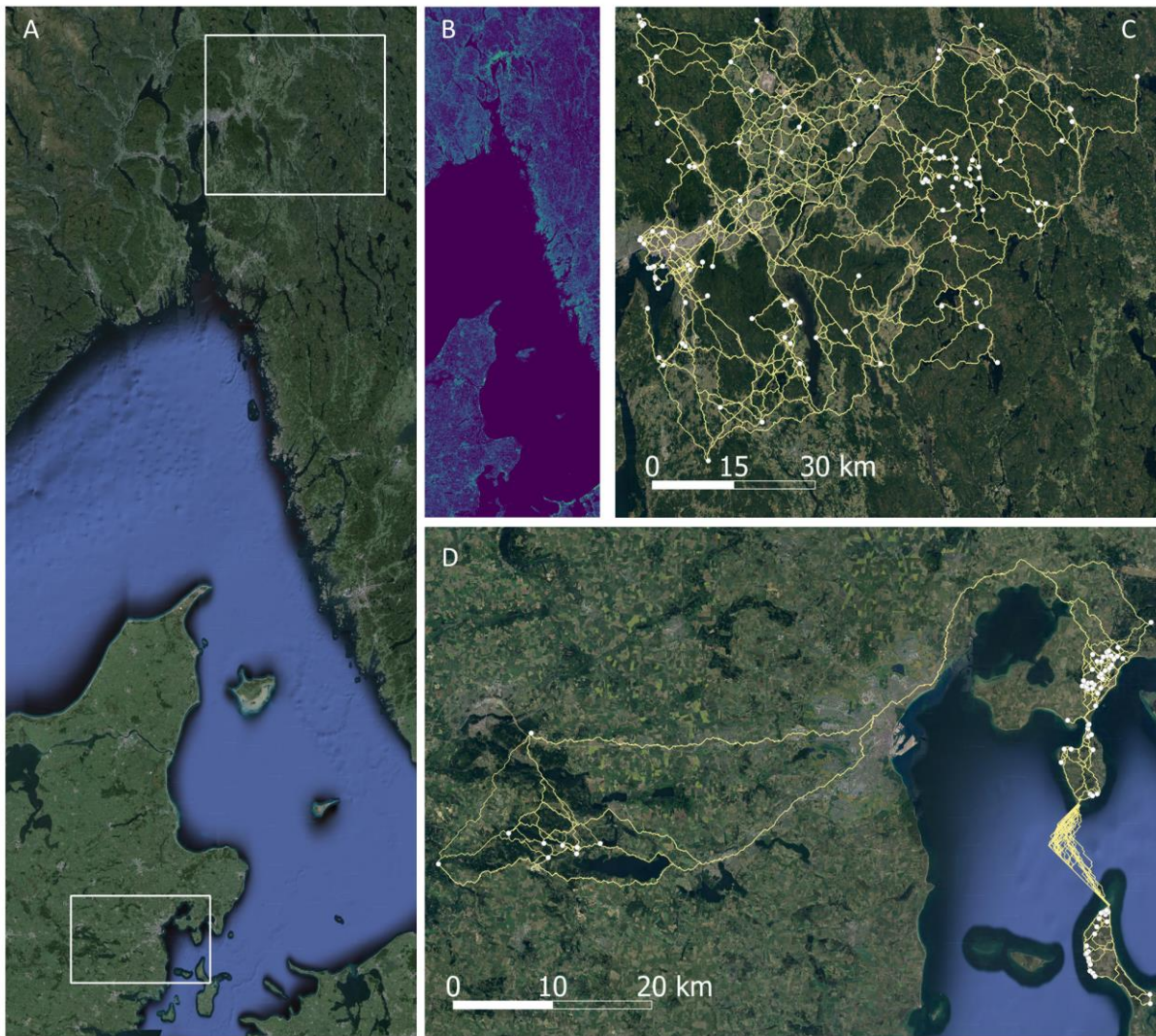
681

682 Figure 2 Marginal effects plots showing that wild bee species richness increased with the
683 proportion of semi-natural habitat edges within 1.5km of sampling sites (A), after controlling
684 for the increase in bee species richness with plant species richness (B), and that this relationship
685 was mainly driven by an increase in be species richness with the proportion of forest edges (C)
686 after controlling for local plant species richness (D).



687

688 Figure 3 Marginal effects plots showing that bee species compositional similarity between pairs
689 of sites decreased with the length of least cost path dispersal corridors (A) while also depending
690 on the plant species richness within the two sites being compared (B). Results were similar
691 when assessing connectivity as the number of shared bee species between site-pairs (C-D).



692

693 Figure 4 Overview map of the Norwegian study region showing the extents of the two study
694 landscapes (A). Within the study region we used a map showing the proportionate contribution
695 of semi-natural habitat-edges within 100m grid cells (B) to identify least cost path corridors
696 between seminatural grasslands (white points) of conservation priority in the Norwegian (C)
697 and Danish (D) study landscapes. Satellite imagery from Map data ©2024 Google via QGIS
698 2024.

699 **Supplementary material S1**

700 Table S1 Summary outputs from Zero-inflated Beta GLMMs used to model wild bee species
 701 compositional similarities between sites and from Generalized Poisson GLMMs used to model
 702 the number of shared species between sites.

Compositional similarity

Fixed effects	Estimate	z-value	p-value
Intercept	-0.612	-11.2	< 0.001
Plant richness site i	0.026	0.6	0.523
Plant richness site j	0.025	0.6	0.564
Geographic distance	-0.111	-5.4	< 0.001
Plant richness site i × Plant richness site j	0.100	4.3	< 0.001
Zero-inflated model	Estimate	z-value	p-value
Intercept	-3.524	-17.4	< 0.001
Random Intercepts (obs = 873)	Name	variance	s.d.
Site i (n = 66)	Intercept	0.06	0.24
Site j (n = 66)	Intercept	0.09	0.30
Fixed effects	Estimate	z-value	p-value
Intercept	-0.614	-11.3	< 0.001
Plant richness site i	0.035	0.9	0.388
Plant richness site j	0.028	0.6	0.524
Least cost path length <small>Seminatural edge habitat</small>	-0.125	-5.9	< 0.001
Plant richness site i × Plant richness site j	0.097	4.1	
Zero-inflated model	Estimate	z-value	p-value

Intercept	-3.524	-17.4	< 0.001
Random Intercepts (obs = 873)	Name	variance	s.d.
Site i (n = 66)	Intercept	0.06	0.23
Site j (n = 66)	Intercept	0.09	0.30
Fixed effects	Estimate	z-value	p-value
Intercept	-0.615	-11.3	< 0.001
Plant richness site i	0.029	0.7	0.475
Plant richness site j	0.025	0.6	0.571
Least cost path length <small>Forest edges</small>	-0.121	-5.7	< 0.001
Plant richness site i × Plant richness site j	0.099	4.24	< 0.001
Zero-inflated model	Estimate	z-value	p-value
Intercept	-3.524	-17.37	< 0.001
Random Intercepts (obs = 873)	Name	variance	s.d.
Site i (n = 66)	Intercept	0.06	0.24
Site j (n = 66)	Intercept	0.09	0.30
Fixed effects	Estimate	z-value	p-value
Intercept	-0.614	-11.3	< 0.001
Plant richness site i	0.039	0.9	0.342
Plant richness site j	0.022	0.5	0.614
Least cost path cost <small>Seminatural edge habitats</small>	-0.116	-5.4	< 0.001
Plant richness site i × Plant richness site j	0.106	4.5	< 0.001
Zero-inflated model	Estimate	z-value	p-value
Intercept	-3.524	-17.37	< 0.001

Random Intercepts (obs = 873)		Name	variance	s.d.
	Site i (n = 66)	Intercept	0.05	0.23
	Site j (n = 66)	Intercept	0.09	0.30
Fixed effects		Estimate	z-value	p-value
	Intercept	-0.615	-11.3	< 0.001
	Plant richness site i	0.030	0.7	0.467
	Plant richness site j	0.019	0.4	0.656
	Least cost path cost _{Forest edges}	-0.113	-5.3	< 0.001
	Plant richness site i × Plant richness site j	0.108	4.6	< 0.001
Zero-inflated model		Estimate	z-value	p-value
	Intercept	-3.524	-17.37	< 0.001
Random Intercepts (obs = 873)		Name	variance	s.d.
	Site i (n = 66)	Intercept	0.05	0.24
	Site j (n = 66)	Intercept	0.09	0.30
Number of shared species				
Fixed effects		Estimate	z-value	p-value
	Intercept	1.086	18.2	< 0.001
	Plant richness site i	0.126	2.6	0.009
	Plant richness site j	0.111	2.5	0.011
	Geographic distance	-0.062	-4.9	< 0.001
	Plant richness site i × Plant richness site j			
Random Intercepts (obs = 873)		Name	variance	s.d.
	Site i (n = 66)	Intercept	0.10	0.32

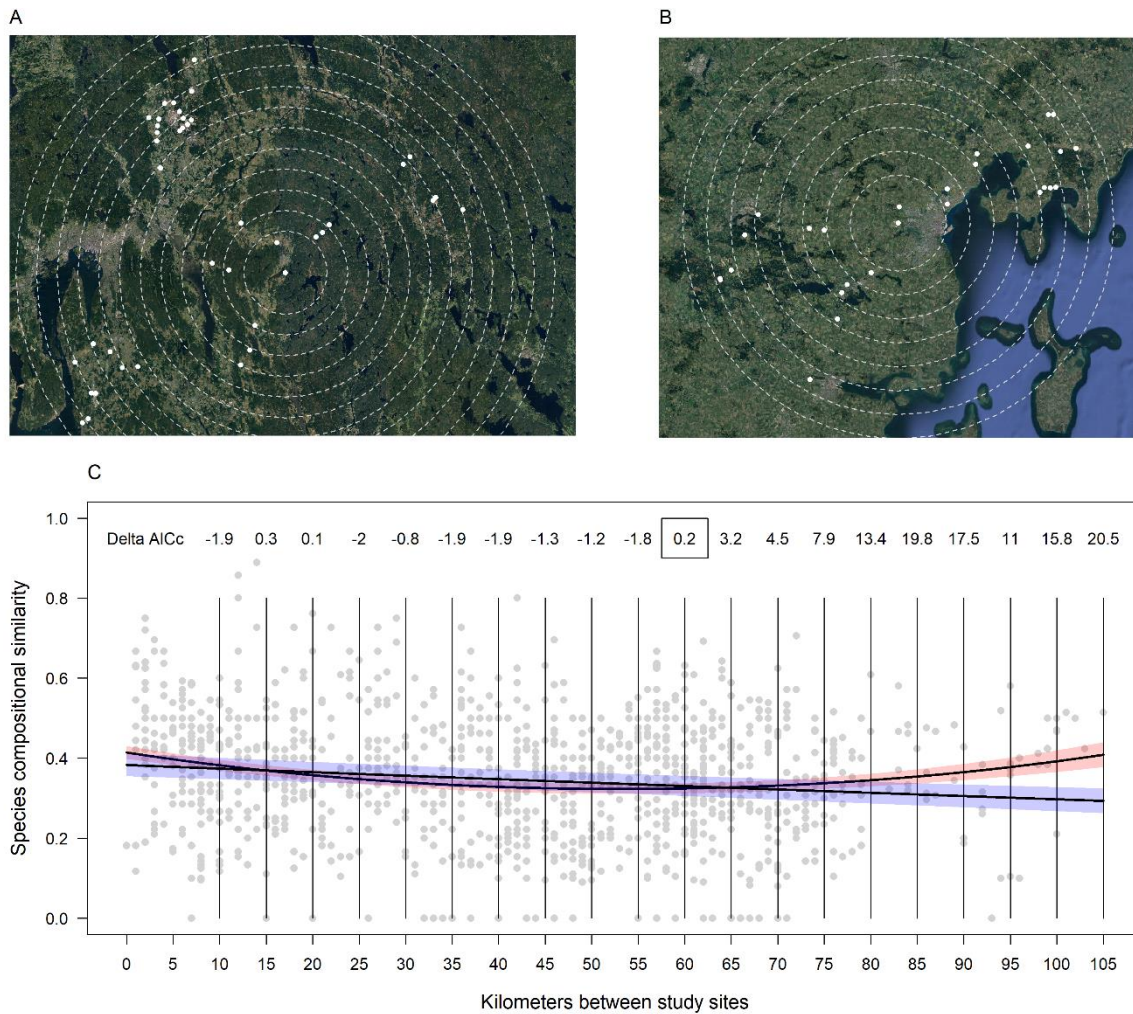
Site j (n = 66)	Intercept	0.10	0.32
Fixed effects	Estimate	z-value	p-value
Intercept	1.084	18.2	< 0.001
Plant richness site i	0.130	2.7	0.007
Plant richness site j	0.112	2.6	0.009
Least cost path length <small>Seminatural edge habitats</small>	-0.069	-5.2	< 0.001
Plant richness site i × Plant richness site j	0.063	4.5	< 0.001
Random Intercepts (obs = 873)	Name	variance	s.d.
Site i (n = 66)	Intercept	0.10	0.32
Site j (n = 66)	Intercept	0.10	0.31
Fixed effects	Estimate	z-value	p-value
Intercept	1.085	18.2	< 0.001
Plant richness site i	0.127	2.6	0.008
Plant richness site j	0.111	2.6	0.010
Least cost path length <small>Forest edges</small>	-0.068	-5.1	< 0.001
Plant richness site i × Plant richness site j	0.064	4.6	< 0.001
Random Intercepts (obs = 873)	Name	variance	s.d.
Site i (n = 66)	Intercept	0.10	0.32
Site j (n = 66)	Intercept	0.10	0.32
Fixed effects	Estimate	z-value	p-value
Intercept	1.085	18.2	< 0.001
Plant richness site i	0.132	2.8	0.006

Plant richness site j	0.109	2.5	0.012
Least cost path cost <small>Seminatural edge habitats</small>	-0.063	-4.7	< 0.001
Plant richness site i × Plant richness site j	0.067	4.8	< 0.001
Random Intercepts (obs = 873)	Name	variance	s.d.
Site i (n = 66)	Intercept	0.10	0.32
Site j (n = 66)	Intercept	0.10	0.32
Fixed effects	Estimate	z-value	p-value
Intercept	1.084	18.2	< 0.001
Plant richness site i	0.127	2.7	0.008
Plant richness site j	0.108	2.5	0.013
Least cost path cost <small>Forest edges</small>	-0.062	-4.6	< 0.001
Plant richness site i × Plant richness site j	0.069	4.9	< 0.001
Random Intercepts (obs = 873)	Name	variance	s.d.
Site i (n = 66)	Intercept	0.10	0.32
Site j (n = 66)	Intercept	0.10	0.32

704 Table S2 Comparisons of zero-inflated Beta GLMMs of wild bee species compositional
705 similarity or generalized Poisson GLMMs of the number of shared species richness between
706 site-pairs i and j as a function of geographic distance, seminatural edge habitat least cost path
707 length, forest edge least cost path length, seminatural edge habitat least cost path cost, and forest
708 edge least cost path cost.

Distance measure between sites	AICc Compositional similarity	AICc Shared species
Geographic distance	-882.5	2773.0
Least cost path length: Seminatural edges	-887.7	2769.3
Least cost path length: Forest edges	-886.4	2770.3
Least cost path cost: Seminatural edges	-882.6	2774.7
Least cost path cost: Forest edges	-881.7	2775.1

709 **All models included an interaction term between plant species richness in the i th and j th site,*
710 *and random intercepts for site i and site j . See Table S1 for full model summary statistics.*



711

712 Figure S1 Location of study sites in Norway (A) and Denmark (B) shown within buffers of
713 increasing 5km distance from the most central site within each region. Zero-inflated Beta
714 GLMMs with km between sites untransformed or using a second order polynomial were used
715 to model bee species compositional similarity between sites and compared using AICc values
716 (C). For analyses restricted to site-pairs within 60km of each other the untransformed and the
717 polynomial models performed equally well ($\Delta AICc = 0.2$), while at greater distances the
718 polynomial model performed best ($\Delta AICc > 2$). Species compositional similarity was
719 calculated as $1 -$ the bray-curtis dissimilarity. Regression lines in (C) show fitted relationships
720 $\pm 2 \times$ standard deviations for the untransformed (blue polygon) and polynomial models (red
721 polygon) including all site distances.