

1 **Effects of climate change on the distribution of hoverfly species (Diptera: Syrphidae) in Southeast Europe**

2

3 Marija Miličić<sup>1,3\*</sup>, Ante Vujić<sup>2</sup>, Pedro Cardoso<sup>3</sup>

4

5 <sup>1</sup>BioSense Institute - Research Institute for Information Technologies in Biosystems, University of Novi Sad, Trg Dr

6 Zorana Đinđića 1, 21000 Novi Sad, Serbia, <sup>2</sup>Department of Biology and Ecology, Faculty of Sciences, University of

7 Novi Sad, Novi Sad, Serbia, <sup>3</sup>Finnish Museum of Natural History, Zoology Unit, University of Helsinki, Helsinki,

8 Finland

9 \*Corresponding author: Marija Miličić, BioSense Institute - Research Institute for Information Technologies in

10 Biosystems, University of Novi Sad, Trg Dr Zorana Đinđića 1, Novi Sad, Serbia. Telephone: +381/644849132. E-

11 mail: marija.milicic@biosense.rs

12

13 **Acknowledgements**

14 We kindly thank John O'Brien for English proofreading and Dr Tamara Jurca for useful comments regarding this

15 paper. This work was supported by the Ministry of Education, Science and Technological Development, Republic of

16 Serbia, under Grant No. 173002 and Grant No. 43002, the Provincial Secretariat for Science and Technological

17 Development under Grant No. 114–457–2173/2011–01 and H2020 project ANTARES under Grant No. 664387.

18

19 **Abstract:** Climate change presents a serious threat to global biodiversity. Loss of pollinators in particular has major

20 implications, with extirpation of these species potentially leading to severe losses in agriculture and, thus, economic

21 losses. In this study, we forecast the effects of climate change on the distribution of hoverflies in Southeast Europe

22 using species distribution modelling and climate change scenarios for two time-periods. For 2041-2060, 19 analysed

23 species were predicted to increase their areas of occupancy, with the other 25 losing some of their ranges. For 2061-

24 2080, 55% of species were predicted to increase their area of occupancy, while 45% were predicted to experience

25 range decline. In general, range size changes for most species were below 20%, indicating a relatively high

26 resilience of hoverflies to climate change when only environmental variables are considered. Additionally, range-

27 restricted species are not predicted to lose more area proportionally to widespread species. Based on our results, two

28 distributional trends can be established: the predicted gain of species in alpine regions, and future loss of species

29 from lowland areas. Considering that the loss of pollinators from present lowland agricultural areas is predicted and  
30 that habitat degradation presents a threat to possible range expansion of hoverflies in the future, developing  
31 conservation management strategy for the preservation of these species is crucial. This study represents an important  
32 step towards the assessment of the effects of climate changes on hoverflies and can be a valuable asset in creating  
33 future conservation plan, thus helping in mitigating potential consequences.

34

35 **Key words:** conservation, global warming, insects, endemism, species distribution modelling

36

### 37 **Introduction**

38 Ecosystems across the world are facing severe modifications due to climate change and many species are facing  
39 extinction risk as a result. Species tolerance to changing climate is critical from ecological, conservation and  
40 evolutionary points of view (Garcia-Robledo et al. 2016). Several studies have shown that climate change influences  
41 many species in different ways: they can move their range to find suitable environment (Hickling et al. 2006;  
42 Parmesan 2006); alter phenology in order to adapt to new conditions (Visser 2008; Gardner et al. 2011); modify  
43 their behaviour, with species opting to change foraging or activity hours, adapt their physiology, or increase  
44 metabolism and growth rates (Hughes 2000); shift their preferred habitat; or eventually undergo evolutionary shifts  
45 (Bradshaw and Holzapfel 2006; Visser 2008; Williams et al. 2008; Daufresne et al. 2009; Maggini et al. 2011). If  
46 none of these is possible or sufficient, extinction is possible (Thuiller et al. 2008; Lurgi et al. 2012).

47 Among range shifts, climate change is expected to force species distributions towards higher elevations and  
48 latitudes, leading to extinction of species whose future habitable climate space becomes too small or too isolated  
49 from their current geographical ranges (Hill et al. 2002; Midgley et al. 2002; Wilson et al. 2005). Limited dispersal  
50 capacity, low reproductive rate and a high degree of habitat specialization are attributes that make species prone to  
51 environmental disturbances (Isaac et al. 2009). Species with a limited distribution often possess most of these  
52 characteristics. Although widespread species may also be endangered, range-restricted species are particularly  
53 vulnerable (Thomas et al. 2004; Wulf et al. 2013).

54 Estimating the effects of climate change on species distributions is an important step in assessing the vulnerability of  
55 species to extinction and can provide useful information about the spectrum of possible consequences (Araújo et al.  
56 2005; Gibson et al. 2010; Yates et al. 2010). Species distribution models (SDM; also called environmental niche

57 models) are often used to predict the effects of climate change and they have been successfully applied in a number  
58 of environmental studies (Hannah et al. 2002; Elith et al. 2006; Peterson 2006). SDM assess the relationship  
59 between species occurrence at sites and the environmental characteristics of those areas (Franklin 2009) in order to  
60 predict the distribution of suitable environmental envelopes for the species in non-sampled areas or time-frames  
61 (Elith and Leathwick 2009; Costion et al. 2015). When used in combination with future climate change scenarios,  
62 these models can indicate the expected effect of changing climate on species distributions.

63 Here, we use SDM to assess the potential effects of climate change on Southeast (SE) European hoverflies.  
64 Hoverflies are Dipteran insects comprising around 6000 described species (Thompson 2013). They are recognized  
65 as an important pollinator group (Fontaine et al. 2005; Petanidou et al. 2011; Jauker et al. 2012; Stenley et al. 2013),  
66 and some species are used as biological control agents (White et al. 1995). SE Europe harbours exceptional hoverfly  
67 diversity. The Balkan Peninsula, occupying the largest part of SE Europe, is considered a hotspot of European  
68 biodiversity (Griffits et al. 2004) owing to its long-term environmental stability (Previšić et al. 2009) and habitat  
69 diversity. The great variety of plants and habitat heterogeneity in this region promotes a high diversity of insect  
70 fauna. Vujić et al. (2001) revealed that the diversity of hoverflies in the Balkan Peninsula is amongst the highest in  
71 Europe. The Aegean islands, a part of our study area, have also been designated as one of the world's hotspots for  
72 hoverflies (Vujić et al. 2012, 2016b; Radenković et al. 2011).

73

74 Our aims were to: (i) analyse the effects of climate change on the distribution of species by examining predicted  
75 changes in range size based on forecasts of current and future potential distribution; (ii) describe and compare  
76 species-richness patterns for both present and future scenarios; (iii) verify if owing to their theoretically higher  
77 vulnerability, the areas of occupancy of range-restricted species decrease proportionally more than those of  
78 widespread species; and (iv) discuss possible consequences to mutualistic networks and implications for  
79 conservation of hoverflies.

80 **Material and methods**

81 **Occurrence data**

82 Species distribution data for all species in SE Europe were extracted from the database of the Department of Biology  
83 and Ecology of the University of Novi Sad, which is the largest database on the region's hoverflies (occurrences of  
84 species used in this study are available at:

85 [http://www.dbe.uns.ac.rs/o\\_departmanu/laboratorije/laboratorija\\_za\\_istrazivanje\\_i\\_zastitu\\_biodiverziteta/prilog/mili](http://www.dbe.uns.ac.rs/o_departmanu/laboratorije/laboratorija_za_istrazivanje_i_zastitu_biodiverziteta/prilog/mili)

86 [cic et al 2017 - species occurrences data](#)). This database comprises data from field collecting in the study area  
87 from 1950-2015, data obtained from different museum and private collections, and published material referring to  
88 this geographic area. Only specimens with precise distributional data were used. If locality coordinates were  
89 available, they were checked for accuracy. Records only with locality names were assigned coordinates using  
90 Google Earth (Google Inc, 2016). For our analysis, we only used species endemic to SE Europe or whose ranges  
91 outside this region do not cover areas with climatic conditions differing from those within the study area (otherwise  
92 SDM would reflect only part of the environmental niche of species and, thus, be potentially biased). For reducing  
93 sampling bias, we applied the thinning procedure, where we used a threshold of 0.01 of the maximum distance  
94 between any two points. The procedure is explained in detail in Miličić et al. (2017). After data processing, all  
95 species with less than five occurrence points were dropped (the number of occurrences per species is assessable in  
96 occurrence data table, provided on the link above in text).

97 **Selection of predictor variables**

98 We used 19 bioclimatic variables plus elevation data (2.5 arc-minutes resolution, approximately 4.5 km<sup>2</sup>) taken from  
99 the WorldClim dataset (Hijmans et al. 2005) for model building. As future bioclimatic variables, we used climate  
100 projections at the same resolution from the global climate models used in the Fifth Assessment report of the  
101 Intergovernmental Panel on Climate Change (IPCC 2013). We chose the HadGEM2-ES model with RCP 8.5  
102 (Representative Concentration Pathway), which is a greenhouse gas concentration trajectory that assumes that  
103 emissions will continue to rise throughout the 21st century. We deliberately choose the “worst case scenario”  
104 because historical and current trends of greenhouse emissions are trailing the RCP 8.5 trajectory (Peters et al. 2013).  
105 Modelling was done in two stages. First, we used all variables. Then, using only the stronger predictors for each

106 species, we built the final models and, in that way, avoiding overfitting the models (see details in Miličić et al.  
107 2017).

108

### 109 **Species distribution modelling**

110 For SDM, we used the maxent function of the *dismo* R package (Hijmans et al. 2016). MAXENT is one of the most  
111 commonly used algorithms for this purpose (Phillips et al. 2006, 2008; Peterson et al. 2007; Ortega-Huerta and  
112 Peterson 2008; Merow et al. 2013). This algorithm shows a generally good performance for presence-only data,  
113 even with small sample sizes (Kumar and Stohlgren 2009; Pearson et al. 2007). There are several examples where  
114 MAXENT has been used for modelling the potential distributions of range-restricted species. For example, Gibson  
115 et al. (2010) used MAXENT to estimate the effect of climate change on a range-restricted marsupial. Costion et al.  
116 (2015) and Krause et al. (2015) used it to assess the effect of climate change on endemic species of plants, and Vujić  
117 et al. (2016a) used MAXENT to identify favourable habitats for hoverflies of conservation interest in Serbia.

118 Dataset was split into training and test data. MAXENT default settings were maintained. For each species, maps of  
119 current and future potential distributions were created for the year 2050 (average of years 2041-2060) and 2070  
120 (average 2061-2080). These maps were then transformed to binary format (showing suitable/unsuitable areas for  
121 species), applying the threshold that maximized the sum of sensitivity and specificity (Liu et al. 2005, 2013).

122 Binary maps were used to calculate the potential area of occupancy (pAOO) for all species in all time-periods. To  
123 assess the predictive performance of the models, we used TSS (True Skill Statistic) as an evaluation measure, which  
124 has been shown to be a good measure of accuracy (Allouche et al. 2006; Liu et al. 2013). TSS values range from -1  
125 to +1, with +1 indicating perfect model agreement and values of zero or less indicating a performance no better than  
126 random (Allouche et al. 2006).

### 127 **Calculation of potential species richness**

128 Our second objective was to describe and compare the species richness patterns for both present and future  
129 scenarios. Maps for each species under the present scenario were overlaid and summed for species richness. We then  
130 did the same for the future scenario. Then, the overall present and future richness maps were subtracted, allowing  
131 changes in diversity per cell between time-periods to be determined (see also Ferreira et al. 2016). All maps were  
132 created using the software DIVA-GIS (version 7.5).

133 Our third objective was to test if the ranges of range-restricted species decrease proportionally more than those of  
134 widespread species. We calculated the Pearson correlation between present pAOO of all species and the respective  
135 predicted relative changes in range size for both time-periods. A significantly negative correlation would indicate  
136 that species with smaller ranges would have higher proportional losses of pAOO, confirming our hypothesis.

137

### 138 **Range expansion and contraction patterns**

139 In order to test whether range expansion and contraction patterns are related with altitude, Spearman rank correlation  
140 among all cells showing difference in species richness (between both future periods and present) and altitude was  
141 calculated.

142

## 143 **Results**

### 144 **Species distribution models**

145 In total, 44 species of hoverflies were included in our analysis (Tab. 1). TSS values used for evaluation of the  
146 models varied between 0.49 and 0.99 (Tab. 1), representing a good fit of the models. The bioclimatic variable  
147 contributing to the highest number of models (n=24) was precipitation seasonality (bio15). Other variables  
148 contributing to more than 10 final models were mean temperature of the wettest quarter (bio8), mean temperature of  
149 the driest quarter (bio9) and precipitation of the driest month (bio14). The list of bioclimatic variables used in each  
150 final model is given in Fig. 1.

151 For 2041-2060, 19 species (43%) were predicted to lose part of their range, while 25 species were predicted to gain  
152 in range. However, for 40% of the species, their pAOO changed by less than 20%. For 2061-2080, 20 species (45%)  
153 were predicted to reduce their area of occupancy, whereas 24 species (55%) would gain occupancy. Variation in  
154 range size for 38% of the species was below 20%. Four different trends can be identified from the overall changes in  
155 pAOO: (1) fifteen species (34%) were predicted to lose part of their range for both time-periods; (2) twenty species  
156 (45%) would expand their pAOO over both time-periods; (3) four species (9%) were predicted to lose part of their  
157 range during the first period and then regain some of it under the second period; and (4) another five species (11%)  
158 would first gain range and then lose it.

159 **Species richness**

160 We predicted the species richness hotspots to be similar across time. The Aegean islands and part of the Dinaric  
161 mountain range stretching through Bosnia and Herzegovina, Serbia and Montenegro were predicted to have the  
162 highest potential number of species in all cases (Fig. 2b, 2c, 2d). The Dinaric mountains, together with the Alpine  
163 region in Slovenia, high mountain peaks in central Peloponnese, part of the Carpathian Mountains in Romania and  
164 the coastal zone along the Black Sea, spreading into the continental areas of Southwest Bulgaria, are predicted to  
165 gain species with time. In contrast, the valleys between the Olympus and Rhodopes mountains, the lowland along  
166 the Dinaric mountain range and the peripheral zone of Strandza Mountain in Bulgaria are each predicted to lose  
167 between 1 and 3 species in the future (Fig. 2e and 2f). In general, higher loss is predicted for 2070 time period.

168 **Loss of area**

169 Our results indicate that the correlations between present ranges of species and proportional changes in range size  
170 for both time-periods were not statistically significant (Tab. 2).

171 Range expansion and contraction patterns for both future time periods showed slight positive statistically significant  
172 correlation with altitude (Tab. 2).

173

174 **Discussion**

175 In this paper, we forecast the effect of climate change on the distribution of hoverflies in SE Europe using SDM and  
176 climate change scenarios for two time-periods. We predict species to be distributed in similar proportions amongst  
177 losers and gainers of areas of occupancy, yet individual species distributions change considerably over time leading  
178 to divergent patterns for various sub-regions of our study area.

179

180 Two recent studies analysed the effects of climate change on the distributions of some species belonging to the two  
181 largest hoverfly genera in the region, *Merodon* and *Cheilosia*. However, in both studies, only widespread species (i.e.  
182 those not limited to the Balkan Peninsula) and with a large number of occurrences (more than 15 and 30 for  
183 *Cheilosia* and *Merodon*, respectively) were included in the analyses. Kaloveloni et al. (2015) predicted *Merodon*  
184 species to be relatively equally divided amongst gainers and losers of areas of occupancy, whereas Radenković et al.

185 (2017) concluded that climate change will have serious consequences for the distributions of almost all studied  
186 *Cheilosia* species, causing severe range losses for these species across the entire Balkan Peninsula. Undoubtedly,  
187 habitat type and the altitude at which a given species occurs influence species distributions of all hoverflies,  
188 regardless of which genus they belong to. Most species included in the analyses of Radenković et al. (2017) are  
189 Alpine, while the *Merodon* species analysed by Kaloveloni et al. (2015) are both high mountain and Mediterranean  
190 in origin, with our analyses confirming the patterns established in these studies. However, endemic species  
191 occurring on some Greek islands, and only included in our analyses, show a mixed response, with some species  
192 increasing their area of occupancy and that of others decreasing. Mediterranean and lowland taxa are predicted to  
193 expand their ranges, as these species can move their range towards higher altitudes if temperatures increase. Thus, it  
194 is not surprising that, in most cases, the regions gaining in terms of species richness are mountainous, such as the  
195 Alpine regions of Slovenia, the Dinaric Mountains, or part of the Carpathian Mountains. The bioclimatic variables  
196 found to mostly affect hoverfly distribution were related to precipitation seasonality and temperature and  
197 precipitation in the driest months, which might be related with these findings. Temperature increases tend to shift  
198 species towards areas of higher altitude, which typically have higher levels of precipitation (Beniston 2006). Climate  
199 change-induced altitudinal shifts have already been reported in numerous studies for different organisms (Penuales  
200 and Boada 2003; Wilson et al. 2005; Hickling et al. 2006; Lenoir et al. 2008). In contrast, lowland areas, such as the  
201 valleys between mountains are predicted to lose species. Global warming may render the climatic conditions in such  
202 regions too harsh (hot and/or dry) for many hoverflies. It should be noted that this loss of species at low altitude  
203 might be compensated by range expansions of species coming from warmer areas in the South and East of Europe,  
204 as these species were not modelled here.

205  
206 Based on our results, three patterns can be established: a) a relatively high resilience of Syrphidae to climate change  
207 disturbance; b) future range expansions of some hoverfly species to new locations, mostly mountainous; and c)  
208 depletion of syrphid species in lowland areas.

209 We predict some species (such as *Merodon virgatus* Vujić et Radenković, 2016; see also Tab. 1) to significantly  
210 expand their range under a feasible climate change scenario. Thus, it seems that projected climate change will create  
211 additional favourable climate space for this and about half the other species we considered here. It is also worth  
212 mentioning that, for a considerable number of species, the variation in range size for both time-periods was below



213 20% (40% and 38% of species for 2050 and 2070, respectively). In addition, we found that range-restricted species  
214 are not predicted to decrease their ranges to a greater proportional extent than widespread species. Together, these  
215 findings might indicate an overall potential inherent resistance to changing climate amongst hoverflies in SE  
216 Europe. If true, hoverflies could become an important alternative leading pollinator group if the number of bees  
217 continues to severely decline as a consequence of changing climate, as has been projected (Biesmeijer et al. 2006;  
218 Dorman et al. 2008). We note that two factors may decisively influence our conclusions regarding the resilience of  
219 species and their future range expansions. These are dispersal capacity and diet specialization. Capacity to disperse  
220 to new climatically-suitable regions is a critical factor in species responses to climatic change, as these potential new  
221 areas may be out of reach for less vagile species. Considering that the vast majority of larvae of the species we  
222 analysed are phytophagous (38 out of 44), contrary to species with saprophagous larvae, the distributions of these  
223 hoverfly species are conditioned by the distribution of their hosts. Host plants of stenotopic species may be  
224 unavailable in the new locations so that even though the climatic envelope of a new area might be suitable, the  
225 habitat perhaps cannot support displaced species. In addition, adult hoverflies are always associated with flowering  
226 plants, their food source, which entails that our predictions are necessarily influenced by how the distributions of  
227 hoverfly host plants will alter in the future. More detailed knowledge about species biology and ecology, namely  
228 functional traits such as dispersal ability and diet, are needed to determine limiting factors for species expansion.

229

230 According to our results, loss of hoverfly species from lowlands and their migration to higher altitudinal areas is to  
231 be expected. Having in mind that lowlands represent significant areas for agriculture used since ancient times  
232 (Turner 1974) because of their higher temperatures and less rugged terrain, these altitudinal shifts might cause a  
233 depletion of potential pollinators from agricultural areas, inevitably causing economic losses. Additionally, even if a  
234 species remain in lowlands, a changing climate may cause temporal (phenological) and spatial (distributional)  
235 mismatches (Hegland et al. 2009), between insect and host plant, leading to partial or complete decoupling of  
236 mutualistic partners (Visser and Both 2005). Such decoupling may result in changes to ecosystem dynamics, which  
237 again lead to economic losses in agricultural communities (Donnelly et al. 2011). Therefore, assessment of the effects  
238 of climate change on mutualistic processes between plants and pollinators is critically needed to fully assess the risk  
239 of climate change and the possible consequences on insect communities.

240 Although predicted future range expansions of some hoverfly species and registered relatively low variations in  
241 range size may indicate high resilience of hoverflies to climate change, there are a number of factors that threaten  
242 current and predicted future locations for Syrphidae conservation. The areas with the highest predicted species  
243 richness for every period, such as the Aegean islands, are dominated by Mediterranean vegetation. Large expanses  
244 of this vegetation type are severely affected by land degradation processes, leading to desertification as a result of  
245 inadequate land use or because of discordance between economic and conservation priorities (Hill et al. 2008).  
246 Many deciduous forests across SE Europe face a similar scenario, harbouring high species richness but are severely  
247 endangered due to forestry and land degradation. Jovičić et al. (2017) indicated that land use has a strong influence  
248 on the species composition of *Merodon* and *Cheilosia* hoverflies. Changes in habitat availability for species and low  
249 tolerance to environmental change increase the risks of severe consequences from climate change. Another factor  
250 that can threaten the potential future expansion of hoverflies is intensive agriculture; multiple examples testify to its  
251 negative effects on biodiversity (Matson et al. 1997; Sotherton 1998; Tilman et al. 2001; Wickramasinghe et al.  
252 2004). Kremen et al. (2002) found that agricultural intensification has a serious effect on bee populations, causing  
253 reductions in both diversity and abundance of species, while Hendrickx et al. (2007) established that total species  
254 richness of hoverflies decreases with increasing management intensity in agricultural fields. Agriculture also causes  
255 fragmentation of natural habitats, which has a ruinous effect, especially on small and isolated populations  
256 (Benton et al. 2003). Tourism also represents serious threat to biodiversity. For example, construction of ski resorts  
257 has a strong negative effect on many plant and animal species, including hoverflies, considering that the majority of  
258 these species are mountainous. Ristić et al. (2012) addressed the negative effects of the construction of a ski resort  
259 on Stara Planina Nature Park in Serbia. As a consequence of the construction of the ski centre, population sizes of  
260 several endemic species of birds and plants were significantly reduced or even disappeared from this area rich in  
261 hoverflies. Similarly, The Valley of Butterflies on the Greek island of Rhodes, which has been designated as a  
262 Natura 2000 site, is predicted to be one of the most species-rich areas for hoverflies under both present and future  
263 climate projections in our analysis. However, the numerous tourists visiting this location severely affect its  
264 environment, and it is unclear how long the species that this site hosts can resist such anthropogenic pressure  
265 (Petanidou et al. 1991). Thus, it might prove crucial to find ways of alleviating the consequences of different  
266 threatening factors to preserve imperilled species and biodiversity in general in these regions.  
267

268 **Conclusion**

269 Undoubtedly, climate change will affect species ranges in the future. Hoverflies are in general conjectured to have a  
270 relatively high resilience to climate change disturbance, with some species predicted to experience future range  
271 expansions to new, mostly mountainous locations, while in lowland areas the depletion of syrphid species is to be  
272 expected. Such range shifts (both expansionary and contractionary) are all the more important for species dependent  
273 on mutualistic networks and that constitute keystone taxa for several ecosystem services such as pollination. Loss of  
274 these species would lead to severe losses in agriculture and, consequently, economic losses. Our study represents an  
275 important step towards the assessment of the effects of changing climate on hoverflies and can help in future  
276 conservation planning, which could mitigate potential economic loss.

277

278 **Data availability**

279 All data generated or analysed during this study are included in this published article [or assessable through the link  
280 provided in the text].

281

282 **Compliance with ethical standards**

283 Funding: This work was supported by the Ministry of Education, Science and Technological Development, Republic  
284 of Serbia, under Grant No. 173002 and Grant No. 43002, Provincial Secretariat for Science and Technological  
285 Development under Grant No. 114–457–2173/2011–01 and H2020 project ANTARES under Grant No. 664387.  
286 The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the  
287 manuscript.

288 Conflict of interest: The authors declare that they have no conflict of interest.

289

290 **References**

291 Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa  
292 and the true skill statistic (TSS). *J Appl Ecol* 43:1223–1232. doi: 10.1111/j.1365–2664.2006.01214.x

293 Araújo MB, Whittaker RJ, Ladle RJ, Erhard M (2005) Reducing uncertainty in projections of extinction risk from  
294 climate change. *Global Ecol Biogeogr* 14:529–538. doi: 10.1111/j.1466–822X.2005.00182.x

295 Beniston M (2006) Mountain weather and climate: a general overview and a focus on climatic change in the Alps.  
296 *Hydrobiologia* 562:3–16. doi: 10.1007/s10750-005-1802-0

297 Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol*  
298 *Evol* 18:182–188. doi: 10.1016/S0169-5347(03)00011-9

299 Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R,  
300 Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and  
301 the Netherlands. *Science* 313:351–354. doi: 10.1126/science.1127863

302 Bradshaw WE, Holzapfel CM (2006) Evolutionary response to rapid climate change. *Science* 312:1477–1478. doi:  
303 10.1126/science.1127000

304 Costion CM, Simpson L, Pert PL, Carlsen MM, Kress WJ, Crayn D (2015) Will tropical mountaintop plant species  
305 survive climate change? Identifying key knowledge gaps using species distribution modelling in Australia. *Biol*  
306 *Conserv* 191:322–330. doi: 10.1016/j.biocon.2015.07.022

307 Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in aquatic ecosystems. *Proc Natl*  
308 *Acad Sci USA*, 106:12788–12793. doi: 10.1073/pnas.0902080106

309 Donnelly A, Caffarra A, O'Neill BF (2011) A review of climate-driven mismatches between interdependent  
310 phenophases in terrestrial and aquatic ecosystems. *Int J Biometeorol* 55:805–817. doi:10.1007/s00484-011-0426-5

311 Dormann CF, Schweiger O, Arens P, Augenstein I, Aviron ST, Bailey D, Baudry J, Billeter R, Bugter R, Bukacek  
312 R, Burel F, Cerny M, De Cock R, De Blust G, DeFilippi R, Diekötter T, Dirksen J, Durka W, Edwards PJ, Frenzel  
313 M, Hamersky R, Hendrickx F, Herzog F, Klotz S, Koolstra B, Lausch A, Le Coeur D, Liira J, Maelfait JP, Opdam  
314 P, Roubalova M, Schermann-Legionnet A, Schermann N, Schmidt T, Smulders MJM, Speelmans M, Simova P,  
315 Verboom J, van Wingerden W, Zobel M, Burel F (2008) Prediction uncertainty of environmental change effects on  
316 temperate European biodiversity. *Ecol Lett* 11:235–244. doi: 10.1111/j.1461-0248.2007.01142.x

317 Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR,  
318 Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM,  
319 Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberon J, Williams S, Wisz MS,

320 Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data.  
321 *Ecography* 29:129–151. doi: 10.1111/j.2006.0906–7590.04596.x

322 Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and  
323 time. *Annu Rev Ecol Evol Syst* 40:677–697 doi: 10.1146/annurev.ecolsys.110308.120159

324 Ferreira MT, Cardoso P, Borges PA, Gabriel R, de Azevedo EB, Reis F, Araújo M, Elias RB (2016) Effects of  
325 climate change on the distribution of indigenous species in oceanic islands (Azores). *Climatic Change* 138:603–615.  
326 doi: 10.1007/s10584–016–1754–6

327 Fontaine C, Dajoz I, Meriguet J, Loreau M (2005) Functional diversity of plant-pollinator interaction webs enhances  
328 the persistence of plant communities. *PLoS Biol* 4: e1. doi:10.1371/journal.pbio.0040001

329 Franklin J (2009) Mapping species distributions: spatial inference and prediction. Cambridge University Press,  
330 Cambridge, UK

331 García-Robledo C, Kuprewicz EK, Staines CL, Erwin TL, Kress WJ (2016) Limited tolerance by insects to high  
332 temperatures across tropical elevational gradients and the implications of global warming for extinction. *Proc Natl*  
333 *Acad Sci USA* 113:680–685. doi: 10.1073/pnas.1507681113

334 Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R (2011) Declining body size: a third universal response to  
335 warming? *Trends Ecol Evol* 26:285–291. doi: 10.1016/j.tree.2011.03.005

336 Gibson L, McNeill A, de Tores P, Wayne A, Yates C (2010) Will future climate change threaten a range restricted  
337 endemic species, the quokka (*Setonix brachyurus*), in south west Australia? *Biol Conserv* 143:2453–2461. doi:  
338 10.1016/j.biocon.2010.06.011

339 Google Inc. Google Earth. Mountain View, California, USA. 2013. <https://www.google.com/earth>. Accessed 15  
340 January, 2016

341 Griffiths HI, Kryštufek B, Reed JM (2004) Balkan Biodiversity Pattern and Process in the European Hotspot.  
342 Kluwer Academic Press, Dordrecht

343 Hannah L, Midgley GF, Millar D (2002) Climate change-integrated conservation strategies. *Global Ecol Biogeogr*  
344 11:485–495. doi: 10.1046/j.1466–822X.2002.00306.x

345 Harrell FE (2001) Regression modelling strategies with applications to linear models, logistic regression and  
346 survival analysis. Springer Series in Statistics, Springer-Verlag, New York

347 Hegland SJ, Nielsen A, Lázaro A, Bjerknæs AL, Totland Ø (2009) How does climate warming affect plant-pollinator  
348 interactions? *Ecol Lett* 12:184–195. doi: 10.1111/j.1461-0248.2008.01269.x

349 Hendrickx F, Maelfait JP, Van Wingerden W, Schweiger O, Speelmans M, Aviron S, Augenstein I, Billeter R,  
350 Bailey D, Bukacek R, Burel F, Diekötter T, Dirksen J, Herzog F, Liira J, Roubalova M, Vandomme V, Bugter R  
351 (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod  
352 diversity in agricultural landscapes. *J Appl Ecol* 44:340–351. doi: 10.1111/j.1365-2664.2006.01270.x

353 Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are  
354 expanding polewards. *Glob Change Biol* 12:450–455. doi: 10.1111/j.1365-2486.2006.01116.x

355 Hijmans RJ, Phillips S, Leathwick J, Elith J (2016) *dismo: Species Distribution Modeling*. R package version 1.1–1.  
356 <https://CRAN.R-project.org/package=dismo>

357 Hijmans RJ, Guarino L, Mathur P (2012) *DIVA-GIS, version 7.5. A geographic information system for the analysis*  
358 *of species distribution data. Manual.* <http://www.diva-gis.org>.

359 Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for  
360 global land areas. *Int J Climatol* 25:1965–1978. doi: 10.1002/joc.1276

361 Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J, Huntley B (2002) Responses of butterflies to twentieth  
362 century climate warming: implications for future ranges. *Proc Roy Soc Lond B Bio* 269:2163–2171. doi:  
363 10.1098/rspb.2002.2134

364 Hill J, Stellmes M, Udelhoven T, Röder A, Sommer S (2008) Mediterranean desertification and land degradation:  
365 mapping related land use change syndromes based on satellite observations. *Glob Planet Chang* 64:146–157. doi:  
366 10.1016/j.gloplacha.2008.10.005

367 Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends Ecol Evol*  
368 15:56–61. doi: 10.1016/S0169-5347(99)01764-4

369 IPCC (2014) Fifth Assessment Report (AR5). Cambridge University Press

370 Isaac JL, Vanderwal J, Johnson CN, Williams SE (2009) Resistance and resilience: quantifying relative extinction  
371 risk in a diverse assemblage of Australian tropical rainforest vertebrates. *Divers Distrib* 15:280–288. doi:  
372 10.1111/j.1472–4642.2008.00531.x

373 Jauker F, Bondarenko B, Becker HC, Steffan–Dewenter I (2012) Pollination efficiency of wild bees and hoverflies  
374 provided to oilseed rape. *Agric For Entomol* 14:81–87. doi: 10.1111/j.1461–9563.2011.00541.x

375 Jovičić S, Burgio G, Diti I, Krašić D, Markov Z, Radenković S, Vujić A (2017) Influence of landscape structure and  
376 land use on *Merodon* and *Cheilosia* (Diptera: Syrphidae): contrasting responses of two genera. *J Insect Conserv* doi:  
377 10.1007/s10841–016–9951–1

378 Kaloveloni A, Tscheulin T, Vujić A, Radenković S, Petanidou T (2015) Winners and losers of climate change for  
379 the genus *Merodon* (Diptera: Syrphidae) across the Balkan Peninsula. *Ecol Model* 313:201–211. doi:  
380 10.1016/j.ecolmodel.2015.06.032

381 Krause CM, Cobb NS, Pennington DD (2015) Range shifts under future scenarios of climate change: dispersal  
382 ability matters for Colorado Plateau endemic plants. *Nat Areas J* 35:428–438. doi:  
383 <http://dx.doi.org/10.3375/043.035.0306>

384 Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural  
385 intensification. *Proc Natl Acad Sci USA* 99:16812–16816. doi: 10.1073/pnas.262413599

386 Kumar S, Stohlgren TJ (2009) Maxent modeling for predicting suitable habitat for threatened and endangered tree  
387 *Canacomyrica monticola* in New Caledonia. *J Ecol Nat Environ* 1:094–098.

388 Lenoir J, Gégout JC, Marquet PA, De Ruffray P, Brisse H (2008) A significant upward shift in plant species  
389 optimum elevation during the 20th century. *Science* 320:1768–1771. doi: 10.1126/science.1156831

390 Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species  
391 distributions. *Ecography* 28:385–393. doi: DOI: 10.1111/j.0906–7590.2005.03957.x

392 Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only  
393 data. *J Biogeogr* 40:778–789. doi: 10.1111/jbi.12058

394 Lurgi M, Lopez B, Montoya J (2012) Climate change impacts on body size and food web structure on mountain  
395 ecosystems. *Philos Trans Roy Soc Lond B Biol Sci* 367:3050–3057. doi: 10.1098/rstb.2012.0239

396 Maggini R, Lehmann A, Kéry M, Schmid H, Beniston M, Jenni L, Zbinden N (2011) Are Swiss birds tracking  
397 climate change? Detecting elevational shifts using response curve shapes. *Ecol Model* 222:21–32. doi:  
398 10.1016/j.ecolmodel.2010.09.010

399 Matson PA, Parton WJ, Power AG, Swift MJ (1997) Agricultural intensification and ecosystem properties. *Science*  
400 277:504–509. doi: 10.1126/science.277.5325.504

401 Merow C, Smith MJ, Silander JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it  
402 does, and why inputs and settings matter. *Ecography* 36:1058–1069. doi: 10.1111/j.1600–0587.2013.07872.x

403 Midgley GF, Hannah L, Millar D, Rutherford MC, Powrie LW (2002) Assessing the vulnerability of species  
404 richness to anthropogenic climate change in a biodiversity hotspot. *Glob Ecol Biogeogr* 11:445–451. doi:  
405 10.1046/j.1466–822X.2002.00307.x

406 Miličić M, Vujić A, Jurca T, Cardoso P (2017) Designating conservation priorities for Southeast European  
407 hoverflies (Diptera: Syrphidae) based on species distribution models and species vulnerability. *Insect Conserv*  
408 *Divers* 10:354–366. doi: 10.1111/icad.12232

409 Ortega-Huerta MA, Peterson AT (2008) Modeling ecological niches and predicting geographic distributions: a test  
410 of six presence–only methods. *Rev Mex Biodiv* 79:205–216

411 Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst*  
412 37:637–669. doi: 10.1146/annurev.ecolsys.37.091305.110100

413 Pearson RG, Raxworthy CJ, Nakamura M, Peterson TA (2007) Predicting species distributions from small numbers  
414 of occurrence records: a test case using cryptic geckos in Madagascar. *J Biogeogr* 34:102–117. doi: 10.1111/j.1365–  
415 2699.2006.01594.x

416 Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny Mountains (NE Spain). *Glob*  
417 *Chang Biol* 9:131–140. doi: 10.1046/j.1365–2486.2003.00566.x

418 Petanidou T, Vokou D, Margaritis NS (1991) *Panaxia quadripunctaria* in the highly touristic Valley of Butterflies  
419 (Rhodes, Greece): conservation problems and remedies. *Ambio*, 20:124–128

420 Petanidou T, Vujić A, Ellis WN (2011) Hoverfly diversity (Diptera: Syrphidae) in a Mediterranean scrub  
421 community near Athens, Greece. *Ann Soc Entomol* 47:168–175. doi: dx.doi.org/10.1080/00379271.2011.10697709



422 Peters GP, Andrew RM, Boden T, Canadell JG, Ciais P, Le Quere C, Marland G, Raupach MR, Wilson C (2013)  
423 The challenge to keep global warming below 2 °C. *Nat Clim Chang* 3:4–6. doi:10.1038/nclimate1783

424 Peterson AT, Papes M, Eaton M (2007) Transferability and model evaluation in ecological niche modeling: a  
425 comparison of GARP and Maxent. *Ecography* 30:550–560. doi: 10.1111/j.0906–7590.2007.05102.x

426 Peterson AT (2006) Uses and requirements of ecological niche models and related distributional models.  
427 *Biodiversity Informatics* 3:59–72. doi: <https://doi.org/10.17161/bi.v3i0.29>

428 Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions.  
429 *Ecol Model* 190:231–259. doi: 10.1016/j.ecolmodel.2005.03.026

430 Phillips SJ, Dudik M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive  
431 evaluation. *Ecography* 31:161–175. doi: 10.1111/j.0906–7590.2008.5203.x

432 Previšić A, Walton C, Kučinić M, Mitrikeski PT, Kerovec M (2009) Pleistocene divergence of Dinaric *Drusus*  
433 endemics (Trichoptera, Limnephilidae) in multiple microrefugia within the Balkan Peninsula. *Mol Ecol* 18:634–647.  
434 doi: 10.1111/j.1365–294X.2008.04046.x

435 Radenković S, Schweiger O, Milić D, Harpke A, Vujić A (2017) Living on the edge: Forecasting the trends in  
436 abundance and distribution of the largest hoverfly genus (Diptera: Syrphidae) on the Balkan Peninsula under future  
437 climate change. *Biol Conserv* 212:216–229. doi: 10.1016/j.biocon.2017.06.026

438 Radenković S, Vujić A, Stahls G, Perez-Banon C, Petanidou T, Šimić S (2011) Three new cryptic species of the  
439 genus *Merodon* Meigen (Diptera: Syrphidae) from the island of Lesvos (Greece). *Zootaxa* 2735:35–56.

440 Ristić R, Kašanin-Grubin M, Radić B, Nikić Z, Vasiljević N (2012) Land degradation at the Stara Planina ski resort.  
441 *Environ Manage* 49:580–592. doi: 10.1007/s00267–012–9812–y

442 Sotherton NW (1998) Land–use changes and the decline of farmland wildlife: an appraisal of the set–aside  
443 approach. *Biol Conserv* 83:259–268. doi: 10.1016/S0006–3207(97)00082–7

444 Stanley DA, Gunning D, Stout JC (2013) Pollinators and pollination of oilseed rape crops (*Brassica napus* L.) in  
445 Ireland: ecological and economic incentives for pollinator conservation. *J Insect Conserv* 17:1181–1189. doi:  
446 10.1007/s10841–013–9599–z

447 Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BF, De Siqueira MF,  
448 Grainger A, Hannah L, Hughes L (2004) Extinction risk from climate change. *Nature* 427:145–148. doi:  
449 doi:10.1038/nature02121

450 Thompson FC (2013) Family Syrphidae. *Systema Dipterorum*, version 1.5. <http://www.diptera.org>. Accessed 28  
451 September 2016

452 Thuiller W, Albert C, Araújo M, Berry P, Cabeza M, Guisan A, Hickler T, Midgley G, Paterson J, Schurr F, Sykes  
453 M, Zimmermann N (2008) Predicting global change impacts on plant species' distributions: future challenges.  
454 *Perspect Plant Ecol Evol Syst* 9:137–152. doi: 10.1016/j.ppees.2007.09.004

455 Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D,  
456 Swackhamer D (2001) Forecasting agriculturally driven global environmental change. *Science* 292:281–284. doi:  
457 10.1126/science.1057544

458 Turner II B L (1974) Prehistoric intensive agriculture in the Mayan lowlands. *Science* 185:118–124.

459 Visser ME (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc Roy*  
460 *Soc Lond B Biol Sci* 275:649–659. doi: 10.1098/rspb.2007.0997

461 Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proc Roy Soc*  
462 *Lond B Biol Sci* 272:2561–2569. doi: 10.1098/rspb.2005.3356

463 Vujić A, Petanidou T, Tscheulin T, Cardoso P, Radenković S, Stahls G, Baturan Ž, Mijatović G, Rojo S, Perez-  
464 Banon C, Devalez J, Andrić A, Jovičić S, Krašić D, Markov Z, Radišić D, Tataris G (2016b) Biogeographical  
465 patterns of the genus *Merodon* Meigen, 1803 (Diptera: Syrphidae) in islands of the eastern Mediterranean and  
466 adjacent mainland. *Insect Conserv Divers* 9:181–191. doi: 10.1111/icad.12156

467 Vujić A, Radenković S, Nikolić T, Radišić D, Trifunov S, Andrić A, Markov Z, Jovičić S, Mudri Stojnić S,  
468 Janković M, Lugonja P (2016a) Prime Hoverfly (Insecta: Diptera: Syrphidae) Areas (PHA) as a conservation tool in  
469 Serbia. *Biol Conserv* 198:22–32. doi: 10.1016/j.biocon.2016.03.032

470 Vujić A, Radenković S, Stahls G, Ačanski J, Stefanović A, Veselić S, Andrić A, Hayat R (2012) Systematics and  
471 taxonomy of the *ruficornis* group of genus *Merodon* Meigen (Diptera: Syrphidae). *Syst Entomol* 37:578–602. doi:  
472 10.1111/j.1365–3113.2012.00631.x

473 Vujić A, Šimić S, Radenković S (2001) Endangered species of hoverflies (Diptera: Syrphidae) on the Balkan  
474 Peninsula. *Acta Entomologica Serbica* 5:93–105.

475 White AJ, Wratten SD, Berry NA, Weigmann U (1995) Habitat manipulation to enhance biological control of  
476 brassica pests by hover flies (Diptera: Syrphidae). *J Econ Entomol* 88:1171–1176. doi:  
477 <https://doi.org/10.1093/jee/88.5.1171>

478 Wickramasinghe LP, Harris S, Jones G, Jennings VN (2004) Abundance and species richness of nocturnal insects on  
479 organic and conventional farms: effects of agricultural intensification on bat foraging. *Conserv Biol* 18:1283–1292.  
480 doi: 10.1111/j.1523–1739.2004.00152.x

481 Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an integrated framework for assessing  
482 the vulnerability of species to climate change. *Plos Biol* 6:2621–2626. doi: 10.1371/journal.pbio.0060325

483 Wilson RJ, Gutiérrez D, Gutiérrez J, Martínez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits  
484 and extent of species ranges associated with climate change. *Ecol Lett* 8:1138–1146. doi: 10.1111/j.1461–  
485 0248.2005.00824.x

486 Wulff AS, Hollingsworth PM, Ahrends A, Jaffré T, Veillon JM, L’Huillier L, Fogliani B (2013) Conservation  
487 priorities in a biodiversity hotspot: analysis of narrow endemic plant species in New Caledonia. *PLoS One*  
488 8:e73371. doi: 10.1371/journal.pone.0073371

489 Yates CJ, McNeill A, Elith J, Midgley GF (2010) Assessing the impacts of climate change and land transformation  
490 on *Banksia* in the South West Australian Floristic Region. *Divers Distrib* 16:187–201. doi: 10.1111/j.1472–  
491 4642.2009.00623.x

492 **Figure legends**

493 **Fig. 1** Contribution of bioclimatic variables related with temperature and precipitation in the final species  
494 distribution models of 44 analysed species of hoverflies in SE Europe. For detailed information on bioclimatic  
495 variables, visit [www.worldclim.org](http://www.worldclim.org)

496 **Fig. 2** Geopolitical map of SE Europe with significant localities (a) and projected potential species richness of  
497 hoverflies for (b) present, (c) 2050, (d) 2070, and differences between (e) 2050 and present and (f) 2070 and present.  
498 Each cell represents the total number of species in defined grid cells

499

500 **Tables**

501 **Tab. 1** TSS values and pAOO values for all time periods, absolute and relative change in pAOO between present  
502 and projected future scenarios for 44 species of hoverflies in SE Europe

503 **Tab. 2** Proportional loss of area and connection of range expansion and contraction patterns with altitude