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ORIGINAL PAPER

Predicted insect diversity declines under climate change in an already impoverished region

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Abstract Being ectotherms, insects are predicted to suffer more severely from climate change than warm-blooded animals. We forecast possible changes in diversity and composition of butterflies, grasshoppers and dragonflies in Belgium under increasingly severe climate change scenarios for the year 2100. Two species distribution modelling techniques (Generalised Linear Models and Generalised Additive Models), were combined via a conservative version of the ensemble forecasting strategy to predict present-day and future species distributions, considering the species as potentially present only if both modelling techniques made such a prediction. All models applied were fair to good, according to the AUC (area under the curve of the receiver operating characteristic plot), sensitivity and specificity model performance measures based on model evaluation data. Butterfly and grasshopper diversity were predicted to decrease significantly in all scenarios and species-rich locations were predicted to move towards higher altitudes. Dragonfly diversity was predicted to decrease significantly in all scenarios, but dragonfly-rich locations were predicted to move upwards only in the less severe scenarios. The largest turnover rates were predicted to occur at higher altitudes for butterflies and grasshoppers, but at intermediate altitudes for dragonflies. Our results highlight the challenge of building conservation strategies under climate change, because the changes in the sites important for different groups will not overlap, increasing the area needed for

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protection. We advocate that possible conservation and policy measures to mitigate the potentially strong impacts of climate change on insect diversity in Belgium should be much more pro-active and flexible than is the case presently.

Keywords Belgium · Butterflies · Dragonflies · Grasshoppers · Species distribution modelling · Species turnover

Introduction

As ectotherms, insects are predicted to react differently to climate change than warm-blooded animals such as birds or mammals (Thomas et al. 2004). Recent changes in insect distributions in northern temperate regions have shown that many species are expanding northwards (e.g., Hickling et al. 2006) or are moving towards higher altitudes (e.g., Konvicka et al. 2003; Wilson et al. 2007) as a reaction to recent climate change. The extent of these changes is expected to become gradually more pronounced with the severity of the projected climate changes, increasing the difficulty of developing strategies for insect conservation. Limited dispersal abilities of insects will prevent most insects from tracking geographic changes in suitable climatic conditions (Menéndez et al. 2006; Parmesan 2006).

Based on the recognition that climate is the main determinant of species distributions over broad regions, bioclimatic envelope modelling techniques are commonly used to investigate species-climate relationships (Pearson and Dawson 2003; Thuiller 2004; Heikkinen et al. 2006), whereby species distributions are correlated with present-day climate variables to describe a 'climate envelope' for the species. The projection of these envelopes under future climatic conditions (i.e. climate scenarios) can provide insights into the potential future range shifts of the species (e.g., Thuiller 2004; Araújo et al. 2006; Schwartz et al. 2006). Therefore, bioclimatic models can be used as a tool to identify sites that will likely remain or become climatically suitable for the conservation of insect diversity under different climate change scenarios. However, the use of bioclimatic envelopes presents some shortfalls which are often neglected (Jiménez-Valverde et al. 2008; Soberón and Nakamura 2009), the available data are often incomplete and geographically biased (Lobo et al. 2007; Hortal et al. 2007, 2008) and the underlying assumptions of these modelling techniques are rarely fulfilled (Kearney 2006; Dormann 2007). Therefore, projections of bioclimatic envelopes should be considered as simulations rather than as accurate predictions of future species distributions (Lawler et al. 2006). In this context, predictions from different techniques or under different climate change scenarios can vary significantly, it being impossible to determine which technique or climate scenario best predicts future species ranges. Therefore, such uncertainty in model predictions should be an integral part of the use of bioclimatic envelopes to forecast the impact of climate change on biodiversity (Thuiller 2004; Araújo et al. 2005; Dormann 2007). Having all this in mind, it is necessary to develop approaches that explicitly account for the uncertainty in predictions and identify their limitations, to help conservation stakeholders with decision-making processes under climate change contexts.

Here, we explore four ways of dealing with this uncertainty in bioclimatic envelope approaches, namely: (a) using modelling techniques with a strong theoretical support for species responses to the environment, which minimize over-fitting to the training data (Austin et al. 1990; Austin 2002); (b) selecting appropriate measures of modelling performance, suited to the conservation context in which model results are used (Lobo et al. 2008); (c) explicitly incorporating prediction uncertainty, by means of an ensemble forecasting strategy (Araújo et al. 2005; Araújo and New 2007); (d) predicting the effects of climate change on a large number of species from several functional and systematic groups with a wide range of ecological requirements, to avoid the lack of relevance of using a single group as a proxy for the whole of biodiversity in systematic conservation planning assessments (Kotze and Samways 1999; Maes and Van Dyck 2005).

Specifically, we model present-day distribution for a number of species pertaining to three insect groups (butterflies, grasshoppers and dragonflies) in Belgium. These groups were selected because they present disparate life histories, are reasonably well surveyed in Belgium and are also expected to react rapidly to climate changes (Parmesan 1996; Thomas et al. 2004). Then, we project their future potential distributions according to increasingly severe climate change scenarios using a conservative version of Araújo and New (2007) ensemble forecasting approach, to evaluate the potential impact of climate change on species diversity (richness and composition) for the different groups.

Methods

Data origin

Distribution data for butterflies (Maes and Van Dyck 2001; Fichefet et al. 2008), grasshoppers (Decleer et al. 2000) and dragonflies (De Knijf et al. 2006) came from volunteer recording schemes conducted from 1991 to 2006, coordinated by the Research Institute for Nature and Forest in Flanders (northern Belgium) and the Research Centre for Nature, Forest and Wood in Wallonia (southern Belgium). All records were attributed to 5 km-resolution cells using the UTM projection (UTM zone 31U-32U of the WGS1984-projection, 1,241 grid cells with >50% of their area in Belgium; hereafter, cells). In total, 98 butterfly species were observed in a total of 1,129 cells, 50 grasshopper species in 1,058 cells and 66 dragonfly species in 1,063 cells.

Species distributions were related to land cover, soil and climate variables (Table 1) via bioclimatic models. Land cover data were derived from CORINE2000 map (Nunes de Lima 2005). For dragonflies, we additionally included watercourses from the hydrological map of Belgium (differentiated in wide, >20 m, and narrow, <20 m, rivers). Due to the unavailability of detailed biotope maps in the southern part of Belgium, ponds and lakes were not included in the analysis. Soil information improves modelling results not only for plants (Coudun et al. 2006), but also for butterflies and grasshoppers (Titeux et al. 2009), so we also included soil data from the Soil Service of Belgium (Marechal and Tavernier 1974). Using GIS, land cover and soil variables were measured as the percentage cover and watercourses were measured as total length within each cell (Table 1). Monthly climate data for the period 1996–2001 from the Royal Meteorological Institute of Belgium was interpolated to all 5-km resolution cells by universal kriging with a linear drift (see Maes et al. 2003 for details), and then aggregated to obtain four seasonal climate variables that are thought to have a prevalent effect on insect species (Roy et al. 2001; Table 1).

Table 1 Mean percentages and range (minimum–maximum) of the spatial coverage of land cover and soil variables and mean values of the climatic variables per cell

Land cover	
Built on area (Corine code 1*)	20.51 (0–100)
Agriculture (Corine code 2* except 231)	45.65 (0–99.32)
Pastures (Corine code 231 + 321)	12.02 (0–77.71)
Deciduous forest (Corine code 311 + 313)	15.48 (0–96.94)
Coniferous forest (Corine code 312)	4.85 (0–68.65)
Sparse vegetation (Corine code 322 + 324 + 331)	1.20 (0–59.32)
Wetlands (Corine code 411 + 412)	0.30 (0–52.14)
Large rivers (>20 m)	0.01 (0–0.13)
Small watercourses (<20 m)	0.13 (0–0.60)
Soil data	
Sandy	28.45 (0–100)
Silty	25.81 (0–100)
Clay	5.98 (0–100)
Peat	2.42 (0–99.4)
Alluvial	5.96 (0–100)
Stony	31.30 (0–100)
Climate	
Spring rain (mm)	204 (154–300)
Summer rain (mm)	233 (188–303)
Winter temperature (°C)	6.0 (2.9–7.4)
Summer temperature (°C)	22.1 (19.4–23.4)

Corine codes refer to the categories in Nunes de Lima (2005). Climate data corresponds to the aggregation of December, January and February for winter, March, April and May for spring and June, July and August for summer

Species distribution modelling

Distribution data rarely include records of species absence, being necessary to identify well sampled areas (e.g., Hortal et al. 2007) to minimize the spurious incorporation of false absences in the data set. Here, we only considered the 25% most species-rich cells per taxonomic group and ecological region (Fig. 1; Dufrêne and Legendre 1991) to build and evaluate the models, assuming that the absence of a species from one of these cells corresponds to a true absence. A possible bias, however, could be the difference in detectability among species, which could make the species surveys more complete for conspicuous species than for others (Dennis et al. 2006). But, according to the relationship between the number of visits and the number of species found in these cells, the species composition of the cells used to build the models is very well documented and can be reasonably considered as almost complete (Fig. 2). For each group, the selected cells were randomly divided into a calibration (70%) and an evaluation (30%) set. Migrant or introduced species as well as species with less than ten presences or absences in the calibration set were excluded from the analyses. This restricted the analyses to 63 butterfly (366 cells), 33 grasshopper (322 cells) and 49 dragonfly species (335 cells).

We used two different techniques with strong theoretical support (Austin 2002) to model present-day species distributions: Generalised Linear Models (GLM, McCullagh and Nelder 1989) and Generalised Additive Models (GAM, Hastie and Tibshirani 1987). Models were calculated with BIOMOD (Thuiller 2003; Thuiller et al. 2009) on the basis of the calibration set, using a binomial distribution of errors with a logistic link function in both GAMs and GLMs, and the AIC criterion to select the most parsimonious models (Burnham and Anderson 2002). We also accounted for the possible curvilinear relationships between the potential distributions of species and the predictors by including their quadratic terms (in the case of GLM) or a cubic smoothing spline with four degrees of freedom (in the case of GAM—Thuiller 2003).

Predicted probabilities of occurrence were transformed into presence-absence data using the prevalence of each species in the calibration set as a probability threshold (Liu et al. 2005; Jiménez-Valverde and Lobo 2006). We then adopted a conservative version of the ensemble forecasting

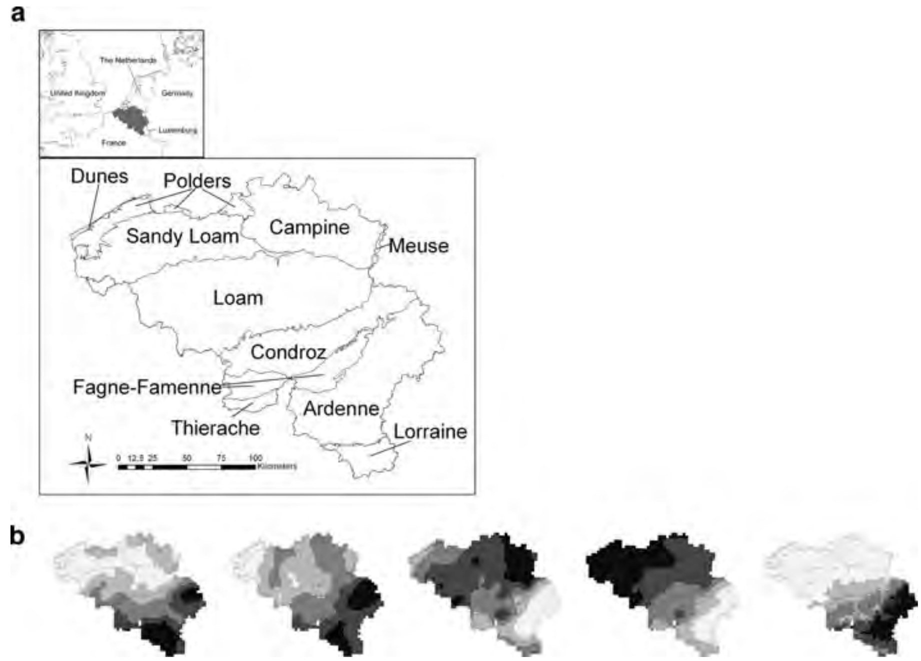

Fig. 1 **a** Ecological regions of Belgium. *Inset*: Location of Belgium (in *dark grey*) in NW Europe. **b** Distribution of climatical variables and altitude in Belgium (from *left to right*: rain in spring, rain in summer (the *darker*, the more rainfall), temperature in summer, temperature in winter (the *darker*, the higher the temperature, topography (the *darker*, the higher the altitude)

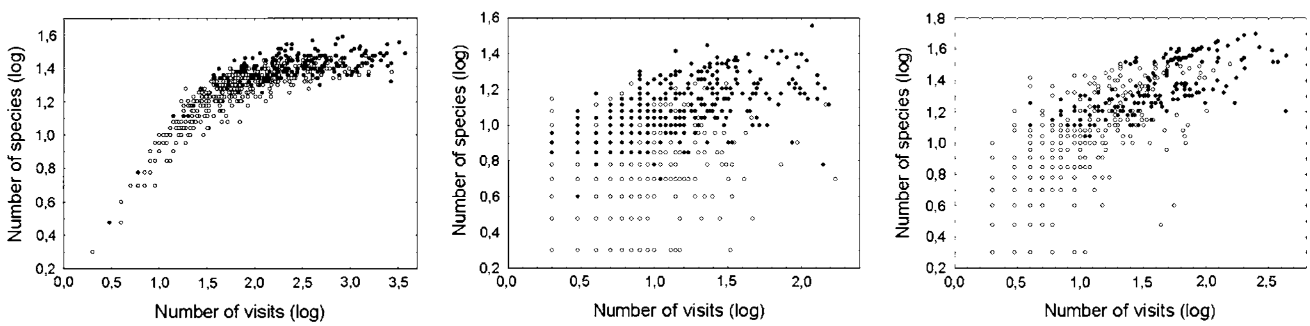

Fig. 2 Relationship between the number of visits per cell and the number of butterfly, grasshopper and dragonfly species found in each cell. *Black dots* represent the cells that were used in the analysis

approach (Araújo and New 2007), considering the species as potentially present in a given cell only if both modelling techniques (GAM and GLM) consistently predicted it. These conservative predictions were evaluated using (a) sensitivity and specificity (i.e., the fractions of correctly predicted presences and absences in the evaluation data, respectively—Lobo et al. 2008), and (b) the area under the curve (AUC) of the receiver operating characteristic plot (ROC) (as a threshold-independent measure for model performance—Fielding and Bell 1997). We aggregated the predicted potential occurrences of all species to calculate species richness in all cells for each group separately and for the three groups altogether.

Climate change projections

We projected the distributions under different climate change scenarios only for those species for which the present-day distribution was well captured (i.e. species that had at least 70% of their presences correctly predicted in the evaluation data, cf. Lawler et al. 2006). This restricted further analyses to 45 butterfly, 22 grasshopper and 21 dragonfly species, for which the models calibrated with present-day data (see above) were used to project their future distribution assuming unlimited dispersal. A complete list of these species and the predictors selected for their models are given in the Supplementary material. Five increasingly severe climate change scenarios were used for these projections (herein, scenarios), based on the predictions of the changes for Belgium by 2100 (National Climate Commission 2006; IPCC (International Panel on Climate Change) 2007; Willems et al. 2009)—gradual increases in winter and summer temperature, constant spring precipitation, and gradual decrease in summer precipitation (Table 2). Since Belgium is a relatively small region, spatial variability in changes in climate variables is negligible (Willems et al. 2009). We, therefore, applied the five scenarios similarly to all cells in Belgium. We also

Table 2 Climate change scenarios for Belgium according to the National Climate Commission (2006)

	Temperature (°C)		Precipitation (%)	
	Winter	Summer	Spring	Summer
Scenario 1	+1	+1	–	−10
Scenario 2	+2	+2	–	−20
Scenario 3	+3	+3	–	−30
Scenario 4	+4	+4	–	−40
Scenario 5	+5	+5	–	−50

applied the same conservative ensemble forecasting approach, considering that a cell hosts adequate conditions for the species under a given scenario only if the projections of both GLM and GAM models predicted it. Land cover and soil data were kept constant under all scenarios to detect the single effect of climate change, and also to limit the additional uncertainties arising from the projections of land use changes.

Additional analyses

We used ANOVA (a) with species as repeated factor, to detect overall differences in AUC, sensitivity and specificity among GAM, GLM and ensemble forecasting results, and (b) with cells as repeated factor, to detect overall differences in species richness among the five scenarios. A multiple comparisons method (Dunnett 1955) was used to test whether species richness in the five individual scenarios differed from the present-day prediction. Species gains and losses in the cells refer to the present-day species pool in Belgium only. We calculated the mean altitude of species-rich cells (i.e., cells in which arbitrarily ≥25% of the total species richness per group in Belgium was predicted) for each taxonomic group and scenario separately. In order to detect altitudinal shifts in species richness, we used a one-way ANOVA testing for differences in elevation within these species-rich cells among the five scenarios, and we used Dunnett's multiple comparisons method to assess if the elevation of these species-rich cells in the scenarios differs from that in the present-day predictions. In addition, we assessed the predicted changes in species composition per cell with the corrected version of Simpson's Beta diversity index, which is independent of variations in richness values (thus identifying true species turnover, see Koleff et al. 2003).

Results

In general, the percentages of correctly predicted presences (sensitivity) and absences (specificity) were relatively high, and the average modelling performance was good for butterflies and fair for grasshoppers and dragonflies, according to AUC (Table 3). For dragonflies, the performance did not differ greatly between modelling techniques. For butterflies and grasshoppers, GLM performed significantly better according to sensitivity and AUC, and just for AUC, respectively. The combination of GLM and GAM outcomes (i.e., ensemble forecasting) significantly decreased sensitivity and increased specificity in all groups, although AUC differed significantly from GLM only in butterflies and grasshoppers (Table 3). Richness values calculated from these model predictions were correlated with the observed richness of both the modelled and all species in all groups (all $P < 0.001$; Fig. 3). A list of selected explanatory variables per species according to GLM and GAM by both models is given in the Supplementary material.

Table 3 AUC and average percentages of correctly predicted presences (sensitivity) and absences (specificity) in the evaluation set for each taxonomic group, as a result of the GAM and GLM models separately and in combination (Ensemble models)

	Butterflies	Grasshoppers	Dragonflies
AUC			
GAM	0.824 ± 0.012^{a}	0.761 ± 0.019^{a}	0.760 ± 0.019
GLM	0.845 ± 0.011^{b}	0.783 ± 0.018^{b}	0.768 ± 0.020
Ensemble models	0.823 ± 0.011^{a}	0.761 ± 0.019^{a}	0.763 ± 0.017
Sensitivity			
GAM	81.0 ± 1.8^{a}	77.2 ± 2.1^{a}	77.4 ± 2.1^{a}
GLM	86.7 ± 2.3^{b}	80.6 ± 1.7^{a}	79.2 ± 2.1^{a}
Ensemble models	76.2 ± 1.9^{c}	68.6 ± 2.6^{b}	70.5 ± 2.3^{b}
Specificity			
GAM	84.2 ± 1.5^{a}	75.0 ± 2.9^{a}	74.9 ± 3.0^{a}
GLM	82.5 ± 1.4^{a}	75.7 ± 2.8^{a}	74.6 ± 2.6^{a}
Ensemble models	88.8 ± 1.0^{b}	83.4 ± 2.2^{b}	82.3 ± 2.1^{b}

Different superscript letters indicate significant differences in the average predictions from GAM, GLM and Ensemble models (ANOVA with species as repeated measure, multiple comparisons using Dunnett's method, $P < 0.05$)

Compared to present-day richness, the overall richness per cell and the number of species-rich cells were predicted to decrease in all scenarios, for each group individually and for all groups altogether (Table 4). Mean altitude of species-rich cells was predicted to increase significantly in all scenarios for butterflies and grasshoppers, and in all but the two most extreme scenarios for dragonflies (Table 4; Fig. 4). In the first scenario, moderate and local butterfly losses were predicted, but severe losses in the presently most species-rich areas at intermediate altitudes (Fagne-Famenne, Lorraine and in the

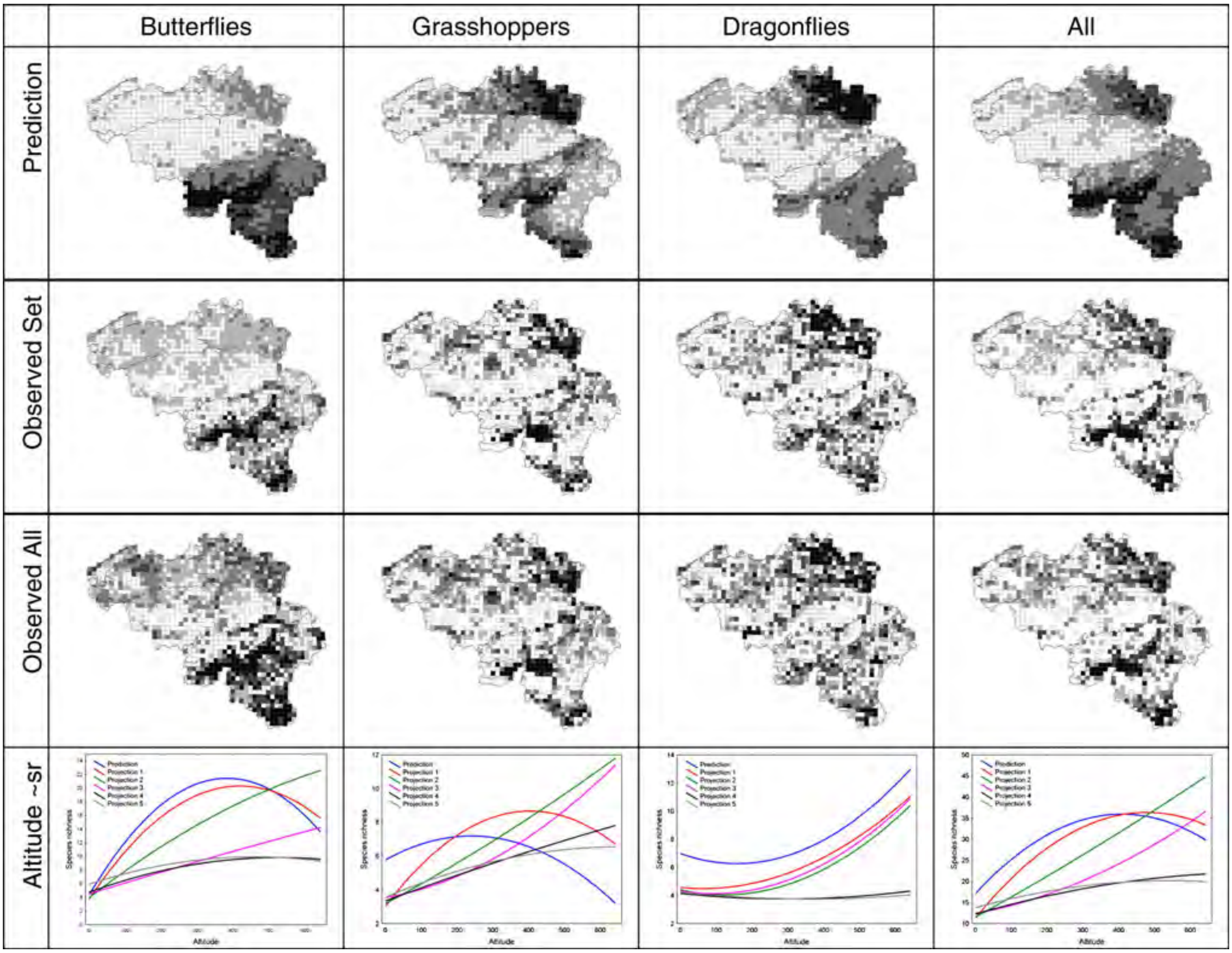

Fig. 3 Predicted species richness (*top row*), observed species richness of the modelled species only (*middle row*) and observed species richness of all species per cell in Belgium (the *darker* the cell, the more species-rich) for butterflies, grasshoppers, dragonflies and for all species together. *Bottom row*: the relation between altitude and the predicted/projected species richness (sr) per scenario

southwest of the Ardenne region) are predicted from the second scenario onwards (Fig. 4). Grasshopper species losses were predicted in the north-eastern Campine region in the northeast and in the Fagne-Famenne region in all scenarios, and to a lesser extent in the Lorraine and Condroz regions, while gains were predicted for the Ardenne region at higher altitudes, together with a gradual elevational shift in the east (Fig. 4). Dragonfly losses are predicted in the presently species-rich Campine region in all scenarios, and also in the Ardenne and the Lorraine regions under the two most severe scenarios (Fig. 4). Increasing changes in species composition are also predicted according to the increasing severity of the scenarios. These compositional changes are predicted to increase linearly in butterflies, while for grasshoppers and dragonflies the ratio of change is predicted to decrease in intensity in the two most severe scenarios (Table 4). Increasingly greater compositional changes are predicted at gradually higher altitudes for butterflies and grasshoppers (mainly in the Ardenne region, Fig. 5), while highest species turnovers were predicted at intermediate altitudes (Condroz region) for dragonflies in all scenarios (Fig. 5).

Discussion

Using a conservative version of the ensemble forecasting approach (Araújo and New 2007), we forecast important changes in the geographical patterns of species diversity under future climate change scenarios for three insect groups in Belgium. The diversity of the species currently living in Belgium is expected to decrease in all three groups and in most scenarios. Additionally, the most species-rich cells are predicted to shift towards higher altitudes. Only in grasshoppers, species richness was predicted to increase at higher altitudes. The most important species

Table 4 Average number of species per cell (N species ± SE), number of cells with ≥25% of the total species richness, mean elevation (±SE) of the cells with ≥25% of the total species richness and mean compositional (±SE) replacement per cell (measured as Simpson beta diversity index ± SE) for butterflies, grasshoppers, dragonflies and for the three groups altogether in the present-day prediction and in the five scenarios (Sc1–5); significant differences with the present-day situation are given in bold (repeated measures ANOVA with cell as repeated measure for Nspecies and one-way ANOVA for mean elevation 25%, multiple comparisons using Dunnett's method, $P < 0.05$), except for compositional replacement, for which significance assessments are not possible

	Prediction	Sc1	Sc2	Sc3	Sc4	Sc5
Butterflies						
N species	12.63 ± 0.23	**11.53 ± 0.22**	**9.54 ± 0.18**	**7.03 ± 0.09**	**6.91 ± 0.06**	**7.76 ± 0.06**
N cells with ≥ 11 species	554	468	364	191	129	163
Mean elevation ≥11 species (m)	290 ± 6	**329 ± 6**	**364 ± 6**	**384 ± 9**	**351 ± 10**	**325 ± 9**
Mean compositional replacement		0.080 ± 0.002	0.143 ± 0.004	0.200 ± 0.005	0.231 ± 0.005	0.290 ± 0.005
Grasshoppers						
N species	6.40 ± 0.10	**5.71 ± 0.10**	**5.16 ± 0.08**	**4.79 ± 0.06**	**4.52 ± 0.05**	**4.65 ± 0.04**
N cells with ≥ 5 species	855	704	546	503	501	624
Mean elevation ≥5 species (m)	177 ± 6	**221 ± 7**	**257 ± 8**	**282 ± 7**	**285 ± 7**	**247 ± 7**
Mean compositional replacement		0.140 ± 0.005	0.228 ± 0.006	0.298 ± 0.006	0.329 ± 0.006	0.346 ± 0.006
Dragonflies						
N species	6.99 ± 0.12	**5.16 ± 0.07**	**4.68 ± 0.05**	**4.80 ± 0.05**	**3.95 ± 0.03**	**4.00 ± 0.03**
N cells with ≥ 5 species	837	674	568	612	361	369
Mean elevation ≥5 species (m)	189 ± 6	**208 ± 7**	**209 ± 8**	**218 ± 8**	125 ± 8	105 ± 6
Mean compositional replacement		0.111 ± 0.006	0.194 ± 0.007	0.236 ± 0.007	0.257 ± 0.007	0.266 ± 0.007
All						
N species	26.03 ± 0.36	**22.40 ± 0.34**	**19.37 ± 0.30**	**16.62 ± 0.17**	**15.38 ± 0.11**	**16.41 ± 0.09**
N cells with ≥ 22 species	667	480	360	261	94	95
Mean elevation ≥22 species (m)	243 ± 7	**311 ± 7**	**362 ± 6**	**395 ± 7**	**356 ± 13**	**297 ± 11**
Mean compositional replacement		0.123 ± 0.003	0.199 ± 0.004	0.258 ± 0.004	0.286 ± 0.004	0.319 ± 0.004

losses are also expected in regions that are currently species-rich, i.e. intermediate altitudes in calcareous or schistose regions for butterflies and low altitude in calcareous and sandy regions for grasshoppers and dragonflies. These regions have relatively large nature reserves with rare and threatened types of biotopes, where some of the most endangered insect species in Belgium occur. The greatest changes in species composition were predicted at higher altitudes for butterflies and grasshoppers, but at intermediate altitudes for dragonflies.

Model performance and data quality

Model performance was better in butterflies than in grasshoppers and dragonflies according to both sensitivity and specificity. This could be due to the less exhaustive recording effort devoted to grasshopper and dragonfly mapping schemes; mapping effort (measured as records per cell) for butterflies was two-fold higher than for dragonflies, and three-fold higher than for grasshoppers. Biodiversity inventories are often spatially and environmentally biased (e.g., Hortal et al. 2007; Lobo et al. 2007), so that the species' responses to environmental gradients are incompletely recorded (Hortal et al. 2008). Even when only the best-surveyed cells per ecological region are used for the model calibration and evaluation (see Fig. 2), differences in survey intensities inevitably produce false absences, yielding a skewed representation of the realized distribution of the species (Dennis and Hardy 1999). A possible bias could come from differences in detectability among species, i.e., brightly coloured species and species with a conspicuous behaviour are more easily detected than dull-coloured or inconspicuous species (Dennis et al. 2006). Therefore, higher quality models should be expected for butterflies, because they are more easily detected and classified than grasshoppers and dragonflies, but also because they have been surveyed more exhaustively, and by a higher number of recorders, than the other two groups. On top of that, the higher mobility of dragonflies compared to the other two groups of insects could cause a limited number of false presences in the data, because some observations might correspond to vagrants rather than actual breeding populations.

Despite the large number of variables with which the models were built, the variables eventually selected usually have clear ecological links with the species in the different taxonomic groups (See Supplementary material; Titeux et al. 2009). Typical woodland species such as the

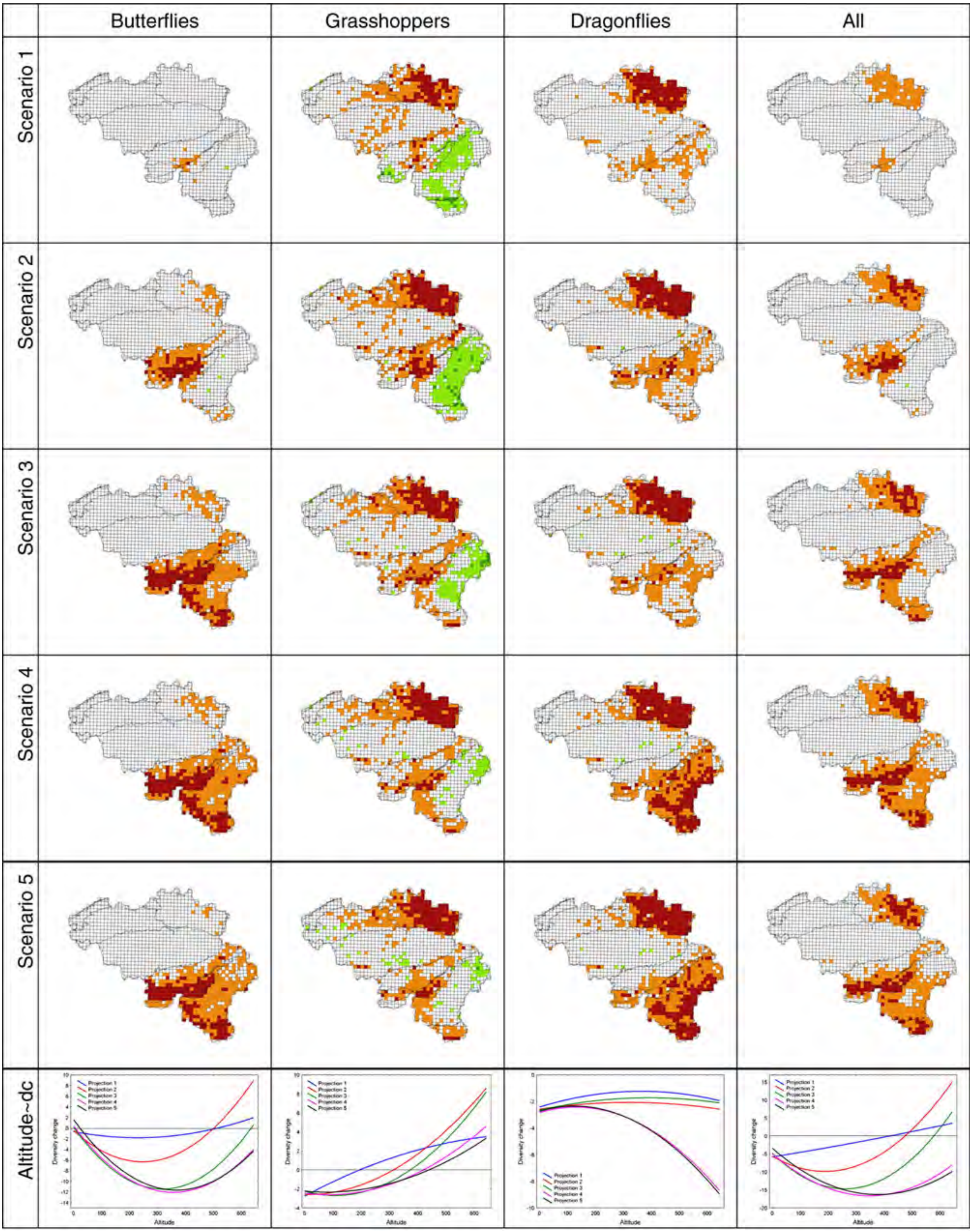

Fig. 4 Diversity changes in the five climate change scenarios for butterflies, grasshoppers, dragonflies and for all species together in Belgium (*red*: ≥30% species loss, *orange*: 15–30% species loss, *light green*: 15–30% species gain, *dark green*: ≥30% species gain). *Bottom row*: the relation between altitude and diversity changes (dc) per scenario

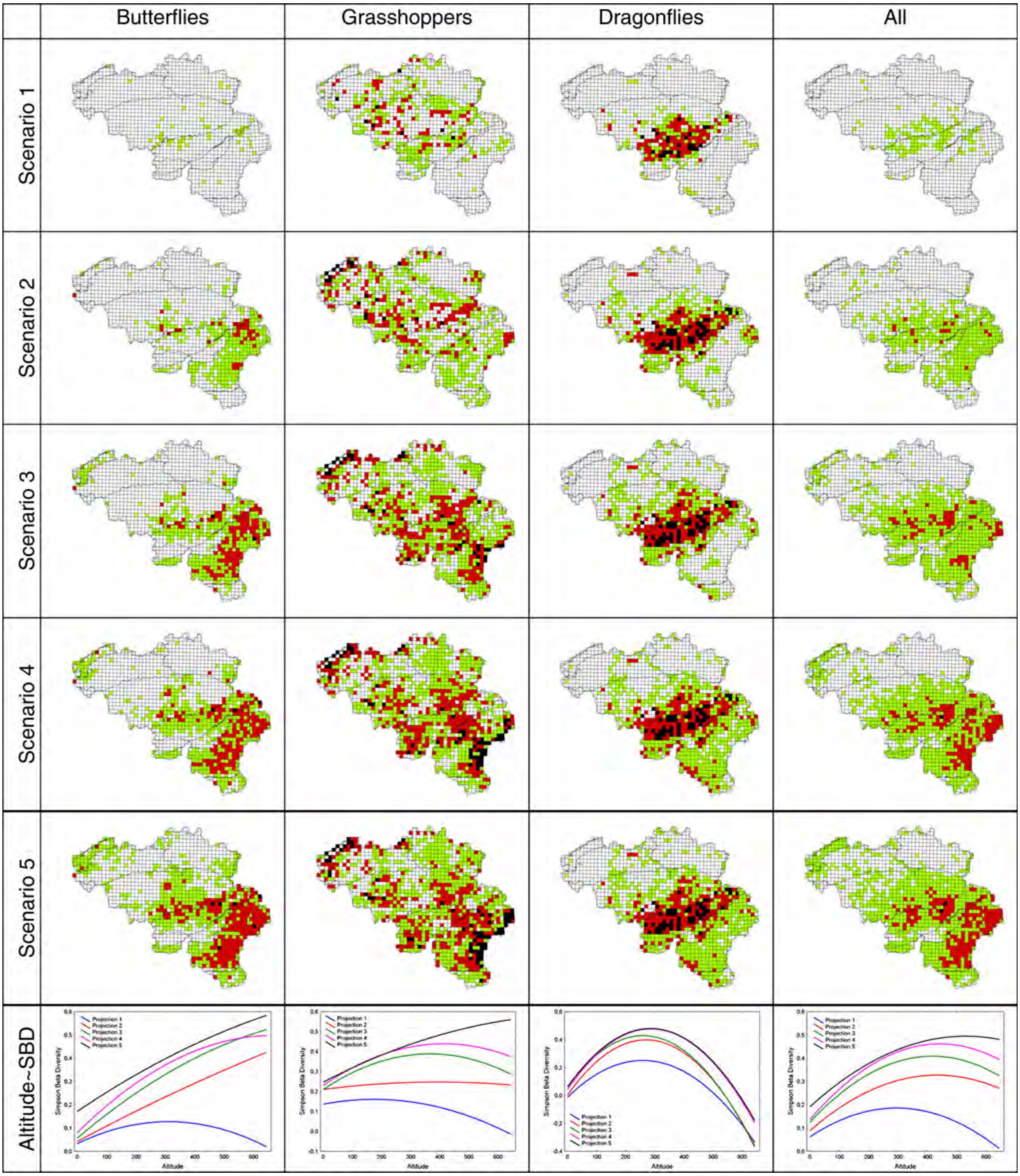

Fig. 5 Predicted compositional changes per cell in the five climate change scenarios for butterflies, grasshoppers, dragonflies and all species together in Belgium. *Green* = 25–50% species turnover, *red* = 50–75% species turnover, *black* = 75–100% species turnover. Turnover values were measured by Simpson's beta diversity index (SBD—see text). *Bottom row*: the relation between altitude and the predicted compositional change per scenario

butterflies *Apatura iris*, *Limenitis camilla*, *Favonius quercus*, *Pararge aegeria* and *Satyrium ilicis*, the dragonflies *Aeshna grandis* and *Cordulegaster boltonii* and the grasshopper *Nemobius sylvestris* all have the variable 'deciduous woodland' selected both by GAM and GLM (Supplementary material). The same holds true for boreo-alpine relict species such as the butterflies *Boloria eunomia*, *Lycaena helle*, *L. hippothoe* and the dragonfly *Aeshna juncea* for which (low) 'winter temperature' was selected as predictor variable by both GAM and GLM. The resolution at which land cover types are inventoried does not allow for the mapping of small (Schmit et al. 2006), but important resources for invertebrates (e.g., nectar sources, food plants, microclimate—Dennis et al. 2003) which might explain the, albeit acceptable, relatively low AUC values for some of the species. The use of proxy data such as broad biotope types, macroclimate variables, soil types and topography is inevitable for large-scale species distribution modelling and can only generate a general framework for understanding the present-day and possible future distribution patterns of species. To understand the mechanisms behind the observed patterns, detailed resource-based habitat research on much smaller scales are needed (Maes et al. 2006). For some regions (e.g., north Belgium, De Blust et al. 1994), land cover maps with a very high resolution, a large number of biotope types and information on biotope quality are available and could improve the predictive power of the models, but such information is not readily available on a larger scale.

Regardless of the differences between groups in data exhaustiveness, these drawbacks are likely to be general for most biodiversity data, including the ones used here (Hortal et al. 2007, 2008; Chefaoui and Lobo 2008; Jiménez-Valverde et al. 2008). Although by discarding the species with poorly performing models for further analyses we partly account for this, the extent of these problems is so general that it is probable that some inaccuracies will remain in model results, yielding limited descriptions of species distributions. Due to this, we adopted a highly restrictive version of the ensemble forecasting approach (Araújo et al. 2005; Araújo and New 2007). By considering a species as potentially present only if both GAM and GLM predicted it, the sensitivity and specificity of the predictions will logically decrease and increase, respectively (see Araújo et al. 2005). This also decreases the chance of over-fitting the models to potentially meaningless records with no clear link to the suitability of environmental conditions. Such a strategy also gives more importance to the most representative environmental conditions, consistently detected by both modelling techniques. The application of species distribution modelling techniques in conservation biology should be a matter of predicting species presences with as much certainty as possible. Thus, a restricted number of presences predicted with confidence is desirable if at the same time the percentage of correctly predicted absences is maximized (Araújo and New 2007). In a context of limited budget for biodiversity conservation, errors of omission (i.e., failing to predict presences) are preferred to errors of commission (i.e., predicting presences in areas where the species is absent). This asymmetric importance of omission and commission errors is not adequately captured when evaluating models with AUC, which amalgamates sensitivity and specificity, two measures that analysed separately (as done here) allow model reliability to be assessed in more detail and more accurately (Lobo et al. 2008).

We have further strengthened our search for the most robust (and thus reliable) climate envelopes by using two modelling techniques (GAM and GLM) with some theoretical support for their ability to capture species responses to environmental gradients (Austin et al. 1990; Austin 2002). Instead of using increasingly complex modelling techniques, which are more likely to over-fit the training data, here we make a plea for the simplicity in the use of climatic envelopes. Using techniques with strong theoretical support increases the likelihood that the relationships captured in the models will actually describe to some extent the potential response of species to environmental gradients, therefore being more likely to forecast the location of suitable conditions for the species under new conditions (Kearney 2006; Jiménez-Valverde et al. 2008; Lobo et al. 2008). Here, it is necessary to point out that we used climate envelopes calibrated in the limited territory of Belgium to forecast possible changes in distribution of butterflies, dragonflies and grasshoppers. We were unable to calibrate our models in a wider region, as it would be desirable to cover the whole environmental response of the studied species (Thuiller 2004), due to the absence of a European distribution database for dragonflies and grasshoppers. Future research using the European butterfly database is needed to ascertain the effect of modelling with national instead of European climate envelopes on the predictions of future distributions in a given region (Bink and Bik 2009). The results of a climate risk analysis for butterflies using European climate envelopes (Settele et al. 2008) showed that strongly declining species (at least 50% decline) outnumbered the strongly increasing species (at least 50% increase) in the present-day species pool in Belgium (Settele et al. unpublished data). Despite the different approach between Settele et al. (2008, using European climate envelopes) and our analysis (using Belgian climate envelopes), there is a high similarity between the decline in butterfly diversity in both analyses. Nevertheless and even if some biases remain present in the projections, using the national climate envelope for all three groups allowed a comparison of their potential future trends. Having said this, all these uncertainties, together with the difference between realized and potential distributions (Thuiller et al. 2004; Jiménez-Valverde et al. 2008; Bink and Bik 2009; Colwell and Rangel 2009) still cast some shadows on the ability of bioclimatic envelops to project future species distributions. Rather, their results must be understood as limited approximations of the areas where species might be able to establish populations in the future. More functional models incorporating species traits, dispersal ability and biotic interactions are needed to forecast their individual responses to changes with higher accuracy (see, e.g., Austin 2007). Nevertheless, bioclimatic envelopes are yet a valuable tool to forecast changes in the geographical distribution of biodiversity, provided that their limitations are understood and explicitly accounted for, and therefore can help identifying areas that might be important for conservation purposes in the future.

Contrasting projected changes among groups

Butterflies and dragonflies from the present-day species pool in Belgium are expected to be the most strongly affected groups, with average decreases in species richness per cell of up to 43–45%. Grasshoppers, on the contrary, are expected to increase their numbers at higher altitudes in the Ardenne region. Despite the low range in elevations in Belgium, we were able to detect elevational shifts in species diversity, probably because of the fine grained resolution of our analyses (cf. Konvicka et al. 2003; Wilson et al. 2005; Hickling et al. 2006). However, we were not able to detect latitudinal shifts, probably due to the reduced geographical extent of Belgium, but also because our assessment is limited to the species currently present in Belgium due to the lack of appropriate distribution data in more southerly regions. Therefore, the possible northward shift of species from southern regions into Belgium could also counterbalance the number of species lost in some areas beyond the predictions from our models (cf. Peterson et al. 2004), at least for species sufficiently mobile so as to reach climatically suitable areas (e.g., the grasshopper *Conocephalis discolour*, Kleukers et al. 1996, or the dragonfly *Crocothemis erythraea*, De Knijf et al. 2006). Specialist species often have high thermal demands for dispersal (Dennis et al. 2003) and it is unlikely that those conditions will be readily available in the highly fragmented Belgian landscape. Nevertheless, we considered unlimited dispersal for all species in the interpretation of our results, which although being reasonable given the relatively small size of Belgium, might be over-optimistic for most of the habitat specialist species. Settele et al. (2008) predicted that Belgium would become climatically suitable for 93 butterfly species that are nowadays absent or extinct from Belgium, of which 25 have populations within a 100 km radius from Belgium. Most of the other species would have to come from the south of France (>400 km) and SE Europe (500–1,000 km) which makes a spontaneous colonization highly unlikely given the limited dispersal capacity of many species. Additionally, most of these species are habitat specialists for which no suitable areas are present in Belgium nowadays.

The highest species turnover was predicted in the Ardenne region for both butterflies and grasshoppers, where most specialist species (e.g., *Boloria eunomia*, *Lycaena helle* in butterflies and *Gomphocerripus rufus*, *Metrioptera bicolor* in grasshoppers) might be lost, being replaced by common ones (e.g., *Pararge aegeria*, *Polygonia c-album* in butterflies and *Tettigonia viridissima*, *Leptophyes punctatissima* in grasshoppers). In the case of dragonflies, species nowadays present in the Condroz region are expected to move towards higher altitudes in the Ardenne region (e.g. *Calopteryx splendens*, *C. virgo*), while species currently present at lower altitudes will instead move to Condroz (e.g. *Erythromma viridulum*, *Pyrrhosoma nymphula*), which explains the high species turnover in this region. Surprisingly, changes in composition are not strong for the first two scenarios (except for dragonflies), being only moderate in the third for butterflies and grasshoppers, and even in the fourth when all three groups are considered. This indicates that most of the areas that are currently important for conservation might remain so for some time, unless changes correspond to the most pessimistic projection, in which case many species would be lost.

Conservation remarks

Conservation evaluation and planning is often restricted to a few taxonomic groups, mostly vertebrates and/or plants. We evaluated the possible impact of climate change on three cold blooded insect groups, one of the most vulnerable units of biodiversity (Thomas 1994). By investigating groups that incorporate different life history traits, dispersal capacities or habitat requirements (Maes and Van Dyck 2005), we show that the impact of climate change might differ spatially in different groups. This highlights the difficulty of building conservation strategies under climate change, because the changes in the sites important for different groups will not coincide, increasing the area needed for protection in the future (Maes et al. 2005; Pressey et al. 2007). Different authors have shown that especially rare and specialised species will be strongly affected by climate change (e.g., Konvicka et al. 2003; Hickling et al. 2005; Franco et al. 2006). Therefore, in the case of radical climate changes, new protected areas will be needed based not only on the requirements of the most vulnerable species (e.g., wetlands, wet heathlands) but also on those of the more common ones. Thus, more pro-active conservation policies should pursue the creation of large reserves or protected area networks that include biotopes where these species are likely to occur in the future, allowing the species to easily shift between locally "warm" and "cold" biotope types. This could mean that suitable biotopes should be created in sites that will become climatically suitable in the future (e.g., transforming present-day coniferous woodland plantations in the higher altitude Ardenne region into semi-natural nutrient poor grasslands). Apart from such areas, an increasingly important feature under climate changes is the management of non-protected areas to allow the dispersal of species tracking their climatically suitable sites (Hannah et al. 2002; Williams et al. 2005). This issue is particularly important in Belgium, where semi-natural areas are highly fragmented (European Environment Agency 2002). Here, dispersal movements could be facilitated through the creation of stepping stones or biotope corridors within the, often limited, dispersal range of the species (Hannah et al. 2007). To summarize, conservation policy-makers need to shift from the current paradigm of protected sites as static entities, to a more pro-active concept of conservation planning, in order to allow the species to shifts their ranges to track changing climate conditions.

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