



## Winners and losers of climate change for the genus *Merodon* (Diptera: Syrphidae) across the Balkan Peninsula



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### ARTICLE INFO

#### Article history:

Received 27 October 2014

Received in revised form 19 June 2015

Accepted 22 June 2015

Available online 16 July 2015

#### Keywords:

Biogeography

Ensemble modelling

Hoverflies

Mediterranean species

Mountainous species

Plant–pollinator mismatch

### ABSTRACT

The implementation of species distribution models on the research of species response to climate change has increased due to the growing vulnerability and extinction rates of various taxa. Reported declines of pollinator population sizes and diversity due to global changes may negatively affect the services they provide. Considering the importance of hoverflies as pollinators, we predict the climate change effect on the potential distribution range of selected species of the genus *Merodon* Meigen, 1803. We used two climate models (ECHAM5, HadCM3) and three climate change scenarios (optimistic, modest, pessimistic), under two time frames (2050 and 2080). We predicted the species spatial distribution as well as the species richness and the percentage turnover for two extreme dispersal hypotheses (limited, unlimited). The analysis was implemented using an ensemble forecasting modelling approach. Species adapted to higher altitudes (i.e. with lower temperature requirements) and/or latitudes were predicted to be more vulnerable to climate change vs. species able to tolerate a wider range of temperatures, by losing a higher percentage of climatically suitable area. Significant differences in distribution ranges were found between mountainous and the remaining species groups each one considered separately (viz. climate-generalists, Mediterranean, and east Mediterranean). Southern Balkans were predicted to experience a preservation of species assemblage across all climate change models, scenarios and dispersal assumptions, while the central and northwestern parts were predicted to be subject to an increased change of their species composition. We emphasize the importance of forecasting distribution shifts of a high number of species for the development of conservation strategies. Furthermore, due to the dependence of *Merodon* fly larvae on geophytes, we highlight the necessity of incorporating biotic interactions to model the potential distribution range shifts of these hoverfly species.

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### 1. Introduction

Global warming has become an important issue during recent years due to the associated changes in ecological processes and environmental elements, posing an increased threat to global biodiversity (Pereira et al., 2010; Thomas et al., 2004). A rapid temperature rise has significant impacts on species populations and thus constitutes a matter of high concern for ecologists. In particular, climate change has been linked to shifts in species' ranges (Chen et al., 2011; Walther et al., 2005), changes in their phenological traits (Parmesan, 2007; Visser and Both, 2005) and temporal and spatial mismatches of interacting species (Burkle and Alarcón,

2011; Schweiger et al., 2008). Extinction risk is predicted to increase for a large number of taxa in the future (Bellard et al., 2012; Pereira et al., 2010), highlighting the vulnerability of many species, as most known species have small geographic ranges and the number of species with restricted distribution range is predicted to increase rapidly even in well-studied taxa (Pimm et al., 2014).

The catastrophic consequence of climate change on terrestrial species is a subject of increased interest during recent years. One of the most widely applied tools to study the effects of climate change on organisms are Species Distribution Models (SDMs), which relate species observations to environmental estimates to predict distribution across landscapes (Elith and Leathwick, 2009). SDMs have been widely used in pollination studies and applied on diverse pollinator species (Giannini et al., 2012; Kuhlmann et al., 2012; Luoto et al., 2006). Pollination is a keystone process with a fundamental role for primary production (Klein et al., 2007), the reproduction of

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large numbers of flowering plant species (Ollerton et al., 2011) and the maintenance of organisms depending on them; besides, the economic value of this ecosystem service is of great significance (Gallai et al., 2009). Increasing declines of pollinator diversity and populations, which are partly associated with the climate change effects (Burkle et al., 2013; Potts et al., 2010), could affect the distribution range of pollinators. Because an increased restriction of pollinators' spatial ranges is associated with high risk of reduction in pollination services, the implementation of SDMs is invaluable to assess the future health of pollination systems.

Most hoverflies feed regularly on pollen and nectar, and thus function as pollinators considered as second in importance after bees (Petanidou et al., 2011). Approximately 6000 hoverfly species have been described worldwide, of which 1200 occur in Europe (Rotheray, 1993). With more than 100 described species, the genus *Merodon* Meigen, 1803 is the second richest in species number on the European continent (Speight, 2013). Especially, the Balkan Peninsula is considered one of the centres of endemism and diversity of *Merodon* (Vujić et al., 2007; Ståhls et al., 2009) with a minimum of 78 recorded species (unpublished data). The high diversity could be a result of the diverse climatic conditions in the Balkans, from Mediterranean to continental, or even an evolutionary result of the high richness and diversity of geophytes in the Mediterranean flora, as *Merodon* species are closely associated with the pollination of, and the larval development in, bulbous plants. Such kinds of interactions are particularly important on small scales, such as at community level, but SDMs are often fitted at larger extents, such as regional to continental. The inclusion of these kinds of interactions into the modelling process for the assessment of climate change effects on species distribution and co-existence is considered essential at every geographical extent, even at the broader scales (Wisze et al., 2013) and, thus, important efforts have been made for the development of ways to account for biotic interactions into the predictive modelling mechanism (Kissling et al., 2012; Wisze et al., 2013).

Our study objectives are to (i) forecast the current distribution of *Merodon* species under a bioclimatic modelling framework, (ii) evaluate the potential range change of *Merodon* species due to climate change effects and (iii) determine the species most threatened by climate change. Regarding the latter aim, we expect that the species encountered in the colder range of the genus' distribution area will be more vulnerable to climate change effects than those occurring in the warmer or in a wide range of the climate gradient. These objectives were assessed by implementing an ensemble modelling approach, in which models with different algorithms are combined to produce more accurate forecasts of species distribution, and hence the use of multi-model ensemble projections has been proposed by several authors (e.g. Araújo and New, 2007; Grenouillet et al., 2011; Marmion et al., 2009).

## 2. Material and methods

### 2.1. Species data set

Current distribution data regarding *Merodon* species were extracted from two databases: the database of the Department of Biology and Ecology of the University of Novi Sad, i.e. the largest hoverfly database of the Balkan Peninsula, with 73 *Merodon* species from a total of 1452 sites; and the database of the Laboratory of Biogeography and Ecology of the Department of Geography of the University of the Aegean (*Melissotheque of the Aegean* cf. Petanidou et al., 2013), with 18 *Merodon* species from 44 sites. Both databases contain long-term observation data, which were checked for their spatial accuracy. We chose species for which a minimum of 30 occurrence points were available to avoid

potential modelling errors associated with small sample sizes (Stockwell and Peterson, 2002; Wisze et al., 2008). In total we applied SDMs to 12 hoverflies (Table 1), classified into four categories: (1) generalist species (*Merodon aberrans* Egger, 1860, *Merodon armipes* Rondani, 1843, *Merodon clavipes* Fabricius, 1781 and *Merodon nigratarsis* Rondani, 1845), (2) mountainous species (*Merodon cinereus* Fabricius, 1794 and *Merodon moenium* Wiedemann, 1822), (3) Mediterranean species (*Merodon albifrons* Meigen, 1822, *Merodon avidus* Rossi, 1790, *Merodon erivanicus* Paramonov, 1925 and *Merodon funestus* Fabricius, 1794) and 4) east Mediterranean/Aegean species (*Merodon spinatarsis* Paramonov, 1929 and *Merodon velox* Loew, 1869). Duplicate records, as well as records before 1950, were removed from the analyses and only one occurrence point per pixel at 2.5 arcmin (ca. ~5 km) resolution was taken into account.

### 2.2. Predictors used for modelling

We assume that at the small spatial scale there is a variety of ecological factors determining a species' absence or presence, such as soil composition, micro-climate, and land cover, while at larger scales we expect the climatic parameters to be more meaningful. The bioclimatic variables (Table 2) for the current conditions (1950–2000) were obtained from the WorldClim database (Hijmans et al., 2005) at 2.5 arcmin resolution. Future bioclimatic variables are generated from Global Climate Models (GCM, also called General Circulation Models), which are provided by the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS, <http://ccafs-climate.org>). There are no objective criteria to rank the performance of climate models (McAvaney et al., 2001). Thus, two climate models, ECHAM5 (Roekner et al., 2003) and HadCM3 (Pope et al., 2000) were used to predict species distributions. For each model we ran three different SRES (Special Report on Emission Scenarios) storylines for the time frames 2050 (averaged across 2040–2069) and 2080 (averaged across 2070–2099). We chose these time frames to represent the near and far future climates, respectively. The A1B is a moderate scenario within the A1 scenario family, assuming a balanced use of fossil and non-fossil energy sources (IPCC, 2007). The A1 scenario family assumes a global population that peaks mid-century and subsequently decreases with a coupled rapid growth of the economy and technology. The A2 scenario describes a strong heterogeneity of the world's economic development and technological change. Finally, the B1 scenario describes a convergent world with the same global population as the A1 scenario but with rapid change in economic structures and the introduction of clean and resource-efficient technology (IPCC, 2007).

The selection of bioclimatic variables to define the habitat suitability for the selected *Merodon* species was based on a multicollinearity assessment using pairwise Pearson correlations coefficient. For each pair of highly correlated variables ( $r \geq \pm 0.75$ ) only the biologically relevant was selected (Appendix A, Table A.1). This resulted in a set of nine bioclimatic variables (see bold variables in Table 2) we used consequently for modelling.

### 2.3. Species distribution modelling process

A number of modelling algorithms has been developed and proposed to identify the relationship between species occurrence and environmental data. We used seven different SDMs within the biomod library (Thuiller et al., 2009) implemented in the R platform (R Development Core Team, 2013). These models have been shown to give accurate results for different samples sizes (Elith et al., 2006; Hernandez et al., 2006). In particular, we ran with default settings (see Thuiller et al., 2013) the: (i) Generalized Linear Model (GLM), (ii) Multivariate Adaptive Regression Splines (MARS),

**Table 1**

Study species and number of occurrences (*N*) at 2.5 arcmin resolution, followed by a short description of preferred environment (PE) and distribution range (DR) (adapted from Speight, 2013).

Study species	<i>N</i>	Description
<i>M. avidus</i>	190	PE: forest/open ground; tracksides etc. in deciduous ( <i>Quercus pubescens</i> ) and evergreen oak forests ( <i>Q. ilex</i> , <i>Q. suber</i> ), <i>Pinus salzmannii</i> and <i>P. halepensis</i> forest (including planted <i>P. halepensis</i> ); old olive groves DR: Mediterranean zone of Europe, from Spain through southern France to Italy, the Balkan Peninsula and Romania
<i>M. albifrons</i>	115	PE: open ground; stony, unimproved, non-calcareous dry grassland and open, tall-herb areas in <i>Q. pubescens</i> and <i>Q. ilex</i> forest on calcareous substrates DR: from central France south to the Mediterranean and N Africa; from western Spain eastwards through central (Switzerland, Austria) and southern Europe (Corsica, Sardinia, Sicily, Italy, former Yugoslavia, Greece, Bulgaria, Romania) to the Crimea and Azerbaijan
<i>M. clavipes</i>	100	PE: open ground; sparsely-vegetated, semi-arid, unimproved, stony pasturage and open, grassy areas within thermophilous <i>Quercus</i> forest DR: from northern France to the Mediterranean (including Corsica, Sardinia, Sicily and Crete) and N. Africa; from Portugal and Spain through central and southern Europe to Greece, Romania, Ukraine and Turkey
<i>M. aberrans</i>	82	PE: unimproved, calcareous montane grassland and patchily-vegetated, herb-rich open areas within the <i>Abies</i> forest zone, in the Alps and Pyrenees. At lower altitudes, including Balkanic thermophilous <i>Quercus</i> forest, in South East Europe DR: through central Europe from Germany, the Czech Republic and the Alps (France, Switzerland, Austria) to Hungary and Romania and on to the Ukraine and southern Russia; in southern Europe from mountainous parts of Portugal and Spain eastwards to Italy, Albania, the former Yugoslavia and Greece and on to Turkey and round the Mediterranean (Lebanon) into N. Africa (Morocco), including Mediterranean islands e.g. Crete
<i>M. moenium</i>	72	PE: forest/open ground; humid <i>Fagus/Picea</i> forest; mesophilous <i>Fagus</i> forest; thermophilous <i>Quercus</i> forest; dry, unimproved, lowland grassland; old almond and cherry orchards DR: probably from southern Sweden south to the Mediterranean; from France through most of central and southern Europe to Turkey and European parts of Russia
<i>M. armipes</i>	66	PE: open ground; thermophilous <i>Quercus</i> forest, thermophilous forest fringes, open areas within dry scrub and dry/semi-arid, closed, unimproved grassland DR: from north-east France (Rhine valley in Alsace) and adjacent parts of Germany, through central Europe (Switzerland) and mountainous parts of northern Italy into the former Yugoslavia and on to Bulgaria, Romania and the Crimea; Greece, Turkey
<i>M. nigritarsis</i>	63	PE: forest/open ground; herb-rich, dry/semi-arid, unimproved grassland and open areas in evergreen <i>Q. ilex</i> and <i>Q. suber</i> forest/maquis, <i>Pinus matorral</i> and Mediterranean scrub DR: Spain, Central Europe from Austria, southern France, Greece, Hungary, Italy, Poland, Switzerland; Balkan Peninsula, Turkey
<i>M. cinereus</i>	48	PE: open ground; from the <i>Picea</i> zone up to 2500 m., in unimproved, calcareous and non-calcareous montane and alpine grassland DR: Massif Central (France), Alps, Apennines (Italy), the former Yugoslavia; southern parts of Russia, the Ukraine and northern Turkey
<i>M. funestus</i>	39	PE: forest/open ground; open areas in evergreen oak forest of <i>Quercus ilex</i> and <i>Q. coccinea/Q. macrolepis</i> ; by seasonal streams in Balkanic thermophilous <i>Quercus</i> forest; tall-herb ruderal communities on sparsely-vegetated open ground, close to seasonal rivers and streams, or drainage ditches DR: most of southern and central Spain and round the Mediterranean basin through southern France, the length of Italy (inc. Sicily), parts of the former Yugoslavia, Albania and Turkey to Israel and Libya; known also from Bulgaria and Romania and, apparently, from Poland
<i>M. spinitarsis</i>	39	PE: forest; grassy open areas in <i>Pinus</i> forest (Vujić et al., 2011) and thermophilous deciduous forest; <i>Castanea</i> forest (Ricarte et al., 2012; Stähls et al., 2009) DR: Greece, Romania, Turkey
<i>M. erivanicus</i>	31	PE: open ground; beside seasonal water-courses with a riparian forest strip of <i>Populus</i> and <i>Salix</i> scrub within otherwise open steppe (Hauser, 1998); alongside rivers, in various habitats, including olive orchards and <i>Castanea</i> forest (Ricarte et al., 2012); phrygana (Petanidou et al., 2011) DR: parts of the former Yugoslavia (Croatia, FYROM), Greece, Caucasus (Armenia), Turkey, Israel, Azerbaijan
<i>M. velox</i>	31	PE: forest/open ground; semi-arid, stony, thinly-vegetated, unimproved grassland and open areas in <i>Abies</i> forest; <i>Castanea</i> forest DR: Greece, Turkey

**Table 2**

Initial set of 19 bioclimatic variables representing annual trends, seasonality and extreme or limiting environmental factors (<http://www.worldclim.org/>). The variables used for modelling are listed in bold.

Code	Bioclimatic variables	Abbreviation
Bio1	Annual mean temperature	
Bio2	Mean diurnal range	
<b>Bio3</b>	<b>Isothermality</b>	<b>Isoth</b>
Bio4	Temperature seasonality	
<b>Bio5</b>	<b>Max temperature of warmest month</b>	<b>MTWM</b>
<b>Bio6</b>	<b>Min temperature of coldest month</b>	<b>MTCM</b>
<b>Bio7</b>	<b>Temperature annual range</b>	<b>TAR</b>
<b>Bio8</b>	<b>Mean temperature of wettest quarter</b>	<b>MTWQ</b>
<b>Bio9</b>	<b>Mean temperature of driest quarter</b>	<b>MTDQ</b>
Bio10	Mean temperature of warmest quarter	
Bio11	Mean temperature of coldest quarter	
Bio12	Annual precipitation	
Bio13	Precipitation of wettest month	
Bio14	Precipitation of driest month	
<b>Bio15</b>	<b>Precipitation seasonality</b>	<b>PSeas</b>
<b>Bio16</b>	<b>Precipitation of wettest quarter</b>	<b>PWQ</b>
<b>Bio17</b>	<b>Precipitation of driest quarter</b>	<b>PDQ</b>
Bio18	Precipitation of warmest quarter	
Bio19	Precipitation of coldest quarter	

(iii) Classification Tree Analysis (CTA), (iv) Flexible Discriminate Analysis (FDA), (v) Generalized Boosting Model (GBM), (vi) Random Forest (RF), and (vii) Maximum Entropy (MaxEnt). Details on the first six models can be found in Thuiller et al. (2009) and on the MaxEnt method in Phillips et al. (2006) and Elith et al. (2011).

Since reliable absences were not available for the implementation of the selected models we generated pseudo-absences. Two sets of 1000 pseudo-absences in each were generated randomly across the entire area in order to conform as far as possible with the recommendations of Barbet-Massin et al. (2012). These authors found that for classification and machine-learning techniques the way pseudo-absences were generated had little influence on model performance, although for regression techniques the predictive accuracy was enhanced by the random selection of pseudo-absences. Conversely, regarding the optimal number of pseudo-absences, they found that a moderate number per replicate had little influence on regression techniques but increased the predictive ability of classification and machine-learning techniques. Equal weights were given to presences and pseudo-absences in order to have the same significance in the calibration process.

The importance of each variable in each modelling algorithm was estimated by applying a randomization procedure, which is independent of the algorithm used, implemented in biomod (Thuiller et al., 2009). This procedure uses Pearson correlation

between the standard predictions (i.e. fitted values) and predictions where the variable under investigation has been randomly permuted. High correlation between predictions indicates low importance of the permuted variable. This procedure was repeated five times and the variable importance was calculated as one minus the mean of correlations (Thuiller et al., 2009).

#### 2.4. Assessing predictive performance

The predictive ability of each model was evaluated by splitting the dataset for each species into two partitions, 80% of the data were used for the calibration of the models and the remaining 20% for evaluation purposes. This procedure was repeated three times to obtain a more robust average estimation of model performance. Two different evaluation metrics, the true skill statistic (TSS, Allouche et al., 2006) and the Area Under the receiver operating characteristic Curve (AUC, Fielding and Bell, 1997), were used. For each species a total of 504 models were generated (7 modelling algorithms  $\times$  3 cross-validation (testing of predictive ability)  $\times$  2 pseudo-absence replicates  $\times$  2 climate models  $\times$  3 climate change scenarios  $\times$  2 time periods).

#### 2.5. Ensemble forecasts—Potential range changes

Instead of choosing a model with the best predictive accuracy, a combination of multiple well predictive models can be implemented, resulting in an ensemble modelling framework. Such an approach was followed to account for the variability in forecasts among different single distribution models and to produce more accurate predictions, reducing the prediction uncertainty derived from different algorithms (Araújo and New, 2007). To avoid the inclusion of weak models we selected only projections with AUC and TSS above 0.8 and 0.6, respectively (Bellard et al., 2013; Gallien et al., 2012). The final current and future ensemble models for each IPCC scenario were obtained by applying a weighted mean consensus method based on the evaluation scores. This method has been shown to provide considerably more robust predictions than the other available methods (Marmion et al., 2009). For each GCM one current and three future ensemble probability distribution maps (one for each emission scenario) were produced for two time periods (2050 and 2080). These consensus models were transformed into binary predictions (suitable/non-suitable) to investigate if the potential range of species was predicted to shrink or expand. The binary transformation was performed by applying a threshold maximizing the True Skill Statistic (Allouche et al., 2006). This is equivalent to the threshold that maximizes the sum of sensitivity and specificity, which has been shown to produce more precise predictions (Jiménez-Valverde and Lobo, 2007) and to outperform other methods for threshold selection for presence only data (Liu et al., 2013).

The impact of climate change to the potential species range change of each climate scenario and time period per ensemble GCM was estimated (Thuiller et al., 2009). The species range change was calculated as the percentage gain, which corresponds to the percentage of predicted new occupied sites in addition to the current potential distribution, minus the percentage loss, which corresponds to the loss of currently predicted occupied sites. For each species we estimated the current and the future range size (number of pixels occupied), assuming no dispersal for the three climate change scenarios of the HadCM3 climate model for the year 2080. The mean differences between the current and the future range sizes for the four species categories ((A) climate-generalist, (B) mountainous, (C) Mediterranean, and (D) east Mediterranean/Aegean), for each climate change scenario were evaluated using a one-way ANOVA. The significant differences between the groups of species were determined by applying a

post-hoc test (Tukey HSD). Furthermore, the spatial niche overlap, i.e. the percentage of potentially common occupied area, defined by current and future predictions, was computed.

#### 2.6. Species richness—Percentage turnover

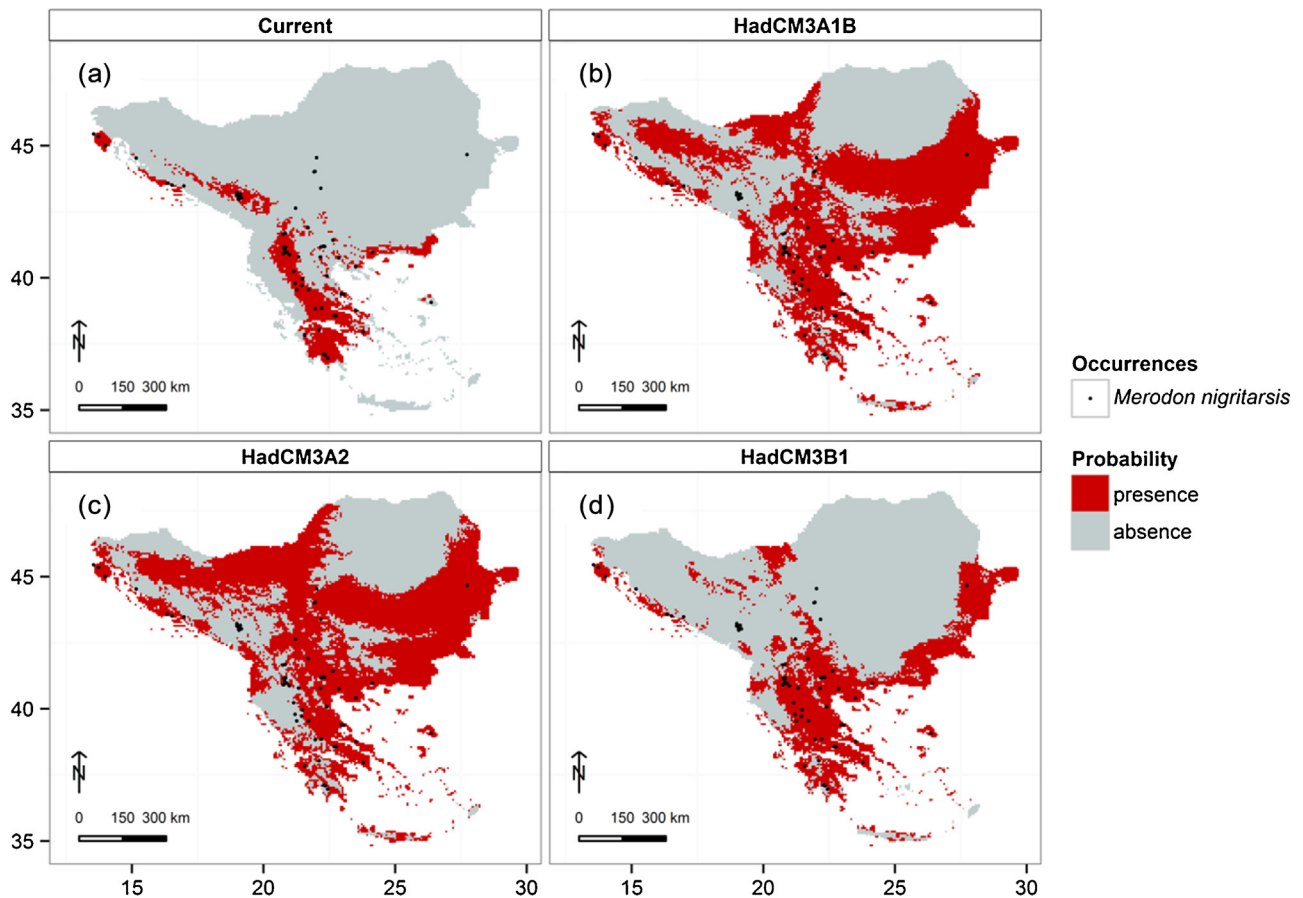
The predicted species richness (SR) was calculated for the current as well as the future conditions. The future SR was estimated under unlimited dispersal scenario (Full Dispersal, FD), assuming that species can disperse to any grid cell with climatically suitable space, and limited dispersal (No Dispersal, ND), assuming that species are incapable of dispersal even if the climatic conditions favour its occupancy. Species turnover is a dissimilarity index, where a value of 0 indicates that the current and future species assemblage is predicted to be the same, whereas a value of 100 indicates changes in species composition. To estimate the species turnover we calculated the number of species lost (L) and gained (G) by pixel. Percentage of species turnover between the two time periods, current and future, for each climate scenario, climate model and time frame, was calculated in each grid cell under the FD scenario by the following equation  $T_{FD} = 100 (L + G) / (SR + G)$  and under ND scenario as  $T_{ND} = 100 (L / SR)$  (Thuiller, 2004), where SR is the current species richness.

### 3. Results

The AUC and TSS values varied mainly among species rather than among algorithms (Appendix A, Figs. A.1 and A.2). The importance of variables, averaged per species across models, is given in Appendix A, Fig. A.3. Species responded differently to potential climate changes according to different climate models and climate change scenarios. For both years two of the climate-generalist species (*M. armipes* and *M. clavipes*) and three of the Mediterranean species (*M. avidus*, *M. erivanicus* and *M. funestus*) were predicted to have small changes regarding their range extent (Appendix B, Fig. B.1). Also, one of the climate-generalist (*M. nigratarsis*), one of the Mediterranean (*M. albifrons*) and both the east Mediterranean species (*M. spinitarsis* and *M. velox*) had extended future potential ranges, especially for the HadCM3 model, whereas the mountainous species (*M. cinereus* and *M. moenium*) were predicted to be the most negatively influenced by potentially losing major extent of their current range (Appendix B, Fig. B.1). Examples of the current potential distribution of the climate-generalist *M. nigratarsis* and the mountainous *M. cinereus* and their predicted response to future climate changes under the HadCM3 climate models of the year 2080 is presented in Figs. 1 and 2, respectively. Our results show that *M. nigratarsis* may be less affected by climate changes as it maintains most of the current extent and gains more suitable habitats across all climate models and scenarios, while *M. cinereus* is predicted to lose a large part of the climatically suitable potential space.

The range change represents the overall predicted trend of species to shrink or expand. The variations of the range change between the projections of the applied climate models and climate change scenarios can be observed for the time frames 2050 and 2080 in Fig. 3. From the twelve studied species, five (*M. aberrans*, *M. avidus*, *M. cinereus*, *M. funestus* and *M. moenium*) are predicted to lose part of their current occupancy, especially the two mountainous species (*M. cinereus* and *M. moenium*) for both time periods. In contrast, the rest of the species are predicted to expand their current range with a notable increased gain of *M. spinitarsis* and *M. velox* for the HadCM3 climate models for 2050 and 2080. The outcomes of the ECHAM5 and HadCM3 climate models varied for the majority of the species. Only the mountainous species had similar results across all the climate models and climate scenarios, as they were predicted to lose over





**Fig. 1.** Predicted potential distribution of the climate-generalist species *Merodon nigritarsis* for the year 2080 under the (a) current and (b) A1B, (c) A2 and (d) B1 climate-warming scenarios of the HadCM3 climate model. The red areas represent the predicted probability of occurrence.

70% of their suitable habitat in all cases. The results for the two climate models were mostly different for *M. aberrans*, as for the case of the ECHAM5 the reduction of the current distribution is higher for both years compared with the HadCM3 results. The ANOVA results of the mean range size differences between groups of species for the HadCM3 climate model for 2080 are presented in Appendix C, Table C.1. The mean range size differences between groups of species are significant for the A2 ( $p < 0.001$ ) and B1 ( $p < 0.01$ ) climate change scenarios. According to the Tukey HSD tests the mean differences between each pair of species categories for all climate scenarios were significant between the mountainous—climate-generalist, Mediterranean—mountainous and east Mediterranean/Aegean—mountainous species ( $p < 0.05$ , Appendix C, Fig. C.1).

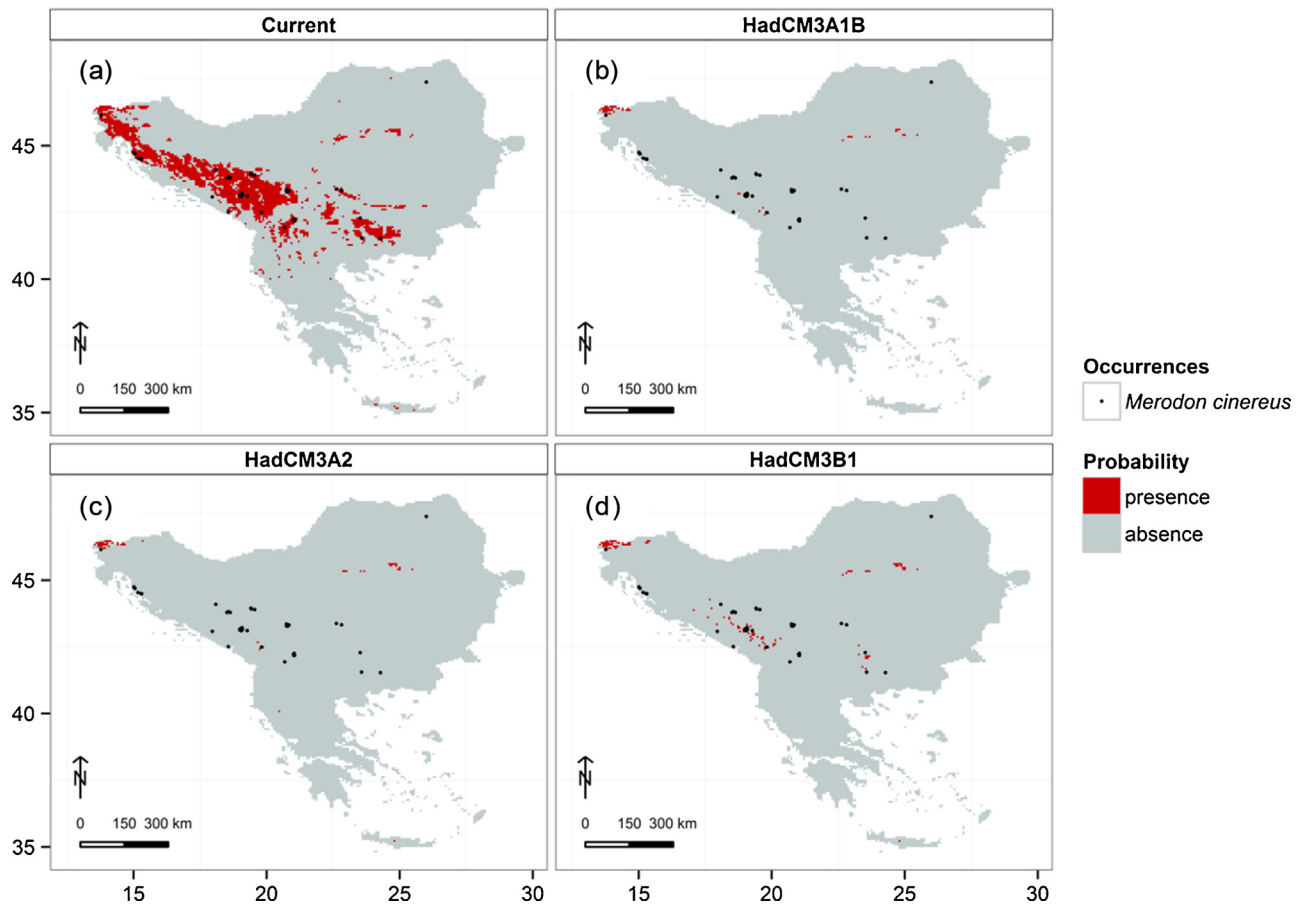
The spatial overlap, which was measured between the predicted current and future suitable habitat, tends to be higher (>21.5%) for all climate models and scenarios for the Mediterranean species (*M. albifrons*, *M. avidus*, *M. erivanicus* and *M. funestus*) and for one of the climate-generalist species (*M. clavipes*) (Table 3). The smallest overlap was found in *M. moenium* for the HadCM3 A2 scenario of the year 2080 (0.51%) and the highest in *M. albifrons* for the ECHAM5 B1 scenario in 2050 (42.52%).

Predicted areas with high species richness in current conditions were detected in the southern, central and northwestern part of the Balkan Peninsula. Under the future climate scenarios the forecasted species richness was higher mostly in the southern and northwestern areas for both years, both climate models and dispersal scenarios with low variations among them (Appendix B, Figs. B.2–B.5). Only the A1B and A2 scenarios of the HadCM3 climate model for 2080 under the full dispersal hypothesis generated

different results with additional predicted areas of high species richness in the northeastern part. Percentage of turnover rate showed similar patterns among climate change scenarios (Appendix B, Figs. B.6–B.7), while highest variability is predicted for the HadCM3 climate model of the year 2080 across dispersal scenarios (Fig. 4). According to the full dispersal results for the HadCM3 model the central, north and northwestern parts would be the most affected as the higher rate of species turnover indicates increased predicted changes of species assemblages. Under the most likely no dispersal scenario the northeastern part was predicted to be the least affected by climate change in terms of species turnover followed by the southern part, while higher turnover values were predicted to the western part. Across all climate change and dispersal scenarios as well as climate models and years the southern areas of Balkans were predicted to be the least influenced regarding the species compositional changes.

#### 4. Discussion

Using different climate models and scenarios for two time frames we predicted the climate impact on the potential current distribution of 12 *Merodon* species. The AUC and TSS values of the most widespread species, *M. aberrans*, *M. armipes* and *M. clavipes*, which appear in different altitudes and thus within a broader range of climatic conditions, were lower than the evaluation scores of the more restricted species (*M. spinatarsis* and *M. velox*). The accurate modelling of narrow-ranged species has been demonstrated by numerous studies (Guisan et al., 2007; Segurado and Araújo, 2004; Stockwell and Peterson, 2002). Lobo and Tognelli (2011) presumed that the improved modelling performance of species with



**Fig. 2.** Predicted potential distribution of the mountainous species *Merodon cinereus* for the year 2080 under the (a) current and (b) A1B, (c) A2 and (d) B1 climate-warming scenarios of the HadCM3 climate model. The red areas represent the predicted probability of occurrence.

a restricted occurrence area might be the result of an increased chance of reliably generated pseudo-absences. This explains the significantly higher evaluation scores of *M. spinitarsis* and *M. velox*, whose distribution range is limited in the Balkans.

We assume that an increase in temperature in the future can potentially have a high impact on the distribution of hoverflies, although the degree of influence of potential climate change to species' distribution depends on their ecological requirements and their adaptation ability. Such characteristics (e.g. preferred habitat types, distribution range, adult behaviour), are available for the study species (Speight, 2013). However, the way their distribution is affected by a potential climate change is currently unidentified and is complemented by the results of this study. Species

occupying regions with extreme climatic conditions, such as mountainous species (*M. cinereus* and *M. moenium*), which appear in higher altitudes, may be the most negatively affected, as they were predicted to lose major extent of the climatically suitable environment. In such cases the ability of species to cope with the adverse effect of climate change depends on their dispersal ability to move outside the modeled region. Indeed, many *Merodon* species have limited dispersal ability (*M. hamifer* Sack 1913, *M. ottomanus* Hurkmans 1993, *M. toscanus* Hurkmans 1993, *M. atratus* Oldenberg 1919, *M. ambiguus* Bradescu 1986, *M. caeruleus* Loew 1869, *M. planifacies* Bezzi 1915, *M. hoplitis* Hurkmans, *M. chalybeatus* Sack 1913 among others, and *M. cinereus*, *M. erivanicus*, *M. funestus*, *M. spinitarsis* among species studied herewith). However, the most effective

**Table 3**

Overlap (%) between the current and the future predicted area under the ECHAM5 and HadCM3 climate models in 2050 and 2080.

Species	ECHAM5 2050			HadCM3 2050			ECHAM5 2080			HadCM3 2080		
	A1B	A2	B1	A1B	A2	B1	A1B	A2	B1	A1B	A2	B1
<i>M. aberrans</i>	12.26	16.52	19.46	12.50	11.53	17.00	10.37	5.87	14.20	9.61	7.75	14.52
<i>M. albifrons</i>	39.24	35.34	42.52	36.62	36.97	34.73	33.86	35.95	39.28	22.63	21.68	35.65
<i>M. armipes</i>	8.66	13.22	3.80	6.71	6.73	5.80	12.93	8.90	13.58	4.03	3.80	5.47
<i>M. avidus</i>	37.39	40.63	40.68	38.14	37.64	39.09	32.31	33.07	34.44	32.22	33.20	35.50
<i>M. cinereus</i>	12.51	14.26	24.38	7.34	9.04	6.41	16.74	5.44	18.25	2.13	1.83	5.29
<i>M. clavipes</i>	36.52	37.50	37.93	30.82	31.29	30.64	35.59	36.59	34.31	22.65	24.45	30.96
<i>M. erivanicus</i>	38.28	37.17	39.37	33.77	36.12	37.87	34.22	34.32	34.70	31.17	24.95	36.65
<i>M. funestus</i>	32.54	39.63	38.27	35.18	34.31	38.06	27.05	30.11	30.12	32.42	34.31	30.81
<i>M. moenium</i>	7.80	9.99	16.54	3.94	4.82	4.88	6.90	0.98	10.88	0.73	0.51	2.99
<i>M. nigritarsis</i>	28.24	31.02	30.94	18.05	19.19	23.89	21.91	23.56	29.63	11.71	9.03	21.05
<i>M. spinitarsis</i>	26.07	19.15	24.97	6.52	9.85	8.08	26.43	4.45	20.68	3.59	3.03	5.43
<i>M. velox</i>	38.11	32.56	7.00	14.75	20.58	21.57	35.98	29.82	38.19	10.42	7.00	25.10

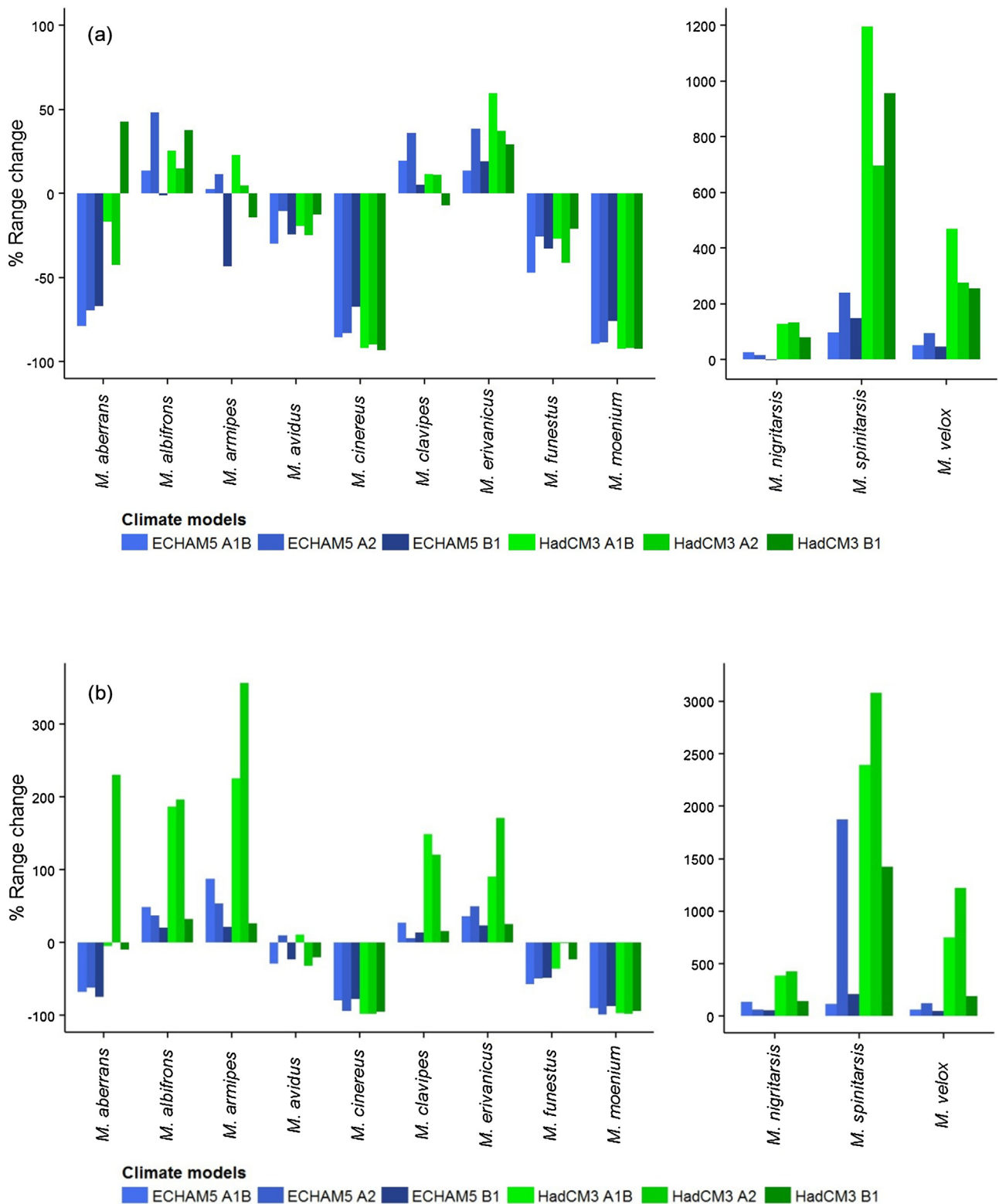
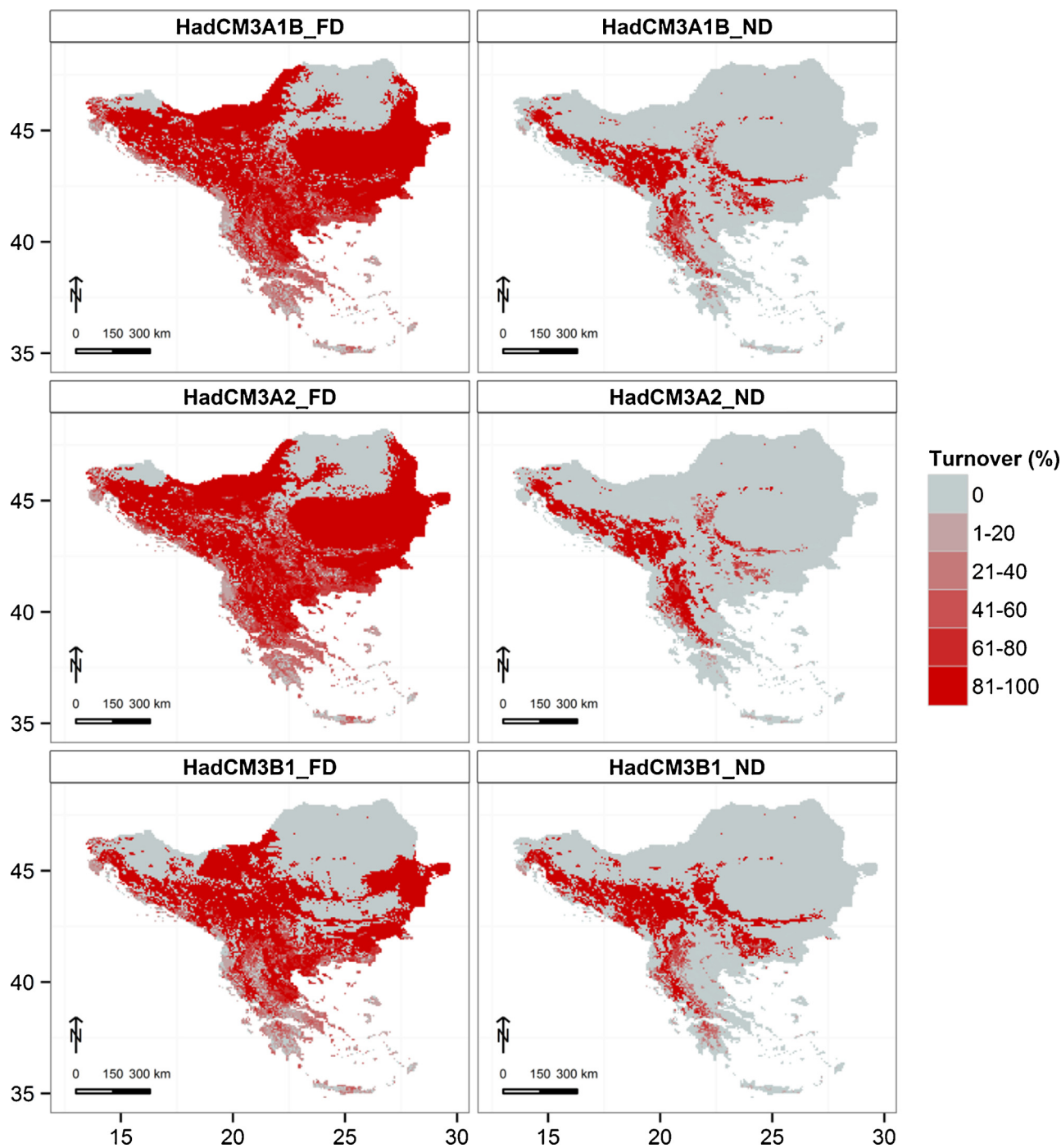


Fig. 3. The range change of the studied species for the years (a) 2050 and (b) 2080 under the A1B, A2 and B1 climate-warming scenarios of ECHAM5 and HadCM3 climate models.

barrier is the association with their geophyte hosts whose bulbs or rhizomes their larvae strictly feed and develop on (Rotheray, 1993). This obligate interaction exacerbates the likelihood of mountainous species in finding suitable habitats outside their current range.

In contrast, according to the results, climate-generalist, Mediterranean and east Mediterranean species appeared to be at an

advantage, since they were forecasted to preserve a higher extent of their potential current suitable environment. Hence, species that also appear at lower altitudes and thereby tolerate a higher temperature range seem to have better survival chances. Especially the Mediterranean species with larger distribution (*M. albifrons* and *M. avidus*) had a larger overlap between the current and future



**Fig. 4.** Percentage turnover of *Merodon* species under full and no dispersal hypothesis (FD and ND, respectively) of the year 2080 for the A1B, A2 and B1 climate-warming scenarios of the HadCM3 climate model.

projections, indicating decreased vulnerability to potential future climate change by maintaining a significant part of their current potential distributional range and in most of the cases even expanding it. Nevertheless, the survival of species in the future depends on various factors and probably the bioclimatic envelope modelling approach partly represents and explains the overall trend of species to contract or expand. Therefore, considering the importance of geophytes for the existence of *Merodon* species at the larval stage as well as the richness and abundance of floral resources for the adults, the inclusion of land cover change could be more informative, resulting in a more integrated knowledge of hoverflies potential future distribution shifts. However, [Martin et al. \(2013\)](#)

found that the incorporation of land cover change scenarios did not contribute significantly to the assessment of species' future distribution ranges. Although they were not discarding their future use, they indicated the necessity of an improvement of the thematic resolution of land cover change scenarios.

Overall, the southern parts of the Balkans, where the future species richness is presently higher, were forecasted to comprise an increased species assemblage in the future under both the extreme assumption of full dispersal and the most pragmatic hypothesis of no dispersal, probably because most of the modeled species occur also at lower altitudes and presumably have adapted to wider temperature ranges, which are predicted to increase at the southern



areas. Likely, the inclusion of further species for the spatial prediction of species richness and percentage turnover rates would be more informative for the estimation of future variations on species composition. However, in the analysis we included species with sufficient sample size in order to produce more accurate forecasts of species future distribution changes, thereby discarding numerous species with inadequate number of localities, which would have proven problematic to model. The exclusion of these species because of lacking data indicates the necessity of an improvement of field-based studies and sampling techniques, and enhancement of SDMs capabilities, since species with fewer observations are usually rare and thus of increased interest of predicting future distribution range shifts. We consider the selected species a representative sample of *Merodon* species in the study area, since they occur in heterogeneous environments and diverse climatic conditions and have an either broad or narrow actual distribution.

The dependence of *Merodon* species on bulbous plants can determine the distribution of both mutualistic partners. However, the relationship of larvae with bulbous plants remains to a big extent unknown and efforts must be targeted on revealing insights on larval feeding habits and host-plant associations. Extreme variations in phenology between species could be driven by climate and such variations may be important in determining the way a community is constituted at species level, especially in diverse communities. An increase in temperature could disrupt the temporal synchrony of plant–pollinator interactions (Memmott et al., 2007), and can lead to phenological (Burkle et al., 2013; Petanidou et al., 2014) or spatial mismatches (Polce et al., 2014; Schweiger et al., 2008), thus, reducing pollination services and in the long run potentially leading to species loss. Moreover, due to the impacts of climate change on flowering phenology, such as earlier onset of flowering (Cleland et al., 2007; Petanidou et al., 1995), the knowledge about larval activity period and development is important as it determines the flight period of the adults. Particularly in the case of specialized species a key determinant of their survival is the ability of larvae to colonize new hosts. Species co-occurrences emerging from such kind of interactions (i.e. mutualism) among species are expected to be manifested at every scale (Araújo and Rozenfeld, 2014) and by not taking into account biotic interactions our ability to predict future responses to global warming is restricted (Gilman et al., 2010). The influence mechanism of biotic interactions in determining species distribution at larger extents, such as regional, continental and beyond, in the face of future predictions has not been sufficiently studied as has been frequently recognized as unimportant (Wisz et al., 2013). However, the importance of local biotic interactions into shaping species distributions and determining species assemblages at macroecological scales has been reported (Araújo and Luoto, 2007; Heikkinen et al., 2007). The inclusion of the complex and dynamic nature of biotic interactions in predicting future distributions in the context of global warming is a challenging task, but notable progress has been made on methods to incorporate them into species distribution modelling tools beyond local spatial scales (see Kissling et al., 2012; Wisz et al., 2013 for a review of methods). Regardless of the importance of biotic interactions at larger scales, the lack of available data about geophytes distribution constrained our ability to investigate their role within the hoverflies modelling framework for the assessment of their potential distribution.

To our knowledge no climate change impact modelling has been carried out for species of the genus *Merodon* on the Balkan Peninsula so far. Our results complement the understanding of the range shifts of the studied species due to climate change by projecting the variations in the availability of suitable future climatic conditions. As hoverfly larvae depend on bulbous plants, knowledge about the potential distribution of hoverflies in relation to the potential distribution of geophytes could be of great importance, providing

useful data for conservation and management purposes. Overall, on research the relationships between hoverflies and the interacting biotic components of their ecological niche is crucial, and under a climate change impact aspect could highlight areas that are expected to suffer most from declines in abundance and diversity of both groups.

## Acknowledgements

The study was funded by the European Union (European Social Fund–ESF) and Greek National Funds through the Operational Program “Education and Lifelong Learning” of the National Strategic Reference Framework (NSRF)—Research Funding Program: THALES—Investing in knowledge society through the European Social Fund (Petanidou et al., 2013). The study material provided by the Department of Biology and Ecology of the University of Novi Sad Part has been collected with funds by the Serbian projects no. 173002 (Ministry of Education, Science and Technological Development) and Genetic diversity of agricultural ecosystems (Provincial Secretariat for Science and Technological Development).

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2015.06.032>

## References

- Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* 43, 1223–1232, DOI 10.1111/j.1365-2664.2006.01214.x.
- Araújo, M.B., Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecol. Biogeogr.* 16, 743–753, DOI 10.1111/j.1466-8238.2007.00359.x.
- Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* 22, 42–47, DOI 10.1016/j.tree.2006.09.010.
- Araújo, M.B., Rozenfeld, A., 2014. The geographic scaling of biotic interactions. *Ecography* 37, 406–415, DOI 10.1111/j.1600-0587.2013.00643.x.
- Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods Ecol. Evol.* 3, 327–338, DOI 10.1111/j.2041-210X.2011.00172.x.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15, 365–377, DOI 10.1111/j.1461-0248.2011.01736.x.
- Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M., Courchamp, F., 2013. Will climate change promote future invasions? *Global Change Biol.* 19, 3740–3748, DOI 10.1111/gcb.12344.
- Burkle, L.A., Alarcón, R., 2011. The future of plant–pollinator diversity: understanding interaction networks across time, space, and global change. *Am. J. Bot.* 98, 528–538, DOI 10.3732/ajb.1000391.
- Burkle, L.A., Marlin, J.C., Knight, T.M., 2013. Plant–pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science* 339, 1611–1615, DOI 10.1126/science.1232728.
- Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333, 1024–1026.
- Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A., Schwartz, M.D., 2007. Shifting plant phenology in response to global change. *Trends Ecol. Evol.* 22, 357–365, DOI 10.1016/j.tree.2007.04.003.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Syst.* 40, 677–697, DOI 10.1146/annurev.ecolsys.110308.120159.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* 17, 43–57, DOI 10.1111/j.1472-4642.2010.00725.x.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49, DOI 10.1017/S0376892997000088.
- Gallai, N., Salles, J.-M., Settele, J., Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* 68, 810–821, DOI 10.1016/j.ecolecon.2008.06.014.

- Gallien, L., Douzet, R., Pratte, S., Zimmermann, N.E., Thuiller, W., 2012. Invasive species distribution models—how violating the equilibrium assumption can create new insights. *Global Ecol. Biogeogr.* 21, 1126–1136, DOI 10.1111/j.1466-8238.2012.00768.x.
- Giannini, T.C., Acosta, A.L., Garófalo, C.A., Saraiva, A.M., Alves-dos-Santos, I., Imperatriz-Fonseca, V.L., 2012. Pollination services at risk: bee habitats will decrease owing to climate change in Brazil. *Ecol. Model.* 244, 127–131, DOI 10.1016/j.ecolmodel.2012.06.035.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. *Trends Ecol. Evol.* 25, 325–331, DOI 10.1016/j.tree.2010.03.002.
- Grenouillet, G., Buisson, L., Casajus, N., Lek, S., 2011. Ensemble modelling of species distribution: the effects of geographical and environmental ranges. *Ecography* 34, 9–17, DOI 10.1111/j.1600-0587.2010.06152.x.
- Guisan, A., Zimmermann, N., Elith, J., Graham, C.H., Phillips, S., Peterson, A.T., 2007. What matters for predicting the occurrences of trees: techniques, data, or species' characteristics? *Ecol. Monogr.* 77, 615–630, DOI 10.1890/06-1060.1.
- Hauser, M., 1998. Zur Schwebfliegenfauna (Diptera, Syrphidae) Aserbaidshans, mit der Beschreibung von zwei neuen Arten. *Volucella* 3, 15–26.
- Heikkinen, R.K., Luoto, M., Virkkala, R., Pearson, R.G., Körber, J.-H., 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecol. Biogeogr.* 16, 754–763, DOI 10.1111/j.1466-8238.2007.00345.x.
- Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29, 773–785, DOI 10.1111/j.0906-7590.2006.04700.x.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978, DOI 10.1002/joc.1276.
- IPCC, 2007. *Climate Change 2007: The Physical Science Basis*. Cambridge University Press, Cambridge, UK.
- Jiménez-Valverde, A., Lobo, J.M., 2007. Threshold criteria for conversion of probability of species presence to either- or presence-absence. *Acta Oecol.* 31, 361–369, DOI 10.1016/j.actao.2007.02.001.
- Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kühn, I., McInerney, G.J., Montoya, J.M., Römermann, C., Schifffers, K., Schurr, F.M., Singer, A., Svenning, J.C., Zimmermann, N.E., O'Hara, R.B., 2012. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *J. Biogeogr.* 39, 2163–2178, DOI 10.1111/j.1365-2699.2011.02663.x.
- Klein, A.-M., Vaisière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc., B* 274, 303–313, DOI 10.1098/rspb.2006.3721.
- Kuhlmann, M., Guo, D., Veldtman, R., Donaldson, J., 2012. Consequences of warming up a hotspot: species range shifts within a centre of bee diversity. *Divers. Distrib.* 18, 885–897, DOI 10.1111/j.1472-4642.2011.00877.x.
- Liu, C., White, M., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* 40, 778–789, DOI 10.1111/jbi.12058.
- Lobo, J.M., Tognelli, M.F., 2011. Exploring the effects of quantity and location of pseudo-absences and sampling biases on the performance of distribution models with limited point occurrence data. *J. Nat. Conserv.* 19, 1–7, DOI 10.1016/j.jnc.2010.03.002.
- Luoto, M., Heikkinen, R.K., Pöyry, J., Saarinen, K., 2006. Determinants of the biogeographical distribution of butterflies in boreal regions. *J. Biogeogr.* 33, 1764–1778, DOI 10.1111/j.1365-2699.2005.01395.x.
- Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W., 2009. Evaluation of consensus methods in predictive species distribution modelling. *Divers. Distrib.* 15, 59–69, DOI 10.1111/j.1472-4642.2008.00491.x.
- Martin, Y., Van Dyck, H., Dendoncker, N., Titeux, N., 2013. Testing instead of assuming the importance of land use change scenarios to model species distributions under climate change. *Global Ecol. Biogeogr.* 22, 1204–1216, <http://dx.doi.org/10.1111/geb.12087>
- McAvaney, B.J., Covey, C., Joussame, S., Kattsov, V., Kitoh, A., Ogana, W., Pitman, A.J., Weaver, A.J., Wood, R.A., Zhao, Z.-C., AchutaRao, K., Arking, A., Barnston, A., Betts, R., Bitz, C., Boer, G., Braconnot, P., Broccoli, A., Bryan, F., Claussen, M., Colman, R., Delecluse, P., Del Genio, A., Dixon, K., Duffy, P., Dümenil, L., England, M., Fifehiet, T., Flato, G., Fyfe, J.C., Gedney, N., Gent, P., Genthon, C., Gregory, J., Guilyardi, E., Harrison, S., Hasegawa, N., Holland, G., Holland, M., Jia, Y., Jones, P.D., Kageyama, M., Keith, D., Kodera, K., Kutzbach, J., Lambert, S., Legutke, S., Mader, G., Maeda, S., Mann, M.E., Meehl, G., Mokhov, I., Motoi, T., Phillips, T., Polcher, J., Potter, G.L., Pope, V., Prentice, C., Roff, G., Semazzi, F., Sellers, P., Stensrud, D.J., Stockdale, T., Stouffer, R., Taylor, K.E., Trenberth, K., Tol, R., Walsh, J., Wild, M., Williamson, D., Xie, S.-P., Zhang, X.-H., Zwiers, F., 2001. *Model evaluation*. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A. (Eds.), *Climate Change 2001: The Scientific Basis*. Cambridge University Press, Cambridge, UK, pp. 471–523.
- Memmott, J., Craze, P.G., Waser, N.M., Price, M.V., 2007. Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* 10, 710–717, DOI 10.1111/j.1461-0248.2007.01061.x.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326, DOI 10.1111/j.1600-0706.2010.18644.x.
- Parmesan, C., 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biol.* 13, 1860–1872, DOI 10.1111/j.1365-2486.2007.01404.x.
- Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for global biodiversity in the 21st century. *Science* 330, 1496–1501, DOI 10.1126/science.1196624.
- Petanidou, T., Ellis, W.N., Margaris, N.S., Vokou, D., 1995. Constraints on flowering phenology in a phryganic (east Mediterranean shrub) community. *Am. J. Bot.* 82, 607–620.
- Petanidou, T., Vujić, A., Ellis, W.N., 2011. Hoverfly diversity (Diptera: Syrphidae) in a Mediterranean scrub community near Athens, Greece. *Ann. Soc. Entomol. Fr.* 47, 168–175.
- Petanidou, T., Ståhls, G., Vujić, A., Olesen, J.M., Rojo, S., Thrasylvoulou, A., Sgardelis, S., Kallimanis, A.S., Kokkini, S., Tschulin, T., 2013. Investigating plant–pollinator relationships in the Aegean: the approaches of the project POL-AEGIS (The pollinators of the Aegean archipelago: diversity and threats). *J. Apic. Res.* 52, 106–117, DOI 10.3896/IBRA.152.2.20.
- Petanidou, T., Kallimanis, A.S., Sgardelis, S.P., Mazaris, A.D., Pantis, J.D., Waser, N.M., 2014. Variable flowering phenology and pollinator use in a community suggest future phenological mismatch. *Acta Oecol.* 59, 104–111, DOI 10.1016/j.actao.2014.06.001.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259, DOI 10.1016/j.ecolmodel.2005.03.026.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344, 1246752, DOI 10.1126/science.1246752.
- Polce, C., Garratt, M.P., Termansen, M., Ramirez-Villegas, J., Challinor, A.J., Lappe, M.G., Boatman, N.D., Crowe, A., Endalew, A.M., Potts, S.G., Somerwill, K.E., Biesmeijer, J.C., 2014. Climate-driven spatial mismatches between British orchards and their pollinators: increased risks of pollination deficits. *Global Change Biol.* 20, 2815–2828, DOI 10.1111/gcb.12577.
- Pope, V.D., Gallani, M.L., Rowntree, P.R., Stratton, R.A., 2000. The impact of new physical parametrizations in the Hadley Centre climate model: HadAM3. *Clim. Dyn.* 16, 123–146, DOI 10.1007/s003820050009.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353, DOI 10.1016/j.tree.2010.01.007.
- R Development Core Team, 2013. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ricarte, A., Nedeljković, Z., Rotheray, G.E., Lyszkowski, R.M., Hancock, E.G., Watt, K., Hewitt, S.M., Horsfield, D., Wilkinson, G., 2012. Syrphidae (Diptera) from the Greek island of Lesvos, with description of two new species. *Zootaxa* 3175, 1–23.
- Roeckner, E., Bäuml, G., Bonaventura, L., Brokopf, R., Esch, M., Giorgetta, M., Hagemann, S., Kirchner, I., Kornblüeh, L., Manzini, E., Rhodin, A., Schlese, U., Schulzweida, U., Tompkins, A., 2003. *The Atmospheric General Circulation Model ECHAM5. Part I: Model Description*. MPI Report 349. Max Planck Institute for Meteorology, Hamburg, Germany, pp. 127.
- Rotheray, G.E., 1993. Colour guide to hoverfly larvae (Diptera, Syrphidae) in Britain and Europe. *Dipterists Dig.* 9, 1–156.
- Schweiger, O., Settele, J., Kudrna, O., Klotz, S., Kühn, I., 2008. Climate change can cause spatial mismatch of trophically interacting species. *Ecology* 89, 3472–3479, DOI 10.1890/07-1748.1.
- Segurado, P., Araújo, M.B., 2004. An evaluation of methods for modelling species distributions. *J. Biogeogr.* 31, 1555–1568, DOI 10.1111/j.1365-2699.2004.01076.x.
- Speight, M.C.D., 2013. *Species Accounts of European Syrphidae (Diptera)*. Syrph the Net, the Database of European Syrphidae, vol. 72. Syrph the Net Publications, Dublin.
- Ståhls, G., Vujić, A., Pérez-Bañón, C., Radenković, S., Rojo, S., Petanidou, T., 2009. COI barcodes for identification of *Merodon* hoverflies (Diptera, Syrphidae) of Lesvos Island, Greece. *Mol. Ecol. Resour.* 9, 1431–1438, DOI 10.1111/j.1755-0998.2009.02592.x.
- Stockwell, D.R.B., Peterson, A.T., 2002. Effects of sample size on accuracy of species distribution models. *Ecol. Model.* 148, 1–13, DOI 10.1016/S0304-3800(01)00388-X.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148, DOI 10.1038/nature02121.
- Thuiller, W., 2004. Patterns and uncertainties of species' range shifts under climate change. *Global Change Biol.* 10, 2020–2027, DOI 10.1111/j.1365-2486.2004.00859.x.
- Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD—a platform for ensemble forecasting of species distributions. *Ecography* 32, 369–373, DOI 10.1111/j.1600-0587.2008.05742.x.
- Thuiller, A.W., Georges, D., Engler, R., 2013. Package “biomod2”, Version 3.1–25. Available at (<http://cran.r-project.org/web/packages/biomod2/biomod2.pdf>).
- Visser, M.E., Both, C., 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc., B* 272, 2561–2569, DOI 10.1098/rspb.2005.3356.
- Vujić, A., Pérez-Bañón, C., Radenković, S., Ståhls, G., Rojo, S., Petanidou, T., Simić, S., 2007. Two new species of the genus *Merodon* Meigen 1803 (Diptera: Syrphidae) from the island of Lesvos (Greece), in the eastern Mediterranean. *Ann. Soc. Entomol. Fr.* 43, 319–326, DOI 10.1080/00379271.2007.10697527.
- Vujić, A., Marcos-García, M.A., Sarıbylık, S., Ricarte, A., 2011. New data on the *Merodon* Meigen 1803 fauna (Diptera: Syrphidae) of Turkey including

- description of a new species and changes in the nomenclatural status of several taxa. *Ann. Soc. Entomol. Fr.* 47, 78–88, DOI 10.1080/00379271.2011.10697699.
- Walther, G.-R., Berger, S., Sykes, M.T., 2005. An ecological 'footprint' of climate change. *Proc. R. Soc., B* 272, 1427–1432, DOI 10.1098/rspb.2005.3119.
- Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., NCEAS Group, 2008. Effects of sample size on the performance of species distribution models. *Divers. Distrib.* 14, 763–773, DOI 10.1111/j.1472-4642.2008.00482.x.
- Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P., Svenning, J.C., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol. Rev.* 88, 15–30, DOI 10.1111/j.1469-185X.2012.00235.x.