

# 1      **Explicit integration of dispersal-** 2                    **related metrics improves** 3      **predictions of SDM in predatory** 4                    **arthropods**

5  
6      Monsimet Jérémy <sup>1\*</sup>, Devineau Olivier <sup>1</sup>, Pétilion Julien<sup>2</sup> & Lafage Denis <sup>2, 3</sup>

7      <sup>1</sup> *Department of Forestry and Wildlife management, Inland Norway University of Applied Sciences,*  
8      *Campus Evenstad, Koppang, Norway*

9      <sup>2</sup> *UMR CNRS 6553 ECOBIO, Université de Rennes, Rennes, France*

10     <sup>3</sup> *Department of Environmental and Life Sciences/Biology, Karlstad University, Karlstad, Sweden*

11     \*Corresponding author: [jeremy.monsimet@inn.no](mailto:jeremy.monsimet@inn.no)

## 12 **ABSTRACT**

13 Fishing spiders (*Dolomedes spp.*) make an interesting model to predict the impact of global  
14 changes because they are generalist, opportunistic predators, whose distribution is driven  
15 mostly by abiotic factors. Yet, the two European species are expected to react differently to  
16 forthcoming environmental changes, because of habitat specialization and initial range. We  
17 used an original combination of habitat and dispersal data to revisit these predictions under  
18 various climatic scenarios. We used the future range of suitable habitat, predicted with  
19 habitat variables only, as a base layer to further predict the range or reachable habitat by  
20 accounting for both dispersal ability and landscape connectivity. Our results confirm the  
21 northward shift in range and indicate that the area of co-occurrences should also increase.  
22 However, reachable habitat should expand less than suitable habitat, especially when  
23 accounting for landscape connectivity. In addition, the potential range expansion was further  
24 limited for the red-listed *D. plantarius*, which is more habitat-specialist and has a lower ability  
25 to disperse. This study highlights the importance of looking beyond habitat variables to  
26 produce more accurate predictions for the future of arthropods populations.

27 **Keywords:** Fishing spiders, Pisauridae, Climate change, Dispersal limitation, Hybrid SDM

## 28 **Introduction**

29 Climate change, which is now threatening all ecosystems worldwide (Bellard et al. 2012), is  
30 a multi-factor problem that goes beyond raising temperatures only (Pereira et al. 2010,  
31 Garcia et al. 2014). Tackling this complexity requires that ecologists obtain realistic  
32 predictions of how species distributions will change in response to global change. In recent  
33 years, species distribution models (SDMs) proved to be an important tool to for this. SDMs  
34 are particularly useful to predict geographic distributions by correlating species occupancy  
35 to environmental variables (Miller 2010). Applications include conservation planning (Guisan  
36 et al. 2013), potential invasion range (Bellard et al. 2013), or forecasting in time (Hijmans  
37 and Graham 2006). SDMs were successfully applied to a large variety of terrestrial (see Hao  
38 et al. 2019 for a review) and marine organisms (see Melo-Merino et al. 2020 for a review).

39 The accuracy of predictions produced by SDMs varies from algorithm to algorithm, even  
40 when considering that the MaxENT algorithm is most often used (Qiao et al. 2015). This  
41 variation in accuracy can be alleviated with ensemble models, which combine algorithms and  
42 produce consensual predictions (Araujo and New 2007, Thuiller 2004). Of course, input data  
43 also influence the predictions (Thuiller et al. 2019), and while most SDMs use only climatic  
44 variables, including other variables such as land-use might improve predictions (Titeux et al.  
45 2016). In order to make projections in time, it is fundamental to carefully select the right  
46 climatic scenario (Thuiller et al. 2019). Right now, the ones produced and updated by the  
47 Intergovernmental Panel on Climate Change (IPCC 2007) are the most widely recognized  
48 and used climatic scenarios.

49 SDMs assume that the species and its environment are at equilibrium (Guisan and Thuiller  
50 2005), so that all suitable locations are occupied. SDMs also assume that the ecological  
51 niche is stable, i.e. that the same factors limit the species in space and time (Richmond et  
52 al. 2010). Under these assumptions, SDMs are used to define habitat suitability, which is the

53 range of physical locations where one species can live (Kearney 2006). However, a properly  
54 constructed and calibrated SDM can provide information about the specie's realized niche,  
55 ie a combination of habitat with other biotic and abiotic factors (Guisan and Thuiller 2005,  
56 Soberon and Peterson 2005). The gold standard of SDMs would be fully mechanistic models  
57 which were used, for example to study seed dispersal in birds (Merow et al 2011) or  
58 population dynamics and evolution of dispersal trait (Bocedi et al. 2017). However, these  
59 models are very data-demanding, and simpler hybrid mechanistic-correlative models are  
60 often more suitable for less well-studied taxa. In particular these hybrid models allow  
61 including active biological processes such as dispersal (Briscoe et al. 2019). Examples  
62 include making predictions under full /no dispersal (Thuiller et al. 2009) or using a buffer of  
63 dispersal around each presence (Mammola and Isaia 2017).

64 As generalist predators, spiders are relatively independent of a specific prey community, and  
65 their assemblage and distribution is mostly influenced by habitat and land use (Lafage et al.  
66 2015), which makes them good study cases for SDMs. Fennoscandia is a potential climatic  
67 refugium for spider populations against the current global warming (Leroy et al. 2014).  
68 Refugia can mitigate the effects of climate change by providing suitable conditions for  
69 species persistence through time (Keppel and Wardell-Johnson 2012). *Dolomedes*  
70 *plantarius* could presumably use Fennoscandia as a refugium, but the ability of the species  
71 to effectively spread northward has not been accounted for in previous predictions (Leroy et  
72 al. 2013, 2014). Moreover, fishing spiders are threatened by the decrease of range and  
73 quality of their wetland and fenland habitats, which are declining globally (Finlayson et al.  
74 2019). The other European fishing spider, *Dolomedes fimbriatus*, also occurs in  
75 Fennoscandia. Co-occurrence of both *Dolomedes*, was considered impossible due to  
76 different habitat requirements (van Helsdingen 1993). Syntopy is possible though, as the two  
77 species can live close to each other (Duffey 2012), for example around the same lake (Ivanov

78 et al. 2017), or in the ecotone habitat between bogs and ponds (Holec 2000). *D. fimbriatus*  
79 has a larger ecological niche: the species is more drought and shade tolerant (Duffey 1995),  
80 and is less sensitive to water quality (Duffey, 2012). Consequently, *D. fimbriatus* could  
81 become a competitor to *D. plantarius* in syntopic sites if global change brings more frequent  
82 drought events

83 Here, we compare the potential range spread of *D. plantarius* and *D. fimbriatus*, and their  
84 ability to use Fennoscandia as a refugium. We aim to provide more conservative predictions  
85 for Fennoscandia than previously predicted at the European scale by Leroy et al (2013). To  
86 do so, we developed hybrid species distribution models including climate and land-use  
87 variables, as well as dispersal and landscape connectivity (figure 1). We expected that:

- 88 1) The distribution of both fishing spiders should expand northward (Parmesan and  
89 Yohe 2003, Parmesan 2006). A larger expansion is expected under more intense  
90 climate change.
- 91 2) Since *D. fimbriatus* is a habitat generalist, the range of habitat it can reach should be  
92 larger and occupied faster, than for *D. plantarius* (Hill et al. 1999).
- 93 3) The area of sympatry between the two species should increase with the range  
94 expansion of the two species.

## 95 **Methods**

### 96 **Occurrence data**

97 We downloaded records of presence for both spider species from the GBIF (GBIF: The  
98 Global Biodiversity Information Facility 2019) via the `rgbif` package (citations for R packages  
99 are provided in Supplementary material, Appendix 1) in R (R Core Team 2019). The GBIF  
100 database gathers volunteer-based naturalist observations (Supplementary material  
101 Appendix 2), which often require a quality check. We used the package `CoordinateCleaner`

102 (Supplementary material Appendix 1) to remove null or duplicate coordinates, and to flag the  
103 records requiring a subjective decision, such as ol records or records located in urban areas,  
104 or at the centroid of a county. Urban records were not necessarily false presence, and we  
105 used aerial photography (ESRI 2009) accessed with packages leaflet and mapedit  
106 (Supplementary material Appendix 1) to decide whether to keep these records or not. We  
107 visually checked, for instance, if a record was not in a recently modified areas in a city. Some  
108 records suggesting co-occurrence of the two species were checked in the field during  
109 summer 2018 and 2019 (25 locations, including four actually syntopic locations). We retained  
110 775 records for *Dolomedes fimbriatus* and 181 records for *Dolomedes plantarius* (Figure 2),  
111 reflecting the GBIF data available until October 2019 in Fennoscandia. When several records  
112 fell in the same raster cell, we kept only one.

## 113 **Species distribution modelling**

### 114 **Predictor variables**

115 For the climatic component of the ecological niche, we included variables which were  
116 biologically relevant for spiders, and not too correlated (Braunisch et al. 2013). Using a  
117 correlation coefficient threshold of 0.7 (Dormann et al. 2012), we selected mean and  
118 maximum annual temperature, mean diurnal temperature range, mean temperature of the  
119 wettest quarter, and annual precipitation, which we extracted from the WorldClim database  
120 (Fick and Hijmans 2017) at a spatial resolution of 30 arc-seconds (Supplementary material  
121 Appendix 4, Tab. A1).

122 To predict the future distribution of *Dolomedes* spiders in Fennoscandia, we used IPCC  
123 projections for 2050 and 2070, under multi-factors “representative concentration pathways”  
124 (RCP) 4.5 and 8.5 (van Vuuren et al. 2011). RCP4.5 corresponds to medium-low greenhouse  
125 gas emissions and air pollution, whereas RCP8.5 considers high greenhouse gas emission,  
126 medium air pollution, and an increase in carbon dioxide (van Vuuren et al. 2011). we

127 downloaded these climatic projections from Wordclim (Hijmans et al. 2005) at a spatial  
128 resolution of 30 arc-seconds.

129 For the habitat component of the ecological niche, we integrated information on ground  
130 wetness, which is an important community driver for the semi-aquatic fishing spiders (Lafage  
131 et al. 2015, Lafage and Pétilon 2016). We also incorporated forest and grassland density,  
132 because the presence of fishing spiders seems to be influenced by the surrounding  
133 landscape (unpublished data). We downloaded the corresponding geographic layers from  
134 the Copernicus Land Monitoring Service at 100-metres resolution (EEA 2018), and upscaled  
135 them to 30 arc-seconds resolution to match the bioclimatic data. The forest layer represents  
136 the density of the tree cover (from 0 to 100 %) in 2015. The 'Water and Wetness' layer  
137 represents the occurrence of wet surfaces from 2009 to 2015, using a water and wetness  
138 probability index, indicating the degree of physical wetness, independently of the vegetation  
139 cover. Finally, the grassland layer represents the percentage of grassland per pixel. We  
140 estimated the change in land use between current and future times with a model which  
141 harmonises scenarios from different integrated assessment models, namely MESSAGE for  
142 RCP8.5 and GCAM for RCP4.5 (Hurtt et al. 2011).

### 143 **Calibration area and pseudo-absences**

144 To use presence-absence models with the presence-only GBIF data, we used a random  
145 sampling procedure with environmental profiling (RSEP; Senay et al. 2013) which creates a  
146 background of absence records for each algorithm. We generated the pseudo-absences in  
147 a different calibration area for each species. *D. plantarius* is a lowland species, so its  
148 calibration area was at low altitude <1000m. For *D. fimbriatus*, we excluded areas >1500m.

### 149 **Model validation**

150 Although there are many SDMs, none stands out as better than the others (Qiao et al. 2015).  
151 To improve the predictions, we therefore used an ensemble forecast approach, which

152 combines several models weighted by their predictive accuracy (Buisson et al. 2010,  
153 Grenouillet et al. 2011).

154 Following recommendations in Barbet-Massin et al. (2012), we built our ensemble model  
155 with 10 runs of gradient boosting models (GBMs), generalized additive models (GAMs) and  
156 Maxent. We used 1000 pseudo-absences for the GBMs, and as many pseudo-absences as  
157 presences for the GAMs. We used 80% of the data for training the ensemble model and  
158 testing the single run of model, and 20% for validation. Each model was cross-validated with  
159 a 5-fold procedure in package biomod2 (Supplementary material Appendix 1), thus leading  
160 to 5 fits for each type of model and each pseudo-absences run. We then evaluated the  
161 predictive accuracy of individual models with the true skill statistic (TSS) and the area under  
162 the receiving operating curve (AUROC). The TSS metric represents the ratio of hit rate to  
163 false alarm rate and varies from -1 to +1 (Allouche et al. 2006). We used a threshold of TSS  
164 = 0.4 to include models into the ensemble forecast (Allouche et al. 2006). The AUROC is a  
165 measure of "separability", which represents the true positive rates graphically against the  
166 true negative rates. Following Fawcett (Fawcett 2006), we retained models with  $AUC > 0.7$  for  
167 the ensemble model. Finally, we converted the probabilities of presence predicted by the  
168 ensemble model into a binary presence/absence, with a cut point based on predictions which  
169 maximized the TSS (Supplementary material Appendix 1). In package biomod2, the relative  
170 variable contribution is assessed based on the correlation between the prediction of a model  
171 including a given variable and the model where this variable was dropped.

172 We built one model with bioclimatic variables only (model Bioc), and one with bioclimatic and  
173 land-use variables (model BLU). We then included dispersal to predict the range of suitable,  
174 but unreachable habitat (model Disp). Finally, we accounted for landscape connectivity into  
175 model dispCS. The framework is summarized in figure 1 (additional details in Supplementary  
176 material Appendix 4, Tab. A1).



## 177 **Including dispersal into SDM**

178 Although they differ in their general dispersal ability, the two species of fishing spider disperse  
179 mostly through ballooning and rappelling, where they catch the wind with a thread of silk,  
180 and passively fly. Laboratory tests suggested that few individuals exhibit long-distance  
181 dispersal behaviour on the water surface (unpublished data). We recorded this behaviour  
182 only in *Dolomedes fimbriatus* through sailing (when spider raised its body and/or abdomen  
183 and/or the legs to catch the wind). However, juveniles of *D. fimbriatus* are generally found in  
184 the surrounding vegetation rather than on the water (Duffey 2012), which makes aquatic  
185 dispersion unlikely.

186 We modelled dispersal ability via the MigClim package (Supplementary material Appendix  
187 1), based on the predicted map of the BLU model. For each species, the MigClim model  
188 evaluates if suitable cells of the raster could become accessible between current time and  
189 2050/2070. The package uses a dispersal kernel, i.e., a vector of probabilities of dispersal,  
190 to simulate the dispersal of the species (Supplementary material Appendix 3, Tab. A1). We  
191 used an imperviousness map (EEA 2018) to locate areas where the species settlement is  
192 highly unlikely. Since both fishing spiders are water-dependent, impervious regions where  
193 the soil seals, are barrier to settlement. Part of the MigClim modelling process is random  
194 (Engler and Guisan 2009), so we replicated each model 30 times and model-averaged the  
195 estimates.

196 In experimental settings, aerial dispersal (ballooning) is usually characterized when the  
197 spider is observed tiptoeing in response to a controlled wind. However, not all tiptoeing  
198 spiders end up ballooning (Bonte et al. 2009, Lee et al. 2015). The distance covered by aerial  
199 dispersal is less than 5 kilometres on average and is not correlated with the duration of the  
200 tiptoeing behaviour (Reynolds et al. 2007). We parametrized the MigClim model with values  
201 from the literature on aerial dispersal distance in spiders (Thomas et al. 2003, Reynolds et

202 al. 2007). We weighed these values by the proportion of individuals we observed rappelling  
203 in our laboratory experiments (Monsimet et al. in prep), namely, 76.6% of *D. fimbriatus* and  
204 59% *D. plantarius*. For long-distance dispersal, we used the proportion of individuals  
205 observed ballooning (*D. fimbriatus*: 14%, *D. plantarius*: 2.9%) for 2019. We considered that  
206 the probability of a settlement was similar for both species. Also, we hypothesized that it  
207 takes two years for a newly colonized area to produce new propagules, based on the >2-  
208 year lifespan of spiders in Northern Europe (Duffey 2012).

### 209 **Accounting for landscape connectivity**

210 We used the Circuitscape software (Shah and McRae 2008) to predict the potential dispersal  
211 corridors that *Dolomedes* could use to colonize their suitable habitat. Circuit theory estimates  
212 multiple pathways based on the resistance and conductance of the landscape (McRae et al.  
213 2008). We used the habitat suitability prediction map from our BLU model to define the  
214 resistance map used by Circuitscape. We transformed the estimates of habitat suitability  
215 according to recommendations in Keeley (Keeley et al. 2017; see also Supplementary  
216 material Appendix 3).

217 We used a "wall-to-wall" approach (Pelletier et al. 2014, Febbraro et al. 2019) which  
218 estimates the conductivity of the landscape from South to North, and from West to East. A  
219 consensus map was produced by multiplying the resistance layers of different directions.  
220 This consensus map was an estimation of the landscape connectivity for the two species.  
221 The consensus map was binarized by considering conductance higher than mean  
222 conductance plus standard deviation as corridors (Febbraro et al. 2019). Areas outside  
223 corridors were then considered as a barrier to short-distance dispersal in Migclim. Migclim  
224 was parametrized as for the model Disp but accounting for the landscape connectivity barrier  
225 to make predictions for model DispCS.

## 226 **Range expansion and geographic overlap in time**

227 We compared suitable habitat predicted across species, models, and scenarios. To estimate  
228 the range expansion or reduction in the future, we used the biomod2 package in R. We  
229 compared the direction of the shift in suitable habitat by calculating the centre of gravity of  
230 the suitable range with the SDMTools package (Supplementary material Appendix 1). To  
231 estimate the overlap of suitable habitat range between species for each time/scenario  
232 combination, we used the Schoeners' D overlap metric (Warren et al. 2008), which ranges  
233 from 0 for no overlap to 1 for full overlap (Rödder and Engler 2011). We estimated the suitable  
234 habitat range overlap and not the full niche overlap here. We calculated D with the ENMtools  
235 package (Supplementary material Appendix 1).

## 236 **Results**

### 237 **Modelling and model validation**

238 The predictive performance of both Bioc and BLU models was higher than the threshold with  
239 either the ROC (>0.7) or the TSS (>0.4) metric (Supplementary material Appendix 4, Tab.  
240 A2). The relative contribution of predictors was the same across models and species, with  
241 mean annual temperature the most important variable with a contribution higher than 60%.  
242 For Bioc, mean temperature of the warmest month was also important, with a higher  
243 contribution for *D. fimbriatus* than for *D. plantarius* (33% and 11%, respectively). Mean  
244 temperature of the wettest quarter, annual precipitation and mean diurnal range contributed  
245 less than 10% to both models. Forest and ground wetness contributed more than grassland  
246 in the BLU models, but their relative contribution was less than 16%.

### 247 **Range expansion and geographic overlap in time**

248 The size of the predicted / projected range was similar for both Bioc and BLU models.  
249 However, range expansion was predicted to be more restricted when also accounting for  
250 land use (BLU) than when considering only climatic variables (Bioc). Indeed, adding land

251 use variables contracted the suitable habitat at the limit of the range. Suitable range was  
252 also smaller for RCP4.5 than for RCP8.5, with similar patterns in time, except for *D. fimbriatus*  
253 where the range was reduced in 2070 compared to current under model BLU (figure 3).

254 Under RCP4.5 scenario, the suitable range was predicted to increase for both species in  
255 2070 with the BLU model (14% for *D. fimbriatus* and 161% for *D. plantarius*). With model  
256 Disp, the range should decrease in 2050 for *D. fimbriatus* (20% decrease) and for *D.*  
257 *plantarius* (66% decrease; figure 3). Both species should be able to fill the suitable range  
258 towards 2070, but both should have a limited spread on the range of suitable habitat under  
259 Disp (figure 3 and 4; 14% increase under BLU and 4% under Disp for *D. fimbriatus*; 161%  
260 and 16%, respectively, for *D. plantarius*). The range of both species should shrink under  
261 DispCS (81% in 2050 and 76% in 2070, compared to current suitable habitat for *D.*  
262 *fimbriatus*; 88% and 53%, respectively, for *D. plantarius*).

263 The southern part of the suitable range should shrink, especially in Sweden and, to a lesser  
264 extent, in Finland. This range should expand in northern Fennoscandia (figure 4). According  
265 to model dispCS, tis shift should occur towards the North-Est, with a limited spread in  
266 southern Finland (figure 3). Similarly, the range of suitable habitat for *D. plantarius* should  
267 also increase towards the North-East under model Disp (figure 5). The shift of the centre of  
268 gravity is at a higher distance for the models which exclude Dispersal (Bioc and BLU) than  
269 model including dispersal (Disp and DispCS). The centre of gravity shifts farther without  
270 dispersal (models Bioc and BLU) than with dispersal (models Disp and DispCS).

271 The predicted distribution overlap between species was higher when considering only  
272 climatic variables than when accounting for land use at current time (Bioc model). Under the  
273 BLU model, the overlap should increase through time and is more important for the scenario  
274 SRCRCP8.5 than the 4.5 one (Schoener's D values ranging from 0.55 at current time to 0.62  
275 in 2070 for RCP4.5, it reached 0.68 under 8.5). The overlap should mainly occur at the

276 Southern range of *Dolomedes fimbriatus* distribution (figure 6; Supplementary material  
277 Appendix 4, Tab. A4).

## 278 **Discussion**

279 Using species distribution models (SDM), we highlighted different range expansions and  
280 shifts of two closely related fishing spiders species in Fennoscandia. According to our  
281 predictions, the range of suitable habitat should spread for both *D. fimbriatus* and *D.*  
282 *plantarius*. Our climatic and habitat models (Bioc and BLU) confirmed the expansion of *D.*  
283 *plantarius* in Fennoscandia predicted by Leroy et al. (2013, 2014). In contrast, our hybrid  
284 models including dispersal and landscape connectivity (Disp and DispCS) predicted a more  
285 limited expansion.

## 286 **Northward range expansion of both *Dolomedes* species**

287 A northward expansion in Fennoscandia is expected for the two species under both Bioc and  
288 BLU models. The range of suitable habitat should increase with the intensity of the climate  
289 change for *D. plantarius* and for *D. fimbriatus* in 2050. This northward expansion is also  
290 predicted in other taxa, as climate change promote an expansion of the range at the colder  
291 margin (Parmesan and Yohe 2003, Parmesan 2006). An increase in annual mean  
292 temperature and in temperature of the warmest month, which are the most important  
293 variables for both models, could impact the lifespan of the two spider species, and affect their  
294 distribution. Higher temperatures could increase the suitable period to produce juveniles,  
295 which could in turn increase the number of juveniles dispersing. The temperature  
296 encountered by juveniles also influences the dispersal ability and mode (ie, long vs short  
297 distance dispersal; Bonte et al. 2008b). Moreover, latitude and climate affect the time at  
298 which the *Dolomedes* reach maturity (Duffey 2012). This could increase the frequency of a  
299 second brood, which we already observed in September (unpublished data). Such an  
300 increase in temperature could, in turn, influence the speed of colonization of new habitats.

301 The inclusion of land use in BLU models shrinks the range of suitable habitat, which confirms  
302 results from other, similar studies (Eskildsen et al. 2013)

303 Under the Disp model, suitable habitat should be less reachable for *D. plantarius* than for *D.*  
304 *fimbriatus*. The size of the area reached under the Disp model should be smaller than the  
305 current area for both species. In 2070, *D. fimbriatus* should have a range slightly equivalent  
306 to the suitable habitat estimated under BLU, whereas it should be smaller for *D. plantarius*.  
307 The limited expansion of *D. plantarius* is explained mainly by dispersal ability. Indeed, we  
308 observe fewer spiderlings of *D. plantarius* showing dispersal behaviours, including long-  
309 distance dispersal through ballooning (unpublished data). Non-filling the suitable range is  
310 usually explained by either or both past and current limited dispersal, as exemplified by trees  
311 species (Svenning and Skov 2004). Some species are trapped in their geographical range,  
312 species which distribution has not changed since the last glaciation. Under a changing  
313 climate, species answer whether through microevolution or adaptive phenotypic plasticity  
314 (Radchuk et al. 2019). Some species are not yet able to adjust their phenology and  
315 physiology to changes induced by climate change. The importance of short-distance  
316 dispersal in fishing spiders should nonetheless maintain genetic exchange, or avoid genetic  
317 drift, at a smaller scale (Bell et al. 2005). A possible prevalence of this behaviour might also  
318 reinforce the importance of shorter dispersal as climate change and other factors like the  
319 increase of habitat fragmentation decrease long-distance dispersal of spiders (Bonte et al.  
320 2006).

## 321 **Geographic range overlap and coexistence**

322 The geographic and climatic niche of *D. plantarius* are included in the realised niche of *D.*  
323 *fimbriatus*. The first is a habitat specialist, the last is a generalist species living in a wider  
324 variety of environmental conditions over its range. Climate change increases the chance of  
325 overlap between these two sister species. However, we did not make predictions at a meso-

326 or microhabitat scale, which would be too fine for SDMs. Yet, field observations suggest that  
327 both *Dolomedes* species also co-occur at finer spatial scales (Duffey 2012). The discrete  
328 nature and propensity to hide and dive of *D. plantarius* (van Helsdingen 1993), together with  
329 possible misidentification (Bellvert et al. 2013, Ivanov et al. 2017) might explain the small  
330 number of records and of co-occurrences. In North America, closely related species of  
331 *Dolomedes* like *D. tritium* and *D. vittatus* were reported to co-occur at small spatial scales  
332 (Carico 1973).

333 Usually, closely related species co-occur less often than moderately related species  
334 (Weinstein et al. 2017). On one hand, an increase in co-occurrence might limit the  
335 distribution by segregation at the landscape scale. Indeed, the number of interactions  
336 between species in the ecosystem increases with climate change (Montoya and Raffaelli  
337 2010), which generates a spatial separation between generalist and specialist species.  
338 Sympatric sister species usually diverge ecologically (Losos 2008), *Dolomedes* species differ  
339 in terms of habitat use (Duffey 2012). *D. plantarius* needs open habitat with slow-flowing  
340 water and water all year, while these factors do not seem to restrict *D. fimbriatus*  
341 (unpublished data). On the other hand, spatial segregation might occur at the micro-habitat  
342 scale. For instance, a study on *Tetragnatha* spiders showed that one of two co-existing spider  
343 species builds nursery webs higher in the vegetation when they co-occur (Williams et al.  
344 1995). Finally, an increase in co-occurrence might lead to phenological shift in co-existence  
345 sites. Our observation in two Swedish locations of *D. fimbriatus* females with juveniles in the  
346 nursery while *D. plantarius* still carried egg sacs could support this. Other closely related wolf  
347 spider species (Lycosidae) also show differences in the timing of their breeding season to  
348 avoid intraguild predation (Balfour et al. 2003).

## 349 **Intrinsic limits of hybrid SDMs**

350 Ideally, a mechanistic model should account for all phases of dispersal, ie, emigration,  
351 transfer, settlement, (Travis et al. 2012, 2013). The SDM accounting for dispersal which we  
352 used here it not a mechanistic model but is rather based on assumptions concerning the  
353 three stages of passive dispersal. Further studies should consider factors which influence  
354 individuals' dispersal such as food availability (Bonte et al. 2008a), presence of  
355 endosymbionts (Goodacre et al. 2009), presence of conspecific in the short-long distance  
356 dispersal allocation (De Meester and Bonte 2010), or genetically inherited boldness (Bonte  
357 and Lens 2007). Since dispersal is not homogeneous within and among species (Clobert et  
358 al. 2009), a more realistic model should include information on dispersal and population size  
359 for each presence observation. The sampling of all sites is necessary to collect this  
360 information. There is a considerable gap between the theory and actual applications of data-  
361 demanding mechanistic SDMs (Briscoe et al. 2019). Knowing that the most used habitat is  
362 not necessarily the most suitable for the fitness of the species (Titeux et al. 2019), we used  
363 a hybrid model based on the lack of sufficient data for a full mechanistic model.

364 Less snow cover leads to less insulation, and thus, to colder subnivean habitat, where fishing  
365 spiders overwinter (Slatyer et al. 2017). Accounting for thermal niche information is possible  
366 with mechanistic models (Ceia-Hasse et al. 2014; Sinervo et al. 2010). However, the current  
367 knowledge of eco-physiological responses of fishing spiders to climate change is too scarce  
368 to allow fully mechanistic models.

## 369 **Conservation of fishing spiders**

370 Fennoscandia may become a climatic refugium for *D. plantarius* as its range in continental  
371 Europe is expected to decrease (Leroy et al. 2013, 2014). The stronger the climate is, the  
372 more likely Fennoscandia will act as a refugium. The overlap between the two *Dolomedes*  
373 species should also increase with the climate change intensity. Arthropods conservation is



374 challenging because of the fine-grain level needed as compared to vertebrates, the low  
375 empathy towards invertebrates, and the lowest number of conservation specialists available  
376 (Cardoso et al. 2020, Samways et al. 2020). Nonetheless, spiders have already been used  
377 as bio-indicators (Marc et al. 1999, Prieto-Benítez and Méndez 2011). Our models suggest  
378 that the conservation of both species is necessary as the reachable range size should  
379 drastically decrease in the future when accounting for dispersal and landscape connectivity.  
380 Conservation of preserved sites in a stepping-stones scheme is an alternative for species  
381 that are not able to use corridors (Noss and Daly 2006). Maintaining interconnected suitable  
382 sites in the first five kilometres around sites with known presence should help conserve  
383 current sites and promote expansion. With respect to fishing spiders, priority should be given  
384 to sites in southern Finland and central Sweden, where there is limited connectivity, and the  
385 spread of *Dolomedes* species is limited. Since *D. fimbriatus* has higher dispersal abilities,  
386 improving the connectivity in the North of the suitable range to make it reachable should  
387 improve the future range.

388 This work, together with other studies on *Dolomedes*, could be used to update the now  
389 outdated range assessment of *D. plantarius* (World Conservation Monitoring Centre 1996).  
390 The species' conservation would benefit from such an update.

## 391 **Acknowledgements**

392 We thank Stefano Mammola for useful comments and discussions on an early version of the  
393 manuscript. We also thank all the landowners who gave access to their properties.

## 394 **Author contributions**

395 All authors contributed to the design and implementation of the research. JM analysed the  
396 data and drafted the manuscript. All authors contributed to writing of the manuscript and  
397 approved of the final version.

## 398 **References**

- 399 Allouche, O. et al. 2006. Assessing the accuracy of species distribution models: prevalence,  
400 kappa and the true skill statistic (TSS). - J. Appl. Ecol. 43: 1223–1232.
- 401 Araújo, M. B. and New, M. 2007. Ensemble forecasting of species distributions. - Trends  
402 Ecol. Evol. 22: 42–47.
- 403 Balfour, R. A. et al. 2003. Ontogenetic shifts in competitive interactions and intra-guild  
404 predation between two wolf spider species. - Ecol. Entomol. 28: 25–30.
- 405 Barbet-Massin, M. et al. 2012. Selecting pseudo-absences for species distribution models:  
406 how, where and how many? - Methods Ecol. Evol. 3: 327–338.
- 407 Bell, J. R. et al. 2005. Ballooning dispersal using silk: world fauna, phylogenies, genetics and  
408 models. - Bull. Entomol. Res. 95: 69–114.
- 409 Bellard, C. et al. 2012. Impacts of climate change on the future of biodiversity: Biodiversity  
410 and climate change. - Ecol. Lett. 15: 365–377.
- 411 Bellard, C. et al. 2013. Will climate change promote future invasions? - Glob. Change Biol.  
412 19: 3740–3748.
- 413 Bellvert, A. et al. 2013. First record of *Dolomedes plantarius* (Clerck, 1758)(Araneae:  
414 Pisauridae) from the Iberian Peninsula. - Rev. Ibérica Aracnol. 23: 109–111.
- 415 Bocedi, G. et al. 2017. RangeShifter: a platform for modelling spatial eco-evolutionary  
416 dynamics and species' responses to environmental changes. - Methods Ecol. Evol.: 388–  
417 396.
- 418 Bonte, D. and Lens, L. 2007. Heritability of spider ballooning motivation under different wind  
419 velocities. - Evol. Ecol. Res. 9: 817–827.

- 420 Bonte, D. et al. 2006. Geographical variation in wolf spider dispersal behaviour is related to  
421 landscape structure. - *Anim. Behav.* 72: 655–662.
- 422 Bonte, D. et al. 2008a. Starvation affects pre-dispersal behaviour of *Erigone* spiders. - *Basic*  
423 *Appl. Ecol.* 9: 308–315.
- 424 Bonte, D. et al. 2008b. Thermal conditions during juvenile development affect adult dispersal  
425 in a spider. - *Proc. Natl. Acad. Sci.* 105: 17000–17005.
- 426 Bonte, D. et al. 2009. Repeatability of dispersal behaviour in a common dwarf spider:  
427 evidence for different mechanisms behind short- and long-distance dispersal. - *Ecol.*  
428 *Entomol.* 34: 271–276.
- 429 Braunisch, V. et al. 2013. Selecting from correlated climate variables: a major source of  
430 uncertainty for predicting species distributions under climate change. - *Ecography* 36:  
431 971–983.
- 432 Briscoe, N. J. et al. 2019. Forecasting species range dynamics with process-explicit models:  
433 matching methods to applications. - *Ecol. Lett.* 22: 1940–1956.
- 434 Buisson, L. et al. 2010. Uncertainty in ensemble forecasting of species distribution. - *Glob.*  
435 *Change Biol.* 16: 1145–1157.
- 436 Cardoso, P. et al. 2020. Scientists' warning to humanity on insect extinctions. - *Biol. Conserv.*  
437 242: 108426.
- 438 Carico, J. E. 1973. The Nearctic species of the genus *Dolomedes* (Araneae: Pisauridae). -  
439 *Bull. Mus. Comp. Zool. Harv. Coll.* 144: 435–488.
- 440 Ceia-Hasse, A. et al. 2014. Integrating ecophysiological models into species distribution  
441 projections of European reptile range shifts in response to climate change. - *Ecography*  
442 37: 679–688.

- 443 Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and  
444 the dynamics of spatially structured populations. - *Ecol. Lett.* 12: 197–209.
- 445 De Meester, N. and Bonte, D. 2010. Information use and density-dependent emigration in an  
446 agrobiont spider. - *Behav. Ecol.* 21: 992–998.
- 447 Dorman, C. et al. 2012. Collinearity: a review of methods to deal with it and a simulation  
448 study evaluating their performance. - *Ecography* 36: 27–46.
- 449 Duffey, E. 1995. The distribution, status and habitat of *Dolomedes fimbriatus* (Clerck) and *D.*  
450 *plantarius* (Clerck) in Europe. - *Proc. 15th Eur. Colloq. Arachnol.*: 54–65.
- 451 Duffey, E. 2012. *Dolomedes plantarius* (Clerck, 1757) (Araneae: Pisauridae): a  
452 reassessment of its ecology and distribution in Europe, with comments on its history at  
453 Redgrave and Lopham Fen, England. - *Bull. Br. Arachnol. Soc.* 15: 285–292.
- 454 EEA, 2018. European Union, Copernicus Land Monitoring Service 2018, European  
455 Environment Agency (EEA)
- 456 Engler, R. and Guisan, A. 2009. MigClim: Predicting plant distribution and dispersal in a  
457 changing climate. - *Diversity and Distributions* 15: 590–601.
- 458 Eskildsen, A. et al. 2013. Testing species distribution models across space and time: high  
459 latitude butterflies and recent warming. - *Glob. Ecol. Biogeogr.* 22: 1293–1303.
- 460 ESRI 2009. World Imagery.
- 461 Etherington, T. R. 2016. Least-Cost Modelling and Landscape Ecology: Concepts,  
462 Applications, and Opportunities. - *Curr. Landsc. Ecol. Rep.* 1: 40–53.
- 463 Fawcett, T. 2006. An introduction to ROC analysis. - *Pattern Recognit. Lett.* 27: 861–874.
- 464 Febbraro, M. D. et al. 2019. Integrating climate and land-use change scenarios in modelling  
465 the future spread of invasive squirrels in Italy. - *Divers. Distrib.* 25: 644–659.

- 466 Fick, S. E. and Hijmans, R. J. 2017. WorldClim 2: new 1-km spatial resolution climate  
467 surfaces for global land areas. - *Int. J. Climatol.* 37: 4302–4315.
- 468 Finlayson, C. M. et al. 2019. The Second Warning to Humanity – Providing a Context for  
469 Wetland Management and Policy. - *Wetlands* 39: 1–5.
- 470 Garcia, R. A. et al. 2014. Multiple Dimensions of Climate Change and Their Implications for  
471 Biodiversity. - *Science* 344: 1247579.
- 472 GBIF: The Global Biodiversity Information Facility 2019. What is GBIF? -  
473 <https://www.gbif.org/what-is-gbif>
- 474 Goodacre, S. L. et al. 2009. Microbial modification of host long-distance dispersal capacity.  
475 - *BMC Biol.* 7: 32.
- 476 Grenouillet, G. et al. 2011. Ensemble modelling of species distribution: the effects of  
477 geographical and environmental ranges. - *Ecography* 34: 9–17.
- 478 Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple  
479 habitat models. - *Ecol. Lett.* 8: 993–1009.
- 480 Guisan, A. et al. 2013. Predicting species distributions for conservation decisions. - *Ecol.*  
481 *Lett.* 16: 1424–1435.
- 482 Hao, T. et al. 2019. A review of evidence about use and performance of species distribution  
483 modelling ensembles like BIOMOD. - *Divers. Distrib.* 25: 839–852.
- 484 Hijmans, R. J. and Graham, C. H. 2006. The ability of climate envelope models to predict the  
485 effect of climate change on species distributions. - *Glob. Change Biol.* 12: 2272–2281.
- 486 Hijmans, R. J. et al. 2005. Very high resolution interpolated climated surfaces for global land  
487 areas. - *International Journal of Climatology* 25: 1965–1978.

- 488 Hill, J. K. et al. 1999. Evolution of flight morphology in a butterfly that has recently expanded  
489 its geographic range. - *Oecologia* 121: 165–170.
- 490 Holec, M. 2000. Spiders (Araneae) of the fishpond eulittoral zone. - *Ekológia Bratisl.* 19:  
491 51–54.
- 492 Hurtt, G. C. et al. 2011. Harmonization of land-use scenarios for the period 1500–2100:  
493 600 years of global gridded annual land-use transitions, wood harvest, and resulting  
494 secondary lands. - *Clim. Change* 109: 117.
- 495 IPCC 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working*  
496 *Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate*  
497 *Change.*
- 498 Ivanov, V. et al. 2017. *Dolomedes Plantarius* (Araneae, Pisauridae) in Belarus: Records,  
499 Distribution and Implications for Conservation. - *Arachnol. Mitteilungen* 54: 33–37.
- 500 Kearney, M. 2006. Habitat, Environment and Niche: What Are We Modelling? - *Oikos* 115:  
501 186–191.
- 502 Kearney, M. and Porter, W. 2009. Mechanistic Niche Modelling: Combining Physiological and  
503 Spatial Data to Predict Species' Ranges. - *Ecology Letters* 12: 334–350.
- 504 Keeley, A. T. H. et al. 2017. Habitat suitability is a poor proxy for landscape connectivity  
505 during dispersal and mating movements. - *Landsc. Urban Plan.* 161: 90–102.
- 506 Keppel, G. and Wardell-Johnson, G. W. 2012. Refugia: keys to climate change management.  
507 - *Glob. Change Biol.* 18: 2389–2391.
- 508 Lafage, D. and Pétilon, J. 2016. Relative importance of management and natural flooding  
509 on spider, carabid and plant assemblages in extensively used grasslands along the Loire.  
510 - *Basic Appl. Ecol.* 17: 535–545.

- 511 Lafage, D. et al. 2015. Disentangling the influence of local and landscape factors on alpha  
512 and beta diversities: opposite response of plants and ground-dwelling arthropods in wet  
513 meadows. - *Ecol. Res.* 30: 1025–1035.
- 514 Lee, V. M. J. et al. 2015. Ballooning behavior in the golden orbweb spider *Nephila pilipes*  
515 (Araneae: Nephilidae). - *Front. Ecol. Evol.* in press.
- 516 Leroy, B. et al. 2013. First Assessment of Effects of Global Change on Threatened Spiders:  
517 Potential Impacts on *Dolomedes Plantarius* (Clerck) and Its Conservation Plans. - *Biol.*  
518 *Conserv.* 161: 155–163.
- 519 Leroy, B. et al. 2014. Forecasted climate and land use changes, and protected areas: the  
520 contrasting case of spiders. - *Divers. Distrib.* 20: 686–697.
- 521 Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship  
522 between phylogenetic relatedness and ecological similarity among species. - *Ecol. Lett.*  
523 11: 995–1003.
- 524 Mammola, S. and Isaia, M. 2017. Rapid poleward distributional shifts in the European cave-  
525 dwelling Meta spiders under the influence of competition dynamics. - *J. Biogeogr.* 44:  
526 2789–2797.
- 527 Marc, P. et al. 1999. Spiders (Araneae) useful for pest limitation and bioindication. - *Agric.*  
528 *Ecosyst. Environ.* 74: 229–273.
- 529 McRae, B. H. et al. 2008. Using Circuit Theory to Model Connectivity in Ecology, Evolution,  
530 and Conservation. - *Ecology* 89: 2712–2724.
- 531 Melo-Merino, S. M. et al. 2020. Ecological niche models and species distribution models in  
532 marine environments: A literature review and spatial analysis of evidence. - *Ecological*  
533 *Modelling* 415: 108837.



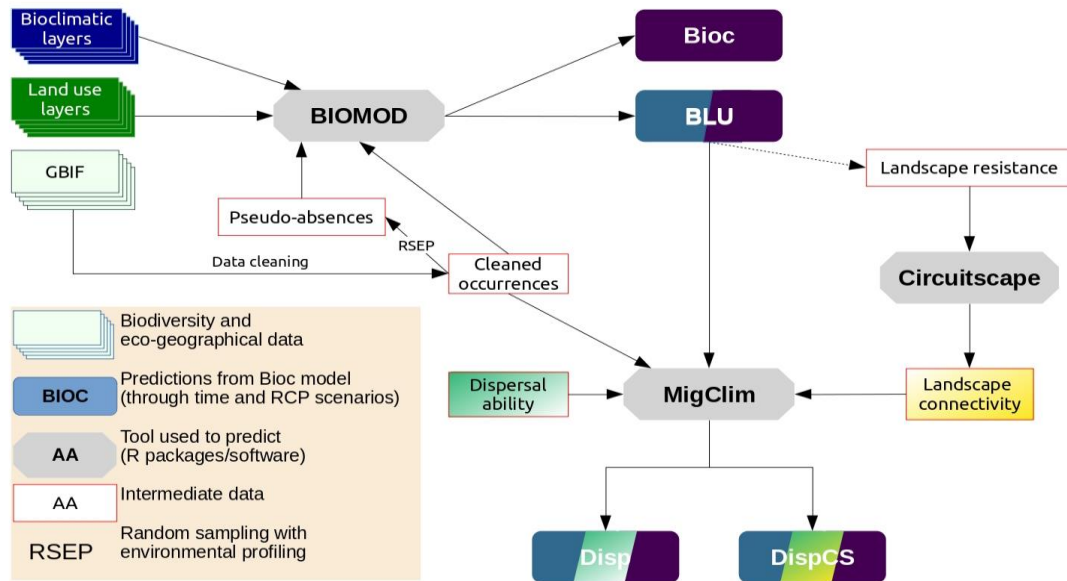
- 534 Merow, C. et al. 2011. Developing Dynamic Mechanistic Species Distribution Models:  
535 Predicting Bird-Mediated Spread of Invasive Plants across Northeastern North America. -  
536 *Am. Nat.* 178: 30–43.
- 537 Miller, J. 2010. Species Distribution Modeling. - *Geogr. Compass* 4: 490–509.
- 538 Montoya, J. M. and Raffaelli, D. 2010. Climate change, biotic interactions and ecosystem  
539 services. - *Philos. Trans. R. Soc. B Biol. Sci.* 365: 2013–2018.
- 540 Noss, R. F. and Daly, K. M. 2006. Incorporating connectivity into broad-scale conservation  
541 planning. - In: Crooks, K. R. and Sanjayan, M. E. (eds), *Connectivity conservation.*  
542 *Conservation biology.* Cambridge University Press, pp. 587–619.
- 543 Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. -  
544 *Annu. Rev. Ecol. Evol. Syst.* 37: 637–669.
- 545 Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts  
546 across natural systems. - *Nature* in press.
- 547 Pelletier, D. et al. 2014. Applying Circuit Theory for Corridor Expansion and Management at  
548 Regional Scales: Tiling, Pinch Points, and Omnidirectional Connectivity. - *PLoS One* 9:  
549 e84135.
- 550 Pereira, H. M. et al. 2010. Scenarios for Global Biodiversity in the 21st Century. - *Science*  
551 330: 1496–1501.
- 552 Prieto-Benítez, S. and Méndez, M. 2011. Effects of land management on the abundance and  
553 richness of spiders (Araneae): A meta-analysis. - *Biol. Conserv.* 144: 683–691.
- 554 Qiao, H. et al. 2015. No silver bullets in correlative ecological niche modelling: insights from  
555 testing among many potential algorithms for niche estimation. - *Methods Ecol. Evol.* 6:  
556 1126–1136.

- 557 R Core Team 2019. R: A language and environment for statistical computing.
- 558 Radchuk, V. et al. 2019. Adaptive responses of animals to climate change are most likely  
559 insufficient. - Nat. Commun. 10: 1–14.
- 560 Reynolds, A. M. et al. 2007. Ballooning dispersal in arthropod taxa: conditions at take-off. -  
561 Biol. Lett. 3: 237–240.
- 562 Richmond, O. M. W. et al. 2010. Is the Climate Right for Pleistocene Rewilding? Using  
563 Species Distribution Models to Extrapolate Climatic Suitability for Mammals across  
564 Continents. - PLoS One in press.
- 565 Rissler, L. J. 2016. Union of Phylogeography and Landscape Genetics. - Proc. Natl. Acad.  
566 Sci. U. S. A. 113: 8079–8086.
- 567 Rödder, D. and Engler, J. O. 2011. Quantitative metrics of overlaps in Grinnellian niches:  
568 advances and possible drawbacks. - Glob. Ecol. Biogeogr. 20: 915–927.
- 569 Samways, M. J. et al. 2020. Solutions for humanity on how to conserve insects. - Biol.  
570 Conserv. 242: 108427.
- 571 Senay, S. D. et al. 2013. Novel three-step pseudo-absence selection technique for improved  
572 species distribution modelling. - PLoS One in press.
- 573 Sinervo, B. et al. 2010. Erosion of Lizard Diversity by Climate Change and Altered Thermal  
574 Niches. - Science 328: 894–899.
- 575 Shah, V. B. and McRae, B. 2008. Circuitscape: a tool for landscape ecology. - Proc. 7th  
576 Python Sci. Conf. 7: 62–66.
- 577 Slatyer, R. A. et al. 2017. Measuring the effects of reduced snow cover on Australia's alpine  
578 arthropods. - Austral Ecology 42: 844–857.

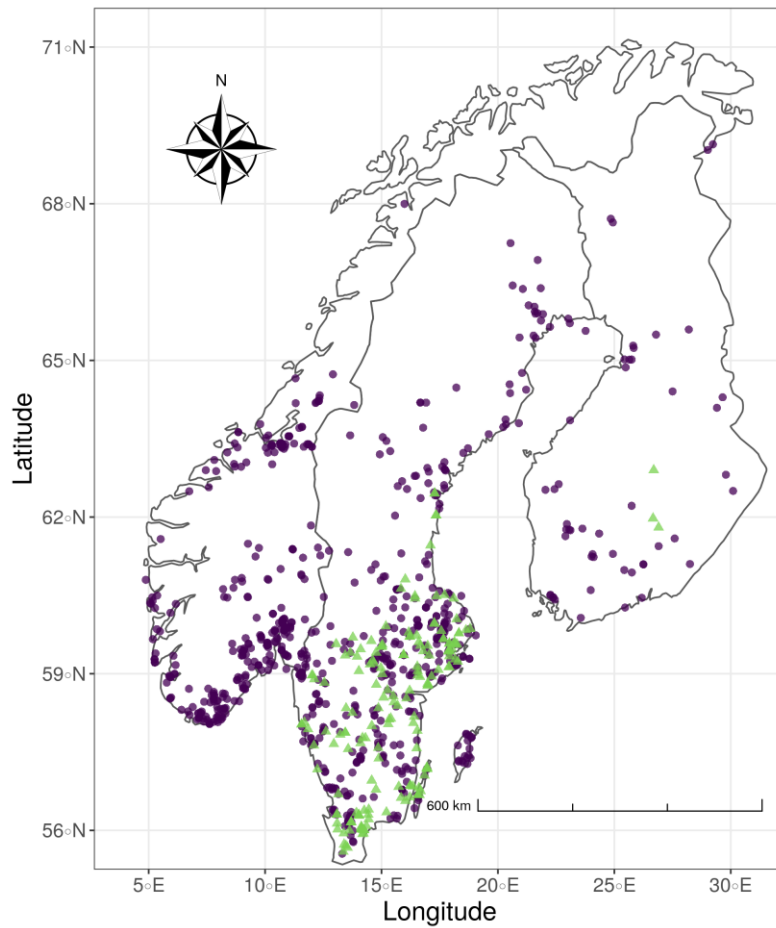
- 579 Soberon, J. and Peterson, A. T. 2005. Interpretation of Models of Fundamental Ecological  
580 Niches and Species' Distributional Areas. - *Biodivers. Inform.* in press.
- 581 Storfer, A. et al. 2007. Putting the 'Landscape' in Landscape Genetics. - *Heredity* 98: 128–  
582 142.
- 583 Svenning, J.-C. and Skov, F. 2004. Limited filling of the potential range in European tree  
584 species. - *Ecol. Lett.* 7: 565–573.
- 585 Thomas, C. F. G. et al. 2003. Aerial activity of linyphiid spiders: modelling dispersal distances  
586 from meteorology and behaviour. - *J. Appl. Ecol.* 40: 912–927.
- 587 Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change.  
588 - *Glob. Change Biol.* 10: 2020–2027.
- 589 Thuiller, W. et al. 2009. BIOMOD – a Platform for Ensemble Forecasting of Species  
590 Distributions. - *Ecography* 32: 369–373.
- 591 Thuiller, W. et al. 2019. Uncertainty in ensembles of global biodiversity scenarios. - *Nat.*  
592 *Commun.* 10: 1–9.
- 593 Titeux, N. et al. 2016. Biodiversity scenarios neglect future land-use changes. - *Glob. Change*  
594 *Biol.* 22: 2505–2515.
- 595 Titeux, N. et al. 2019. Ecological traps and species distribution models: a challenge for  
596 prioritizing areas of conservation importance. - *Ecography* in press.
- 597 Travis, J. M. J. et al. 2012. Modelling dispersal: an eco-evolutionary framework incorporating  
598 emigration, movement, settlement behaviour and the multiple costs involved. - *Methods*  
599 *Ecol. Evol.* 3: 628–641.
- 600 Travis, J. M. J. et al. 2013. Dispersal and species' responses to climate change. - *Oikos* 122:  
601 1532–1540.

- 602 van Helsdingen, P. J. 1993. Ecology and Distribution of Dolomedes in Europe (Araneida:  
603 Dolomedidae). - *Boll Acc Gioenia Sci Nat* 26: 181–187.
- 604 van Vuuren, D. P. et al. 2011. The representative concentration pathways: an overview. -  
605 *Clim. Change* 109: 5.
- 606 Wagner, H. H. and Fortin, M.-J. 2013. A conceptual framework for the spatial analysis of  
607 landscape genetic data. - *Conserv. Genet.* 14: 253–261.
- 608 Warren, D. L. et al. 2008. Environmental Niche Equivalency versus Conservatism:  
609 Quantitative Approaches to Niche Evolution. - *Evol. Int. J. Org. Evol.* 62: 2868–2883.
- 610 Weinstein, B. G. et al. 2017. The role of environment, dispersal and competition in explaining  
611 reduced co-occurrence among related species. - *PLoS One* 12: e0185493.
- 612 Williams, D. D. et al. 1995. Trophic dynamics of two sympatric species of riparian spider  
613 (Araneae: Tetragnathidae). - *Can. J. Zool.* 73: 1545–1553.
- 614 World Conservation Monitoring Centre 1996. The IUCN Red List of Threatened Species  
615 1996. in press.

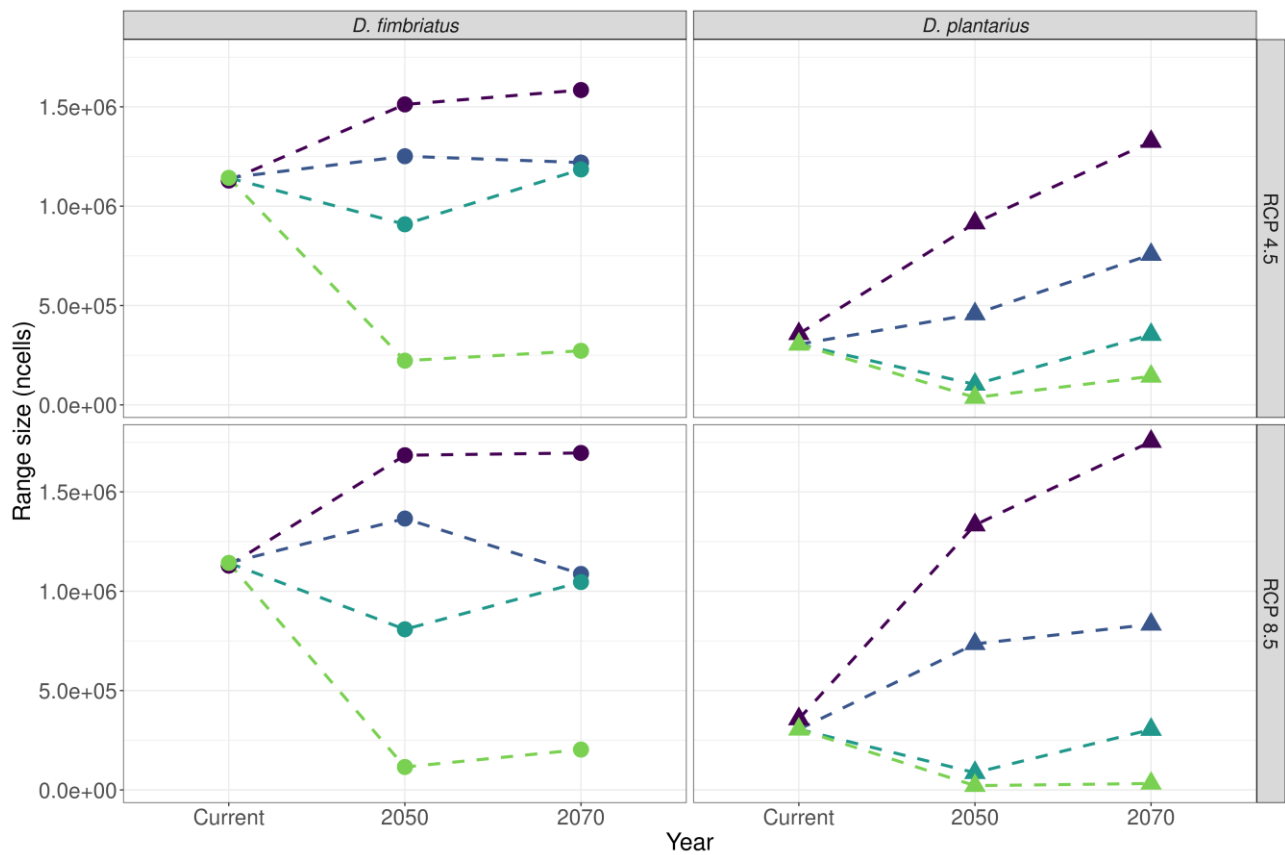
## 616 Figures



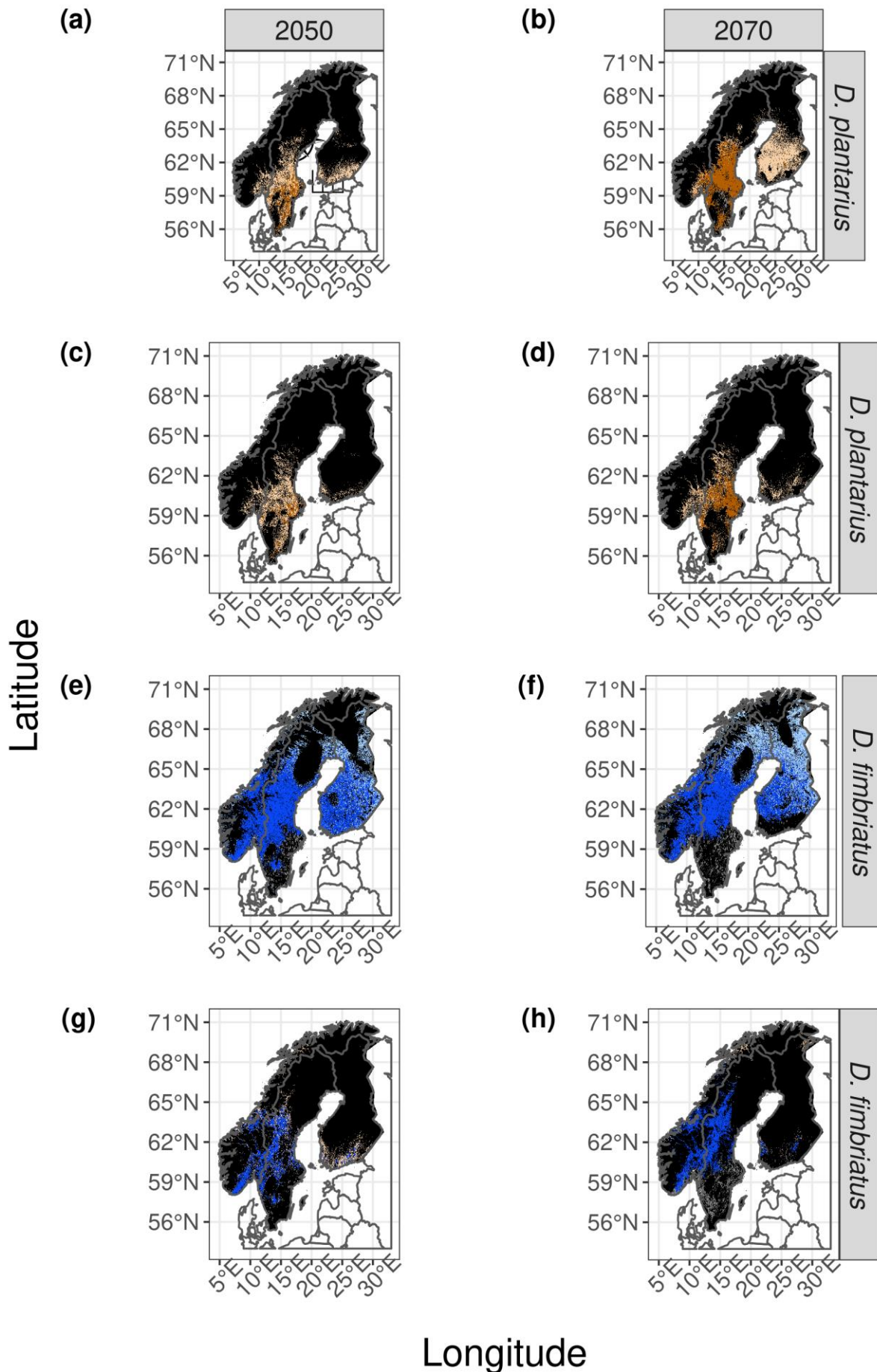
617 Figure 1: Flowchart of the framework used to study the future distribution of the two European  
618 fishing spiders (Bioc: bioclimatic only model, BLU: bioclimatic and land use model, Disp:  
619 dispersal model, DispCS: dispersal and landscape connectivity model).



620 Figure 2: *Dolomedes plantarius* (green triangles) and *Dolomedes fimbriatus* (purple dots)  
621 records in Fennoscandia as of October 2019. Data were extracted from the GBIF database  
622 and supplemented by field samplings.



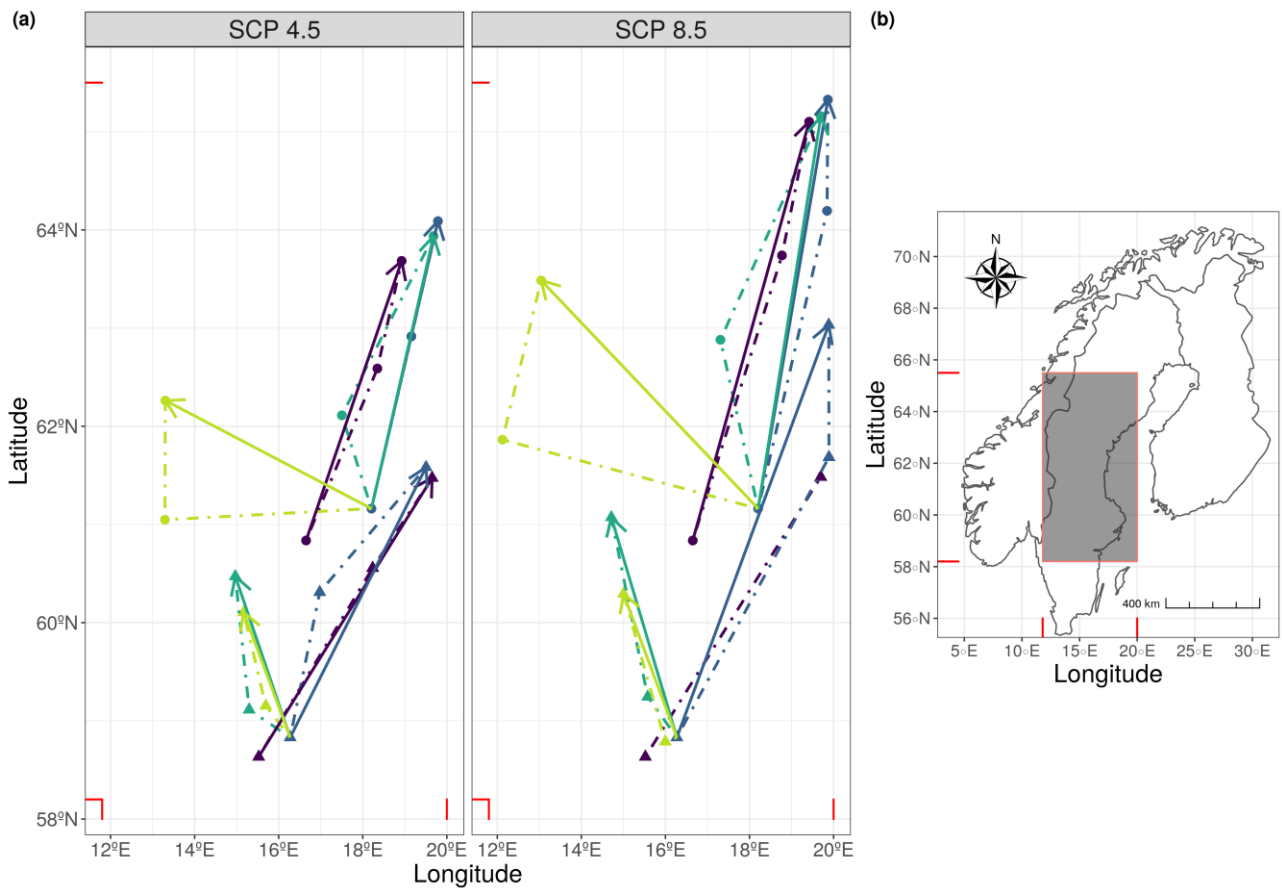
623 Figure 3: Range size in number of cells of suitable habitat predicted by the different SDMs  
624 in time per species and scenarios. (dark purple: Bioc model: bioclimatic variables only; dark  
625 blue: BLU model, bioclimatic + land use; Turquoise: Disp model with dispersal; green:  
626 DispCS model: dispersal and landscape connectivity).



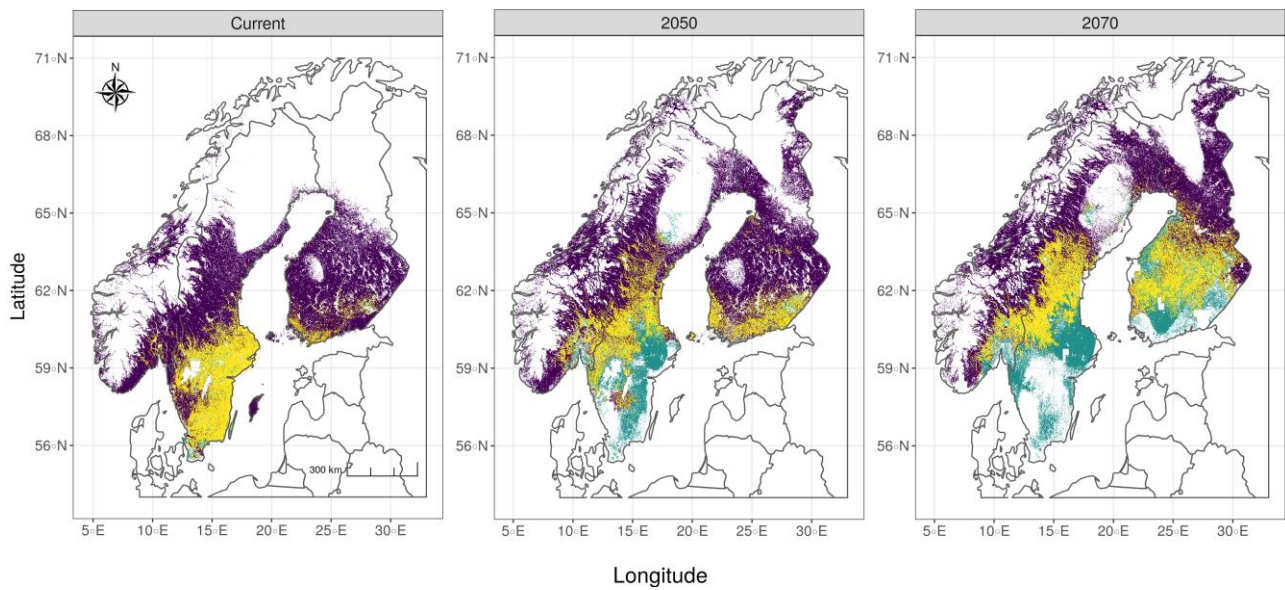
627 Figure 4: Map of the forecasted suitable habitat with an estimation of the reachable range



628 predicted by the dispersion model (Disp) and reachable area from the connectivity model  
629 (DispCS) under the RCP4.5 scenario (RCP: Representative Concentration Pathway; in dark  
630 brown the reachable habitat for *D. plantarius* under Disp (a and b) and DispCS (c and d); in  
631 dark blue the reachable for *D. fimbriatus* under Disp (e and f) and DispCS (g and h); in black:  
632 unsuitable habitat; in grey: previously occupied habitat lost; in light brown and light blue:  
633 suitable but non reachable habitat).



634 Figure 5: Shift in the centre of gravity of the two species distributions predicted by the four  
635 SDMs; solid lines: shift from current to 2070; dashed lines: shift from current time to 2050  
636 and from 2050 to 2070. Dark purple: Bioc model; dark blue: BLU model; turquoise: Disp  
637 model; green: DispCS model.



638 Figure 6: Range overlap predicted by model BLU from current time to 2070 under scenario  
639 RCP4.5. In addition to overlap of suitable range, suitable habitat for each species is  
640 represented. dark purple: suitable habitat for *D. fimbriatus*; green: suitable habitat for *D.*  
641 *plantarius*; yellow: suitable habitat overlapping between the 2 species.