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Climatic suitability ranking of biological control candidates: a biogeographic approach for ragweed management in Europe

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Abstract. Biological control using natural antagonists has been a most successful management tool against alien invasive plants that threaten biodiversity. The selection of candidate agents remains a critical step in a biocontrol program before more elaborate and time-consuming experiments are conducted. Here, we propose a biogeographic approach to identify candidates and combinations of candidates to potentially cover a large range of the invader. We studied *Ambrosia artemisiifolia* (common ragweed), native to North America (NA) and invasive worldwide, and six NA biocontrol candidates for the introduced Europe (EU) range of ragweed, both under current and future bioclimatic conditions. For the first time, we constructed species distribution models based on worldwide occurrences and important bioclimatic variables simultaneously for a plant invader and its biocontrol candidates in view of selecting candidates that potentially cover a large range of the target invader. Ordination techniques were used to explore climatic constraints of each species and to perform niche overlap tests with ragweed. We show a large overlap in climatic space between candidates and ragweed, but a considerable discrepancy in geographic range overlap between EU (31.4%) and NA (83.3%). This might be due to niche unfilling and expansion of ragweed in EU and the fact that habitats with high ragweed occurrences in EU are rare in NA and predicted to be unsuitable for the candidates. Total geographic range of all candidates combined is expected to decrease under climate change in both ranges, but they will respond differently. The relative geographic coverage of a plant invader by biocontrol candidates at home is largely transferable to the introduced range, even when the invader shifts its niche. Our analyses also identified which combination of candidates is expected to cover the most area and for which abiotic conditions to select in order to develop climatically adapted strains for particular regions, where ragweed is currently unlikely to be controlled.

Key words: *Ambrosia artemisiifolia;* biological invasions; climate change; niche overlap; species distribution model.

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INTRODUCTION

Biological invasions by alien plants are among the most important drivers of environmental change (Gurevitch et al. 2011). Accordingly, management and control of invasive alien species is considered one of the greatest challenges that conservation biologists will face in the next decades (Kettenring and Adams 2011). Biocontrol using natural antagonists from the invaders' native range has been a most successful management tool and is currently the curative and sustainable control measure of choice against alien invasive plants, owing to its effectiveness and relatively high environmental safety (Müller-Schärer and Schaffner 2008, Seastedt 2015).

Species distribution models (SDMs) provide statistical inference on drivers of species ranges by relating geo-located observations of occurrence data to environmental variables that contribute to a species' survival and propagation (Guisan and Zimmermann 2000). Recently, SDMs have been increasingly used to predict the spatial extent of invasions and identify at-risk habitats under current climate and ongoing environmental change (Peterson 2003). The use of SDMs to project most suitable ranges of biocontrol agents also provides an effective way to identify collection locations in the home range (Mukherjee et al. 2011) and release sites in the introduced area as climate clearly influences their establishment and performance due to underlying biophysical factors (Hoelmer and Kirk 2005). A number of studies showed that biocontrol agent with optimal climatic match between home and release locations established better and became more efficient than agents with a less good match (Hoelmer and Kirk 2005). SDMs predicting suitable areas and potential future spread of invasive alien plants and their biocontrol candidates have thus become an important tool in successful invasion management. In addition, ordination techniques that allow for direct comparisons of species–environment relationships in environmental space, and employ various maximization criteria to construct synthetic axes from associated environmental variables (Broennimann et al. 2012), provide important complementary information. Such approaches, which can reduce the dimensionality of the data set without losing much information, are becoming widely used because of the simplicity and reliability of the statistical procedure and can explain accurately the associations between climate variables (Lorenz 1956). Ordination techniques for quantifying niche overlap, therefore, are recommended over others that use geographical projections derived from SDMs (Broennimann et al. 2012).

Climate change (IPCC 2013) is expected to impact significantly the distribution of species and the resource dynamics of ecosystems, with particular importance for biological invaders and associated consumers used for biocontrol. This is because many invasive species are opportunists adapted to a wide range of conditions and good at coping with environmental change (Theoharides and Dukes 2007), for example, through minimal reliance on specialized mutualists (Van Kleunen et al. 2008), and high environmental tolerance and phenotypic plasticity (Davidson et al. 2011). In this context, climate change may facilitate the invasion processes enabling invasive alien species to expand into new ranges (Walther et al. 2009). Climate change may also determine the distribution and thus impact of biocontrol agents (Coetzee et al. 2007), but plants and arthropods might react differently to climate change (Gillson et al. 2013). As a cost-effective approach, bioclimatic models widely used to predict the spatial and temporal scale of invaders and their antagonists can be extended to predict potential climate match under future climate scenarios.

Common ragweed, *Ambrosia artemisiifolia* L. (Asteraceae), has uniquely raised the awareness of invasive plants in Europe (Kettunen et al. 2009). It is an annual native to North America, but has become widespread in many continents (e.g., Asia, Australia, and Europe). In Europe, *A. artemisiifolia* has been reported since the mid-1800s and has been considered a weed since the late 1920s. To date, it has become invasive in more than 30 countries (Essl et al. 2015). A main problem with *A. artemisiifolia* is its particularly large production of highly allergenic pollen, generating huge medical costs that are increasing in many countries (Burbach et al. 2009). Furthermore, it is the major weed in various cropping systems, especially in spring-sown crops. The majority of infested land in Europe is, however, non-crop land and both the spread and impact of *A. artemisiifolia* are likely to increase with changing climate, posing a significant risk even in countries presently not yet affected (Hamaoui-Laguel et al. 2015). Herbicides and mechanical control treatments are well in place for short-term management, such as to reduce biomass of *A. artemisiifolia* in crops (Essl et al. 2015); yet, flowering, pollen production, and seed set can only rarely be prevented (Gerber et al. 2011). A promising management option for long-term and sustainable control is classical biocontrol. This option so far has not yet widely been used in Europe (but see Croatia: Winston et al. 2014 and former USSR: Kovalev and Runeva 1970), but has proven to be most successful against *A. artemisiifolia* in China (Zhou et al. 2014) and Australia (Palmer et al. 2010).

No studies yet exist that predict simultaneously the distribution of a plant invader and of its potential biocontrol candidates to provide a cost-effective pre-release assessment before more elaborate and time-consuming experiments are conducted. Our main objective was to predict the overlap of potential suitable areas of *A. artemisiifolia* with those of six biocontrol candidates prioritized for Europe. More specifically, we asked (1) what percentage of the suitable *A. artemisiifolia* range is also suitable for the six agents, both under current and future bioclimatic conditions, (2) does the relative overlap of the geographic distribution of the six agents with the *A. artemisiifolia* distribution in North America correlate with their projected overlap with *A. artemisiifolia* distribution in Europe, and (3) which combination of agents would cover the most area, and which particular biotypes would be needed to fill in the yet uncovered part of the suitable *A. artemisiifolia* range in Europe? Besides SDMs, we also performed a principal component analysis (PCA) of both the plant species and the six biocontrol candidates to assess their overlap in climatic space.

METHODS

Study species

Building on the extensive studies on antagonists of *A. artemisiifolia* in its native range and capitalizing on successful biocontrol activities in Australia and China, a recent review prioritized six candidate insects and one fungus as agents for classical biocontrol in Europe (Gerber et al. 2011). Previous research of biocontrol of plant invaders in general (Winston et al. 2014) and of *A. artemisiifolia* specifically suggests that defoliators can be effective in controlling invasive *A. artemisiifolia* populations (Zhou et al. 2014). Among the prioritized potential biocontrol agents (Gerber et al. 2011), we focus on five leaf feeders (*Ophraella communa*, *Ophraella slobodkini*, *Zygogramma disrupta*, *Zygogramma suturalis*, and *Tarachidia candefacta*) and one stem miner (*Epiblema strenuana*). A detailed description of the biocontrol candidates considered in our study is given in Appendix S1.

Species occurrences and bioclimatic data

We collected all available occurrences in the literature for *A. artemisiifolia* and the six potential biocontrol candidates worldwide. Geo-referenced occurrence records of *A. artemisiifolia* and the six insect species from online resources and from many additional sources for occurrences are given in Appendix S2. Data are deposited in the Figshare: 10.6084/m9.figshare.4602313.

We used WORLDCLIM climate data (developed by Hijmans et al. 2005) at 5-min spatial resolution (~10 km close to the equator) to derive a set of meaningful predictors that are considered critical to plant or insect physiological function and survival of each of our species. In preliminary analyses, we modeled the species (see *Species distribution modeling* section) with 19 variables of WORLDCLIM climatic factors (Appendix S4: Table S1) and growing degree days (GDD > 8° for *A. artemisiifolia* following the baselines of sunflower and GDD > 10° for six insect species because this is the most common baseline for insects; Pruess 1983) to select the most important variables for each species under various climatic scenarios (Appendix S4: Table S2). Based on the response curves of the models (i.e., showing how the predictions changed along each bioclimatic variable), we eliminated variables that showed no variability in the response. We eventually chose different variables for each species under current climatic condition and four future scenarios (Appendix S4: Table S3). For the four "future" scenarios projections for the 2050 time slice (averages for 2041-2060), we adopted two general circulation models (HadGEM2-AO and IPSL-CM5A-LR), under two representative concentration pathways, RCP26 and RCP85 (Giorgetta et al. 2013). Data were developed for the Coupled Model Intercomparison Project Phase 5 (CMIP5, IPCC Fifth Assessment, IPCC, 2013). In all the "future" scenarios, the same 19 bioclimatic variables as used for the "current" scenario were extracted from each projection, HadGEM2-AO, rcp26 (HD-26); HadGEM2-AO, rcp85 (HD-85); IPSL-CM5A-LR, rcp26 (IP-26); IPSL-CM5A-LR, rcp85 (IP-85), respectively.

Species distribution modeling

Based on worldwide occurrences and important bioclimatic variables, we modeled the current and future potential habitats for each species, using the integrative modeling framework Biomod2 (Thuiller et al. 2013) in both the native (North America; NA) and introduced (Europe; EU) range. A combination of different modeling techniques to adjust for the inherent uncertainty of these models was suggested to find the optimal solution from an ensemble of predictions (Araújo and New 2007) or each species; therefore, generalized linear models (GLM), generalized boosting models (GBM), random forest (RF), and maximum entropy (MAXENT) were calibrated on a random sample of the initial data (80) and tested on the remaining data sets with both the receiver-operating characteristic curve and the true kill statistic (TSS; Pearce and Ferrier 2000) and we then estimated their response curve (Elith et al. 2005). Above techniques were chosen because they have proven to presently be among the most effective species distribution models (Elith et al. 2006). Duplicated presences within a raster pixel were removed. As only occurrences were available, random pseudo-absences were generated (Graham et al. 2004) to fill the absence component of models (the number of absences was set to be the same as the number of cleaned presences of each species). The entire training-evaluation procedure was repeated 100 times (25 times for each model), using a different set of calibrated presences and absences within each iteration to ensure robustness of the predictions and provide uncertainty estimates (e.g., Broennimann and Guisan 2008). The suitability of species distribution was then binary-transformed using species-specific thresholds maximizing the rate of the number of corrected predicted presences to number of false absences (i.e., to transform the probabilities of presence into presence and absence). For the predictions under future bioclimatic conditions, we produced maps with mean values and standard deviations from four scenarios of each species. The overlap maps of the six insect species on *A. artemisiifolia* were then produced based on their current binary maps and the mean binary maps of the four future climate scenarios. Based on the current binary maps, we listed the percentage of range suitable for *A. artemisiifolia* and also suitable for six insect candidates of each European country. We also calculated the most optimal combinations of insect biocontrol candidates expected to cover the most area of *A. artemisiifolia* in Europe under current climate condition.

The predictive power of the models was tested using the area under the receiver operator characteristic function (area under the curve criteria, AUC) for evaluation (Pearce and Ferrier 2000). We then assessed the effects of species, models, and climate scenarios on the AUC scores using Tukey's honest significant difference (HSD) post hoc comparison after analysis of variance (ANOVA). Planned contrasts, which allow us to determine significant differences among levels, were then used to identify differences among species, models, and climate scenarios.

Finally, we used Spearman's rank correlation (*spearman.test* function obtained from R package *psperman*; Savicky 2014; i.e., for small sample sizes with pre-computed null distribution and exact approximation) to test for the relationship between the percentage of spatial overlap between the six insect species with *A. artemisiifolia* in EU and that in NA under current and future climatic conditions. To verify the appropriateness of using the mean of four future bioclimatic scenarios of the plant and six insect species to predict their overlap, we also correlated the overlap percentage between the plant and the insect species under each of the four future bioclimatic scenarios independently and presented their average with the standard deviation.

Bioclimatic niche analyses

Niche overlap between *A. artemisiifolia* in the native NA and invaded EU range was estimated using ordination techniques in the *ecospat* package in R (Broennimann et al. 2014). Niches were quantified along the two-first axes of a PCA-env based on a correlation matrix of the same nine bioclimatic variables selected for the SDMs of *A. artemisiifolia* (Appendix S4: Table S3). We then ran niche equivalency and similarity tests. The niche equivalency examines whether the niche overlap is constant when randomly reallocating the occurrences of both entities among the two ranges, which is repeated 100 times. The niche similarity tests address whether the overlap between observed niches in the two ranges is higher than the overlap between the observed niche in one range and a niche selected at random from the other range. The test was done in both direction (NA ↔ EU) using 100 repetitions (Broennimann et al. 2012).

Table 1. AUC power of all species using four models under current climate scenarios, showing acceptable AUC scores.

Modeling	*Ambrosia artemisiifolia*	*Ophraella slobodkini*	*Ophraella communa*	*Zygogramma disrupta*	*Zygogramma suturalis*	*Epiblema strenuana*	*Tarachidia candefacta*
GLM	0.929 ± 0.001	0.933 ± 0.017	0.867 ± 0.004	0.953 ± 0.01	0.841 ± 0.022	0.856 ± 0.009	0.88 ± 0.006
GBM	0.941 ± 0.001	0.957 ± 0.013	0.896 ± 0.003	0.987 ± 0.004	0.899 ± 0.013	0.88 ± 0.008	0.9 ± 0.006
RF	0.958 ± 0.001	0.965 ± 0.011	0.901 ± 0.004	0.991 ± 0.005	0.895 ± 0.013	0.877 ± 0.009	0.904 ± 0.006
MAXENT	0.935 ± 0.001	0.878 ± 0.012	0.833 ± 0.005	0.94 ± 0.011	0.773 ± 0.019	0.807 ± 0.011	0.818 ± 0.009

Note: AUC, area under the curve; GBM, generalized boosting models; GLM, generalized linear models; RF, random forest; MAXENT, maximum entropy.

All analyses were performed using R statistical software, version 3.2.2 (R Development Core Team 2015).

RESULTS

Performance of species distribution models

Area under the curve evaluates the discriminatory power of model predictions. In our models, AUC ranged from 0.77 to 0.99 across the seven species and four model types, and more than 90% of AUC values were larger than 0.8 (Table 1). Specifically, species of *A. artemisiifolia*, *O. slobodkini*, and *Z. disrupta* had on average higher AUC than the other four species (Tukey's HSD, $P < 0.001$); GBM and RF were generally equally predictive (Tukey's HSD, $P = 0.54$), and both tended to be more predictive than GLM and MAXENT (Tukey's HSD, $P < 0.001$; Appendix S4: Fig. S1). In general, given the high AUC scores (AUC = 0.5 indicates that model performance is equal to that of a random prediction, while AUC = 0.8 means that in places where a species is present, in 80 of cases the predicted values will be higher than where the species has not been recorded; Wisz et al. 2008) achieved in each modeling approach for all species, our models thus yielded high AUC scores and provided useful information for an analysis of climate suitability of the studied biocontrol agents through modeling of the species distributions. Those predictions exhibit potential distributions very close to the observed ones. The high AUC of all insect species also suggests that it is possible to obtain reasonable distribution predictions in a specific introduced area using the data from native range or other introduced range. This is most helpful in pre-release assessment.

Geographical overlap between suitable areas for Ambrosia artemisiifolia *and those for insect species*

Within the 150 yr after its introduction into central Europe (Essl et al. 2015), the range of *A. artemisiifolia* already extends well above the 50° latitude (Appendix S6: Figs. S1, S4), which corresponds to climatic conditions at the very northern limit of the distribution in North America. Under climate change, *A. artemisiifolia* is expected to expand its range in Europe even further north and east, whereas its native range is predicted to expand very little (Appendix S6: Figs. S2, S5).

Model predictions based on current climate and four future climate scenarios indicate that *O. slobodkini* has no suitable area in EU and the smallest overlap with the area suitable for *A. artemisiifolia* among the six candidate agents (0% and 3.6% for current climate and 0% and 3.8% for future climate of EU and NA, respectively; Figs. 1A, 2A, 3A, 4A). *Tarachidia candefacta* has the largest overlap percentage with the suitable area for *A. artemisiifolia* among the six candidates (25.5% and 78.2% for current climate and 24.8% and 57.7% for future climate of EU and NA, respectively; Figs. 1F, 2F, 3F, 4F). *Ophraella communa* and *E. strenuana* have a relatively large overlap with the suitable area for *A. artemisiifolia* in both EU and NA (*O. communa*: 18.1% and 62.0% for current climate, respectively, and 7.6% and 52.0% for future climate, respectively; *E. strenuana*: 25.5% and 69.4% for current climate, respectively, and 24.8% and 56.9% for future climate, respectively; Figs. 1B, E, 2B, E, 3B, E, 4B, E), while *Z. suturalis* has relatively small overlap in EU (5.5% and 2.6% for current and future climate, respectively), but relatively high

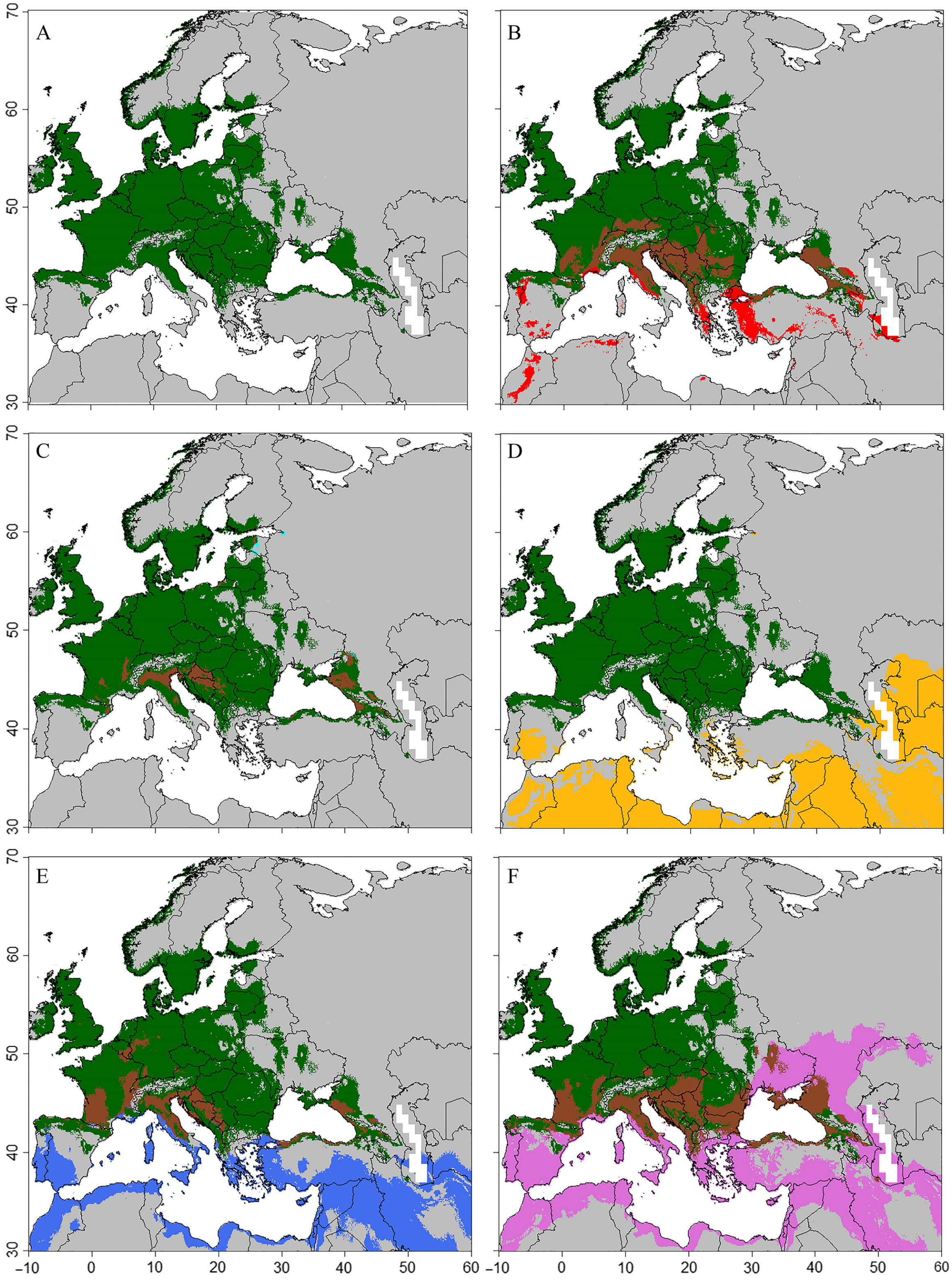

Fig. 1. Geographical predictions of *Ambrosia artemisiifolia* and its potential biocontrol agent herbivores under

(*Fig. 1. Continued*)
present climatic scenarios. The climatic suitability indicates the optimal threshold of the percentage of models predicting each species: (A) dark green, *A. artemisiifolia*; yellow, *Ophraella slobodkini*; overlap, 0%. (B) Dark green, *A. artemisiifolia*; red, *O. communa*; overlap, 18.1%. (C) Dark green, *A. artemisiifolia*; cyan, *Zygogramma suturalis*; overlap, 5.5%. (D) Dark green, *A. artemisiifolia*; goldenrod, *Z. disrupta*; overlap, 0.04%. (E) Dark green, *A. artemisiifolia*; blue, *Epiblema strenuana*; overlap, 11.5%. (F) Dark green, *A. artemisiifolia*; orchid, *Tarachidia candefacta*; overlap, 25.5%. The "overlap" region of the invasive *A. artemisiifolia* and its potential biocontrol agents is given (sienna). Models calibrated in Europe only.

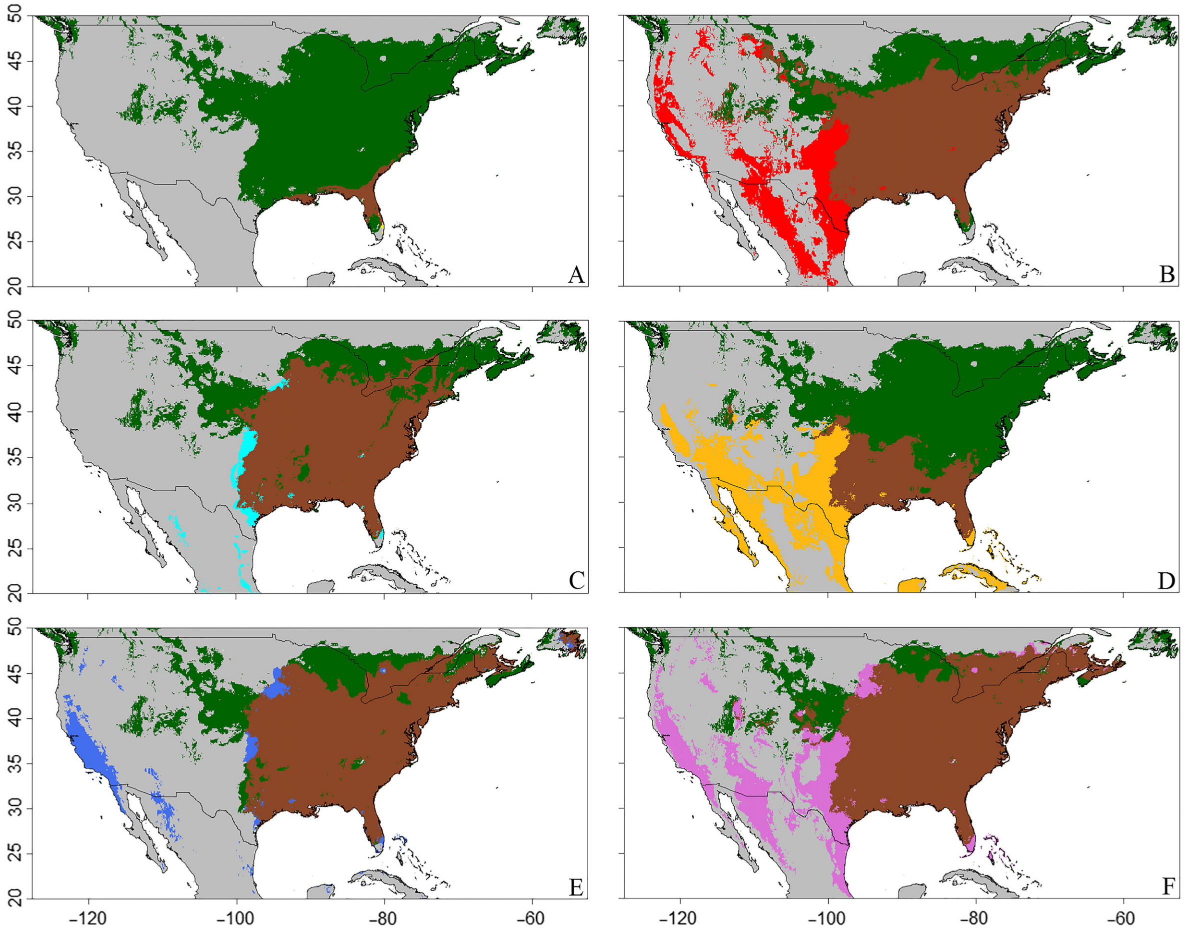

Fig. 2. Geographical predictions of *Ambrosia artemisiifolia* and its potential biocontrol agent herbivores under present climatic scenarios. The climatic suitability indicates the optimal threshold of the percentage of models predicting each species: (A) dark green, *A. artemisiifolia*; yellow, *Ophraella slobodkini*; overlap, 3.6%. (B) Dark green, *A. artemisiifolia*; red, *O. communa*; overlap, 62.0%. (C) Dark green, *A. artemisiifolia*; cyan, *Zygogramma suturalis*; overlap, 60.3%. (D) Dark green, *A. artemisiifolia*; goldenrod, *Z. disrupta*; overlap, 23.1%. (E) Dark green, *A. artemisiifolia*; blue, *Epiblema strenuana*; overlap, 69.4%. (F) Dark green, *A. artemisiifolia*; orchid, *Tarachidia candefacta*; overlap, 78.2%. The "overlap" region of the invasive *A. artemisiifolia* and its potential biocontrol agents is given (sienna). Models calibrated in USA only.

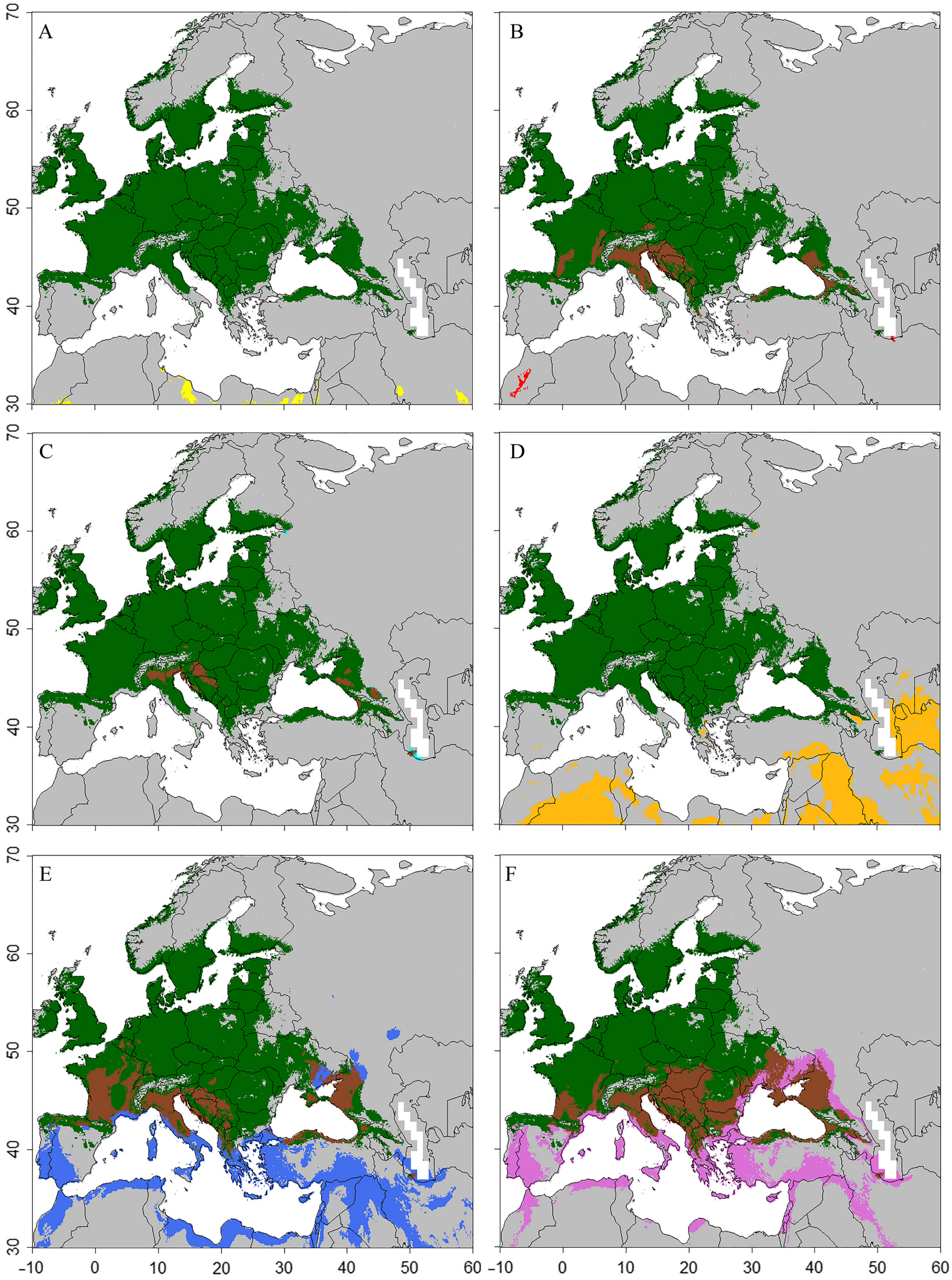

Fig. 3. Geographical predictions of *Ambrosia artemisiifolia* and its potential biocontrol agent herbivores under

(*Fig. 3. Continued*)
future climatic scenarios. The climatic suitability indicates the optimal threshold of the percentage of models predicting each species: (A) dark green, *A. artemisiifolia*; yellow, *Ophraella slobodkini*; overlap, 0%. (B) Dark green, *A. artemisiifolia*; red, *O. communa*; overlap, 7.6%. (C) Dark green, *A. artemisiifolia*; cyan, *Zygogramma suturalis*; overlap, 2.6%. (D) Dark green, *A. artemisiifolia*; goldenrod, *Z. disrupta*; overlap, 0.04%. (E) Dark green, *A. artemisiifolia*; blue, *Epiblema strenuana*; overlap, 15.9%. (F) Dark green, *A. artemisiifolia*; orchid, *Tarachidia candefacta*; overlap, 24.8%. The "overlap" region of the invasive *A. artemisiifolia* and its potential biocontrol agents is given (sienna). Models calibrated in Europe only.

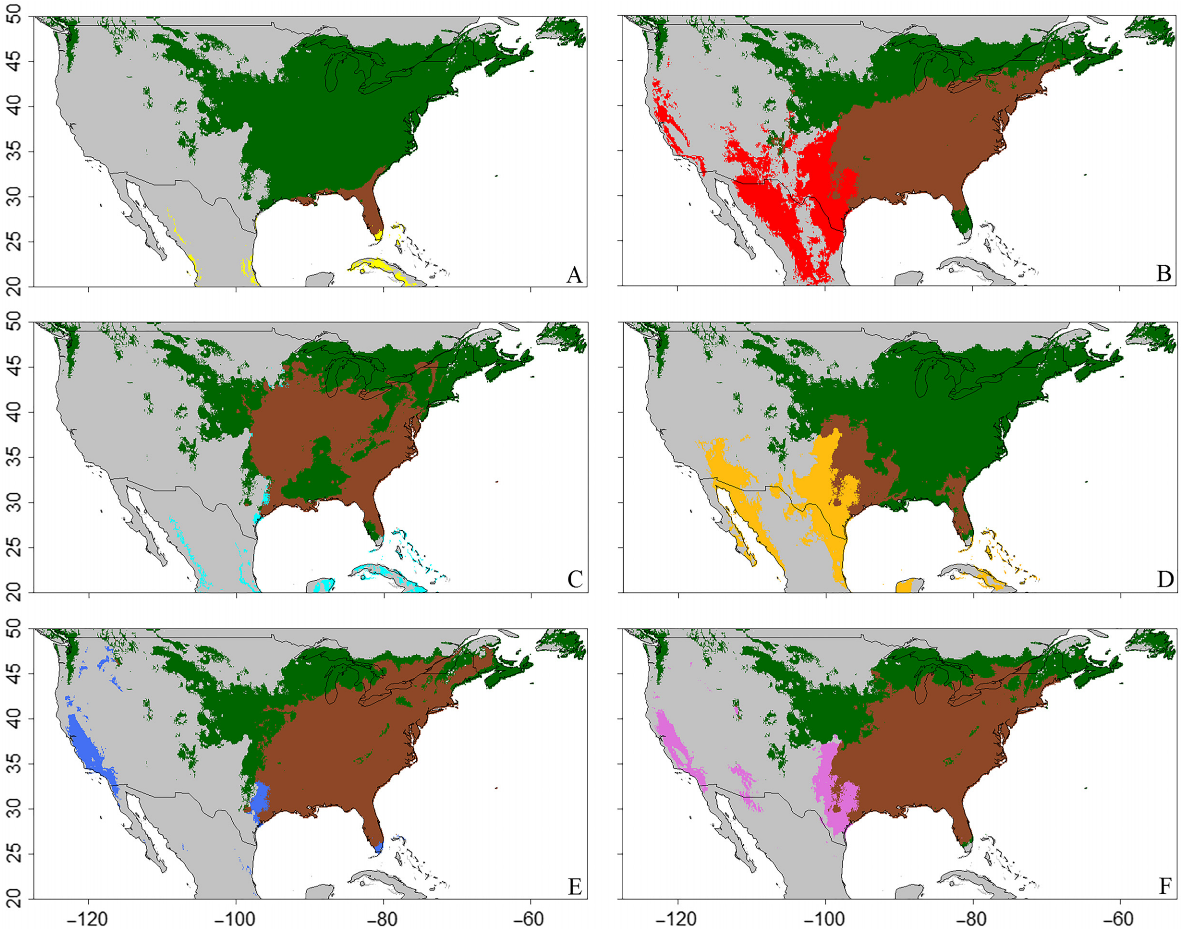

Fig. 4. Geographical predictions of *Ambrosia artemisiifolia* and its potential biocontrol agent herbivores under future climatic scenarios. The climatic suitability indicates the optimal threshold of the percentage of models predicting each species: (A) dark green, *A. artemisiifolia*; yellow, *Ophraella slobodkini*; overlap, 3.8%. (B) Dark green, *A. artemisiifolia*; red, *O. communa*; overlap, 52.0%. (C) Dark green, *A. artemisiifolia*; cyan, *Zygogramma suturalis*; overlap, 44.2%. (D) Dark green, *A. artemisiifolia*; goldenrod, *Z. disrupta*; overlap, 13.2%. (E) Dark green, *A. artemisiifolia*; blue, *Epiblema strenuana*; overlap, 56.9%. (F) Dark green, *A. artemisiifolia*; orchid, *Tarachidia candefacta*; overlap, 57.7%. The "overlap" region of the invasive *A. artemisiifolia* and its potential biocontrol agents is given (sienna). Models calibrated in USA only.

overlap in NA (60.3% and 44.2% for current and future climate, respectively; Figs. 1C, 2C, 3C, 4C); and *Z. disrupta* has relatively small overlap in both EU and NA (0.04% and 23.1% for current climate, respectively, and 0.04% and 13.2% for future climate, respectively; Figs. 1D, 2D, 3D, 4D). In the native North American range, a total of 83.3% (current) and 68.5% (future) of the *A. artemisiifolia* suitable area will also be climatically suitable for at least one of the six potential biocontrol candidates (Appendix S6: Figs. S1, S2), while this is much smaller with only 31.4% (current) and 29.1% (future) for the invaded European area (Appendix S6: Figs. S1, S2). Additionally, the overlap between areas suitable for *A. artemisiifolia* and at least one of the six insect candidates varied drastically (i.e., from 0% to 100%; Table 2) in each European country under current climatic conditions.

We found significant positive correlations between the predicted *A. artemisiifolia* cover by the six potential agents on *A. artemisiifolia* suitable area in NA and that in EU under current climate condition (Spearman's $\rho = 0.943$, $P = 0.008$; Fig. 5), under mean future climate scenarios (Spearman's $\rho = 0.99$, $P = 0.001$; Fig. 5), as well as under each of the four future climate scenarios (Spearman's $\rho = 0.99$, $P = 0.001$; Fig. 5). Variation in overlap between the four future climate scenarios of the different insect species indicates that the overlap of *E. strenuana* on *A. artemisiifolia* is more sensitive to the different scenarios in EU (y-axis error bar is larger than x-axis error bar; Fig. 5), while more sensitive in NA for the other five insect species (y-axis error bar is smaller than x-axis error bar; Fig. 5).

Observed occurrences and suitable areas predicted for each of seven species under current climate conditions and under the four future climate scenarios are shown in Appendix S6: Figs. S4, S5.

Combining biocontrol candidates to increase geographical overlap with suitable areas for Ambrosia artemisiifolia

Under current climate conditions, the best combination of two potential agents includes *O. communa* and *T. candefacta* and is predicted to cover 29.39% of the potential distribution of *Ambrosia* (Appendix S6: Fig. S3). With three

Table 2. Percentage of *Ambrosia artemisiifolia* suitable areas covered by a least one insect for each European country under current climatic conditions.

Country	Percent coverage (%)
Albania	83.67
Andorra	60.00
Austria	22.02
Belarus	0.00
Belgium	35.88
Bosnia and Herzegovina	88.80
Bulgaria	79.34
Croatia	96.26
Cyprus	NA
Czech Republic	1.55
Denmark	0.00
Estonia	10.16
Faroe Islands	NA
Finland	1.23
France	41.00
Germany	15.60
Gibraltar	NA
Greece	93.94
Hungary	67.90
Iceland	NA
Ireland	0.00
Italy	81.95
Latvia	0.11
Liechtenstein	50.00
Lithuania	0.00
Luxembourg	21.28
Macedonia	77.20
Malta	NA
Moldova	34.01
Monaco	NA
Netherlands	0.43
Norway	0.00
Poland	0.26
Portugal	0.00
Romania	48.80
Russia-European part	82.86
San Marino	100.00
Serbia	88.33
Slovakia	5.31
Slovenia	84.59
Spain	34.69
Sweden	0.00
Switzerland	68.75
Ukraine	43.88
United Kingdom	0.11
Vatican city	NA
Isle of Man	0.00
Kosovo	78.53
Montenegro	74.13

Note: NA represents no *A. artemisiifolia* suitable area.

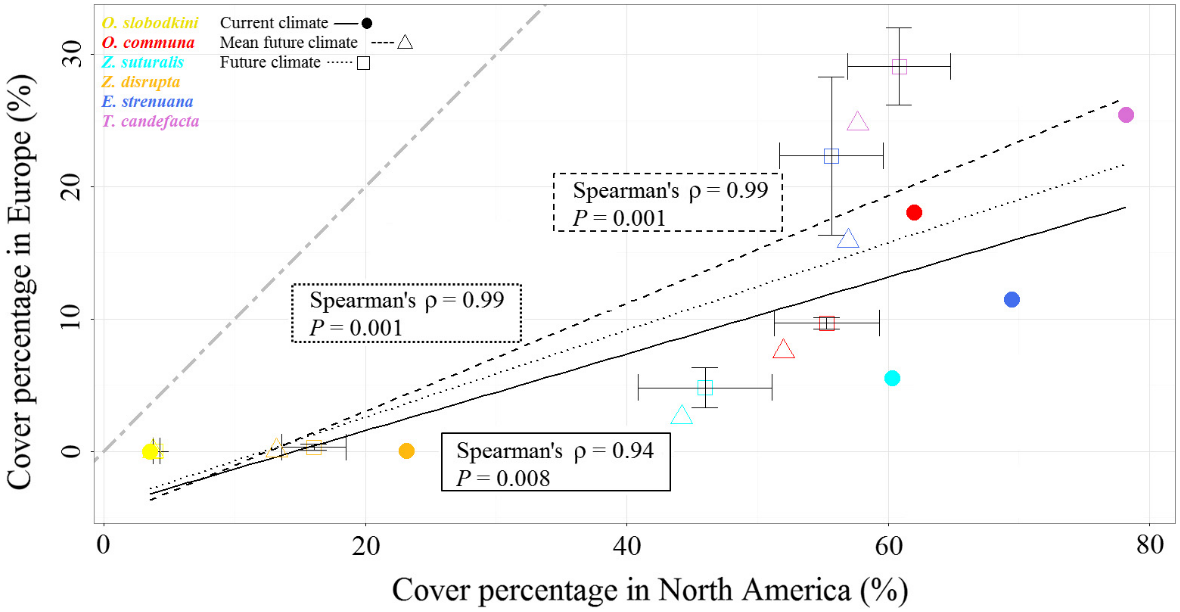

Fig. 5. Relationships between the cover of the suitable area of *Ambrosia artemisiifolia* by its six potential insect biocontrol agents in North America and that in Europe under current climate condition (solid line and dot), the mean of four future climate scenarios (dash line and triangle), and four future climate scenarios (dotted line and square, data are presented as means ± SE, *x*-axis error bar represents the overlap variation among four future climate scenarios in North America, and *y*-axis error bar represents variation in Europe). The agents are *Ophraella slobodkini* (yellow), *O. communa* (red), *Zygogramma suturalis* (cyan), *Z. disrupta* (goldenrod), *Epiblema strenuana* (blue), and *Tarachidia candefacta* (orchid). The four future climates are HadGEM2-AO, rcp26; HadGEM2-AO, rcp85; IPSL-CM5A-LR, rcp26; and IPSL-CM5A-LR, rcp85. Rho values and *P*-values for Spearman's rank correlation are given. The 45° line is included for reference (gray dashed-dotted line).

potential agents, which include *O. communa*, *T. candefacta*, and *E. strenuana*, this percentage would only slightly increase to 31.19% (Appendix S5: Table S1) and be close to 31.4% when all agents are combined (cf. above).

Bioclimatic niche analyses

The first two PCs explained 84.18% of the variation in the data (PC1 = 63.19%, PC2 = 20.99%; Fig. 6). Interestingly, the introduced EU niche exhibits a niche expansion relative to its native NA range (even at its center; Fig. 6A vs. Fig. 6B), mainly due to high *A. artemisiifolia* occurrences in EU in habitats with less distinct seasonality, smaller annual temperature range, and higher precipitations in the driest month (Fig. 6E). Furthermore, the PCA plot also shows unfilling of the NA niche in EU along the temperature and toward less precipitation in the driest month (Fig. 6A, B, E). Both niche equivalency and niche similarity (both ways) are rejected between NA and EU ($P \geq 0.1$), showing that *A. artemisiifolia* has undergone significant alteration of its environmental niche during the invasion process (Fig. 6F–H). This niche change also mirrors the results showed above with regard to the geographic range of *A. artemisiifolia* (Appendix S6: Figs. S1, S2). We also find that habitats with high *A. artemisiifolia* occurrences in EU above the 50° latitude are rare in NA (red points in Fig. 6D vs. Fig. 6A). Moreover, this same area in NA is not covered by insect species, as indicated by their occurrences in NA (blue points in Fig. 6C vs. Fig 6B).

Identifying abiotic conditions not covered by candidates

We chose United Kingdom (UK), Germany, and Poland among the countries with low geographical overlap between *A. artemisiifolia* and the six candidate insects (Table 2) to further explore for ecotypes of the candidate species needed for specific abiotic conditions suitable for *A. artemisiifolia* in

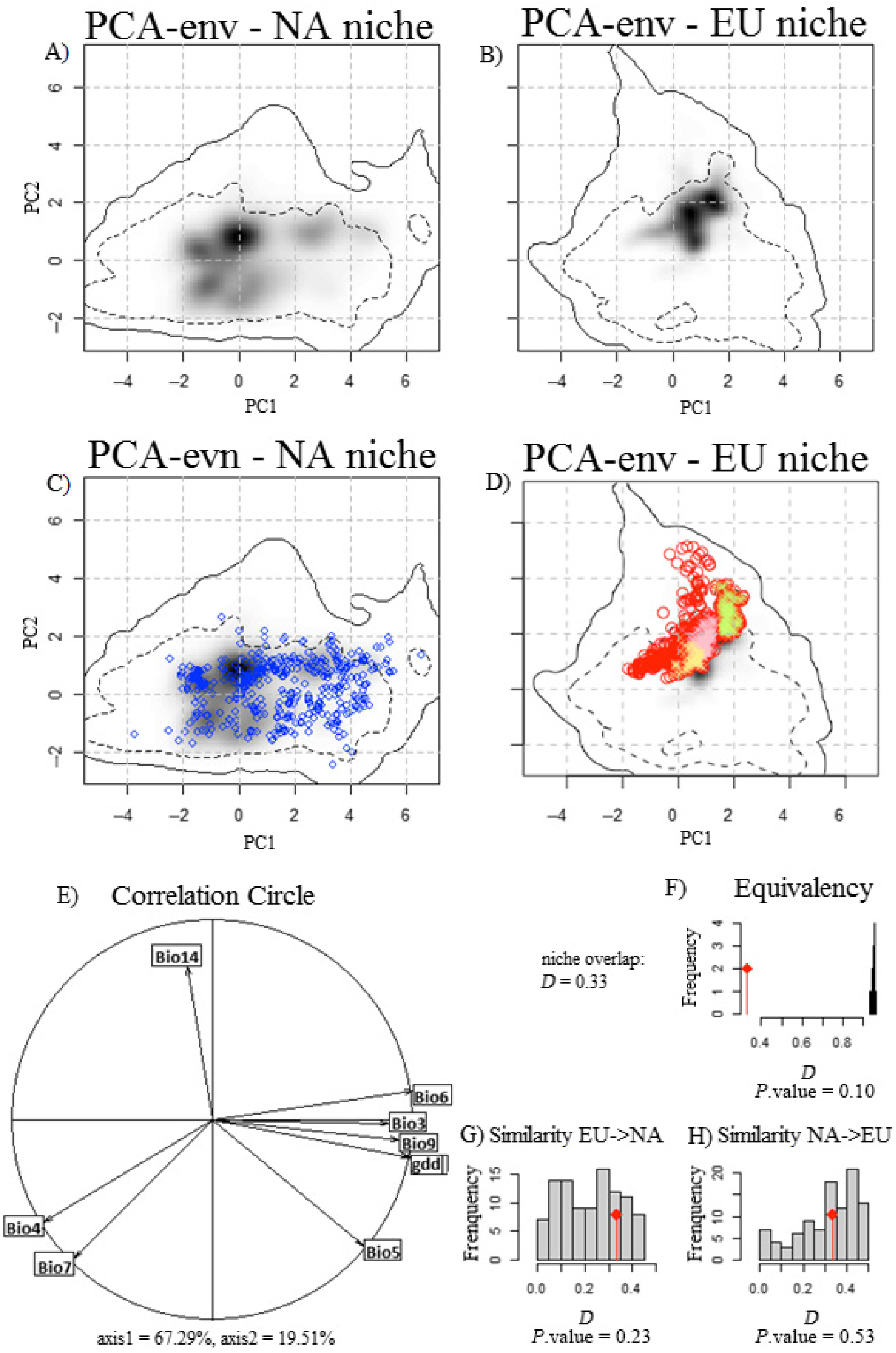

Fig. 6. Niche of *Ambrosia artemisiifolia* in climatic space using principal component analysis (PCA-env). Panels (A) and (B) represent the niche of the species along the two-first axes of the PCA for the native North American (NA) and introduced European (EU) range, respectively. Gray shading shows the density of the occurrences of the species by cell. The solid contour lines illustrate 100% of the available environment, and dashed contour lines

(*Fig. 6. Continued*)
indicate the 50% of most common background environment. Blue circles in (C) give the occurrences of all six insect species in NA and red circles in (D) the occurrences of *A. artemisiifolia* in northern part of EU (>50° latitude, where no insect species are predicted to be suitable, see Fig. 1), green, pink and yellow crosses in (D) give occurrences of *A. artemisiifolia* in UK, Germany, and Poland, respectively; (E) the contribution of the climatic variables on the two axes of the PCA and the percentage of inertia explained by the two axes. Histograms (F–H) show the observed niche overlap D between the two ranges (bars with a diamond) and simulated niche overlaps (gray bars) on which tests of niche equivalency (F), niche similarity of EU to NA (G), and niche similarity of NA to EU (H) are calculated from 100 iterations, with the significance level of the tests.

Europe, but that are not covered yet by any candidates. Comparing occurrences of *A. artemisiifolia* in UK, Germany, Poland, and North America (green, pink, and yellow crosses in Fig. 6D) clearly shows that the conditions occupied by *A. artemisiifolia* in these EU countries are at the margin of the niche of the species in the North America and correspond to cooler and wetter conditions in the three countries, as compared to the NA range (i.e., higher values on bio6, bio9, and bio14, lower values on bio4 and bio7).

DISCUSSION

For the first time, the distributions of an invasive alien plant species and of its potential biocontrol candidates are modeled simultaneously and both under current and future climatic conditions in view of selecting agents with the potential to cover a large range of the target invader species, or with high suitability for specific geographic areas in the invaded range.

Predicted species distributions

The potential distribution maps suggest that the suitable areas for *A. artemisiifolia* area that are also suitable for the selected six most promising biocontrol agents in North America can be usefully transferred to the introduced European area, both for present and for future climatic conditions. Thus, biocontrol agents that can cover larger parts of the suitable area of the target plant species in the native range will also cover larger parts in the introduced range. Interestingly, this holds true despite yet considerable unfilled areas and the identified significant niche expansion (Fig. 6) of the target plant invader in the introduced range. Our analysis further identified *T. candefacta* as the best candidate with regard to maximal cover of the target plant invader. Cover of the *A. artemisiifolia* area by the biocontrol candidates is far higher in the native North American range as compared to the introduced European range (Appendix S6: Fig. S1), but this cover does not vary with climate change. Large areas in EU are unsuitable for all agents, while few areas were predicted to be unsuitable for them in NA. These unsuitable EU areas are located in central, western, and northern Europe, where *A. artemisiifolia* faces lower temperature seasonality and more precipitation compared to the main conditions occupied in North America. This is likely due to the effects of the Gulf Stream, which strongly buffers the climate of the western and northern Europe. Hence, limitation of insect presence by climate appears a likely explanation, but no differentiation between the plant invader and its potential agents is found in the climatic space (Appendix S3: Fig. S1), as those EU habitats are rare in NA, but still exist (Fig. 6).

The rejection of equivalence and similarity, and the centroid shift in the realized niche between European and North American *A. artemisiifolia* indicate that invasive populations in Europe have shifted toward a more continental climate (Fig. 6). The centroid position shift suggests a change in the density of occurrences between the native North American and introduced European niche. More importantly, niche expansion in EU mainly occurred in northern Europe (Fig. 6D, red points), partly explaining the large discrepancy in the geographic range overlap between EU and NA. Petitpierre et al. (2012) found substantial niche shifts to be rare in invasive plants, but important exceptions have recently also been documented (e.g., expansion of *Lactuca serriola*; Alexander 2013, and a shift of *Centaurea stoebe*; Broennimann et al. 2007, in their invaded range). Our observation for *A. artemisiifolia* slightly differs from the finding of Petitpierre et al. (2012), who also reported niche unfilling in Europe for *A. artemisiifolia*, but in contrast to our analysis no niche expansion, which might be due to the slightly reduced set of bioclimatic variables used in their analysis.

Using the mean of the four future bioclimatic scenarios well represents the predicted future overlap between the plant and the insects, although there is some variation when considering the species-specific differences among the future climate conditions in EU or NA. The spatial mismatch of *A. artemisiifolia* and its potential agents is further amplified by climate change for North America, but only slightly for Europe (NA: 83.3% vs. 68.5% and EU: 31.4% vs. 29.1%, for current and future climate; respectively). Especially, the cover of *O. communa* on the suitable *A. artemisiifolia* area is reduced from 18.1% to 7.6% in Europe. One possible reason is that warmer summers and later autumn frosts in the future will allow northward and uphill spread of *A. artemisiifolia* in Europe (Figs. 1, 3; and also see Cunze et al. 2013, Chapman et al. 2014, Essl et al. 2015), but this might not hold true for the insects; for example, insect species will spread more slowly or even being squeezed by climate change (Björkman and Niemelä 2015).

Management implications

We found that a large part of the geographic range of *A. artemisiifolia* in central, western, and northern Europe will not be suitable for the six selected potential biocontrol agents. The observed niche shift of *A. artemisiifolia* in Europe and the fact that widespread habitats in northeastern Europe are rare and do not overlap with the environmental niches of the biocontrol candidates in NA imply that none of the studied candidate agents could presently cover the more northern and eastern area in Europe under present and more so under future climatic conditions. Niche analyses, however, clearly indicate the abiotic conditions to select for in the studied or in additional agents in order to develop specifically adapted strains for the yet uncovered *A. artemisiifolia* areas in Europe. For this, genetic variation in relevant performance traits will be crucial. Measures of genetic variation in functional traits, however, have rarely been studied in biocontrol agents to predict their evolvability, that is, the speed of evolutionary changes and their adaptive potential to abiotic conditions (Roderick et al. 2012).

Previous research with *O. communa*, one of our study species, did find genetic variation in relevant performance traits. For example, Tanaka (2009) found genetic variation for flight activity, and Tanaka et al. (2015) reported rapid evolution in photoperiod response to environmental conditions in different colonized regions, both indicating the potential for local adaptation to different abiotic conditions. In line with these findings, Zhou et al. (2013) were able to select for strains of *O. communa* adapted to colder temperatures by cold acclimation in previous generation to facilitate their range expansion toward northern China and thus to track their host plants into colder climate. This indicates the potential to select for strains that could cover the *A. artemisiifolia* range in northern Europe presently unsuitable for the insects.

Our analysis thus helps to identify the combination of agents that cover most of the area in Europe (Appendix S5: Table S1) and to choose appropriate agents for specific geographical areas. For instance, *O. communa*, *E. strenuana*, and *T. candefacta* appear to be most suitable agents in Italy and France, while *E. strenuana* also has potential to expend toward southern Russia under future climatic conditions (Figs. 1, 3). We also identified two important bioclimatic factors that might restrict establishment, performance, and population build-up of the biocontrol agents in the yet less covered part of the suitable *A. artemisiifolia* range of UK, Germany, and Poland, that is, increased precipitation and decreased temperature. This is well in line with findings by Szűcs et al. (2012), who observed limited establishment of population of the chrysomelid *Longitarsus jacobaeae* originating from low elevations in Italy when introduced as a biocontrol agent against *Jacobaea vulgaris* into cooler areas and higher elevations of the Rocky Mountains in Oregon, United States. Interestingly, these beetles became adapted to the cooler conditions within 30 yr. Specific selection regimes during commercial mass productions could thus greatly speed up the development of strains adapted to the yet uncovered *A. artemisiifolia* areas in Europe.

By using species distribution models, our study provides a cost-effective pre-evaluation of suitable biocontrol agents before time- and cost-intensive experimental studies are conducted. Our analyses also instruct for which abiotic conditions to select in the studied or in additional agents in order to develop specifically adapted strains for the yet uncovered *A. artemisiifolia* areas in Europe and also under future climatic conditions. We acknowledge that studies on the demographic interactions between the invasive alien plant and its biocontrol agents are important to further improve the accuracy of predictions of the distribution dynamics and thus the management success of this prominent plant invader.

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