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

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Abstract: Climate change presents a serious threat to global biodiversity. Loss of pollinators in particular has major implications, with extirpation of these species potentially leading to severe losses in agriculture and, thus, economic losses. In this study, we forecast the effects of climate change on the distribution of hoverflies in Southeast Europe using species distribution modelling and climate change scenarios for two time-periods. For 2041-2060, 19 analysed species were predicted to increase their areas of occupancy, with the other 25 losing some of their ranges. For 2061-2080, 55% of species were predicted to increase their area of occupancy, while 45% were predicted to experience range decline. In general, range size changes for most species were below 20%, indicating a relatively high resilience of hoverflies to climate change when only environmental variables are considered. Additionally, range-restricted species are not predicted to lose more area proportionally to widespread species. Based on our results, two distributional trends can be established: the predicted gain of species in alpine regions, and future loss of species from lowland areas. Considering that the loss of pollinators from present lowland agricultural areas is predicted and that habitat degradation presents a threat to possible range expansion of hoverflies in the future, developing conservation management strategy for the preservation of these species is crucial. This study represents an important step towards the assessment of the effects of climate changes on hoverflies and can be a valuable asset in creating future conservation plan, thus helping in mitigating potential consequences.

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

Introduction

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

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

Estimating the effects of climate change on species distributions is an important step in assessing the vulnerability of species to extinction and can provide useful information about the spectrum of possible consequences (Araújo et al. 2005; Gibson et al. 2010; Yates et al. 2010). Species distribution models (SDM; also called environmental niche models) are often used to predict the effects of climate change and they have been successfully applied in a number of environmental studies (Hannah et al. 2002; Elith et al. 2006; Peterson 2006). SDM assess the relationship between species occurrence at sites and the environmental characteristics of those areas (Franklin 2009) in order to predict the distribution of suitable environmental envelopes for the species in non-sampled areas or time-frames (Elith and Leathwick 2009; Costion et al. 2015). When used in combination with future climate change scenarios, these models can indicate the expected effect of changing climate on species distributions.

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

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

Material and methods

Occurrence data

Species distribution data for all species in SE Europe were extracted from the database of the Department of Biology and Ecology of the University of Novi Sad, which is the largest database on the region's hoverflies (occurrences of species used in this study are available at: http://www.dbe.uns.ac.rs/o_departmanu/laboratorije/laboratorija_za_istrazivanje_i_zastitu_biodiverziteta/prilog/milicic_et_al__2017_-_species_occurrences_data). This database comprises data from field collecting in the study area from 1950-2015, data obtained from different museum and private collections, and published material referring to this geographic area. Only specimens with precise distributional data were used. If locality coordinates were available, they were checked for accuracy. Records only with locality names were assigned coordinates using Google Earth (Google Inc, 2016). For our analysis, we only used species endemic to SE Europe or whose ranges outside this region do not cover areas with climatic conditions differing from those within the study area (otherwise SDM would reflect only part of the environmental niche of species and, thus, be potentially biased). For reducing sampling bias, we applied the thinning procedure, where we used a threshold of 0.01 of the maximum distance between any two points. The procedure is explained in detail in Miličić et al. (2017). After data processing, all species with less than five occurrence points were dropped (the number of occurrences per species is assessable in occurrence data table, provided on the link above in text).

Selection of predictor variables

We used 19 bioclimatic variables plus elevation data (2.5 arc-minutes resolution, approximately 4.5 km^2) taken from the WorldClim dataset (Hijmans et al. 2005) for model building. As future bioclimatic variables, we used climate projections at the same resolution from the global climate models used in the Fifth Assessment report of the Intergovernmental Panel on Climate Change (IPCC 2013). We chose the HadGEM2-ES model with RCP 8.5 (Representative Concentration Pathway), which is a greenhouse gas concentration trajectory that assumes that emissions will continue to rise throughout the 21st century. We deliberately choose the "worst case scenario" because historical and current trends of greenhouse emissions are trailing the RCP 8.5 trajectory (Peters et al. 2013). Modelling was done in two stages. First, we used all variables. Then, using only the stronger predictors for each species, we built the final models and, in that way, avoiding overfitting the models (see details in Miličić et al. 2017).

Species distribution modelling

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

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

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

Calculation of potential species richness

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

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

Range expansion and contraction patterns

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

Results

Species distribution models

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

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

Species richness

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

Loss of area

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

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

Discussion

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

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

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

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

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

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

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

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

Conclusion

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

Data availability

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

Compliance with ethical standards

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Figure legends

Fig. 1 Contribution of bioclimatic variables related with temperature and precipitation in the final species distribution models of 44 analysed species of hoverflies in SE Europe. For detailed information on bioclimatic variables, visit www.worldclim.org

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

Tables

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

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