

## Biological control opportunities of ragweed are predicted to decrease with climate change in East Asia

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**Abstract:** The control of invasive alien plants (IAP) that jeopardize our ecosystems and economy constitutes a significant challenge for natural resource management. Classical biological control referring to the introduction of specialist antagonists from the native range has proven to be a highly cost-effective management tool against IAP. A critical issue in biological control research is to guide informed decision-making on the potential spread and distribution and thus impact of biological control candidates, especially under climate change. Here we propose a biogeographic modeling approach to predict the cover of the suitable area of a plant invader in East Asia (EA) by two biological control agents and their combinations. Our study system is *Ambrosia artemisiifolia*, native to North America and invasive worldwide, and two North American biological control agents, *Ophraella communa* and *Epiblema strenuana* that were accidentally and deliberately introduced into East Asia (EA) in the late 20th century, respectively. Specifically, we ask: (1) what percentage of the suitable *A. artemisiifolia* area is also suitable for the two agents in EA, and (2) which part of the suitable *A. artemisiifolia* area in EA is likely to remain uncovered by these two agents, both under current and future climatic scenarios; and (3) which particular biotypes would be needed to fill in the yet uncovered part of the suitable *A. artemisiifolia* range in EA? For this, we simultaneously modelled the species distributions based on worldwide occurrences and important bioclimatic variables for the target invasive plant and its two biological control agents. Ordination techniques were used to explore climatic constraints of each species and to perform niche overlap and similarity tests with *A. artemisiifolia* between its native North American and introduced EA range. Our results show that *O. communa* has a larger overlap with the geographic range of *A. artemisiifolia* than *E. strenuana*, both under current and future climatic scenarios. Importantly, climate change is expected to reduce the total geographic overlap of *A. artemisiifolia* by the two agents combined, with a higher reduction by *O. communa* than by *E. strenuana*. Our analyses also identified for which abiotic conditions to select in order to develop climatically adapted strains for particular regions, where *A. artemisiifolia* is presently unlikely to be covered.

**Key words:** biological invasions; *Epiblema strenuana*; *Ophraella communa*; biological control; niche overlap; species distribution

## Introduction

Biological invasions by alien plants, i.e. plants that are introduced intentionally or unintentionally outside their native geographical range, are among the most important drivers of global change and can have devastating impacts on ecosystems and economy (Vilà et al, 2011). Management and control of invasive alien plants have thus become a great challenge for ecologists, conservation biologists and environmental practitioners involved in natural resource management (Walker & Steffen, 1997; Kettenring & Adams, 2011).

In this respect, ‘classical’ biological control by releasing specialist natural antagonists from the invaders’ native range has been a most successful management tool to reduce the abundance of invasive plants, owing to its cost-effectiveness and relatively high environmental safety (Müller-Schärer & Schaffner, 2008; Winston et al, 2014; Seastedt, 2015).

Species distribution models (SDMs) relating geo-located observations of occurrence data to a variety of environmental data sets that contribute to a species’ survival and propagation allow identifying ecological characteristics that define the species range and

distribution (Guisan & Zimmermann, 2000). Furthermore, SDMs are also a very useful tool for predicting the response of species distributions to climate change (Peterson, 2011). Recently, SDMs have been increasingly used to predict the spatial extent of invasions and identify at-risk habitats under current climate and on-going environmental change (Peterson, 2003). In analogy, SDMs also provided a most helpful tool to predict most suitable ranges of biological control agents in the introduced ranges (Sun et al, 2017). It further allowed to identify both suitable collection locations of biological control agents in the home range (Mukherjee et al, 2011) and of release sites in the introduced area, as climate clearly influences their establishment and performance due to underlying biophysical factors (Hoelmer & Kirk, 2005). Indeed, biological control agent with an optimal climatic match between home and release locations were found to better establish and become more efficient than agents with a less good match (Goolsby et al, 2005). Important complementary information from species occurrences that are relevant for invasion management can be deduced from ordination techniques that allow for direct comparisons of species-environment relationships in the environmental space (Broennimann et al, 2012).

Climate change (IPCC, 2013) is expected to significantly impact the distribution of species and the resource dynamics of ecosystems, with particular importance for biological invaders and associated consumers used for biological control (Theoharides & Dukes, 2007; Walther et al, 2009). Climatic factors are also of major importance in determining the outcome of species interactions for species distributions and thus also for biological control programmes (Messinger & Van den Bosch, 1971), as plants and arthropods might react differently to climate change (Hannah et al, 2002; Gillson et al, 2013). An understanding of the impact of future climate variability on invasive alien species and on their biological control agents is thus of fundamental importance for predicting sustainable biological control management. For this, bioclimatic models provide a cost-effective approach that further allows considering both present and future climatic conditions.

Common ragweed, *Ambrosia artemisiifolia* (Asteraceae), is an annual wind-pollinated monoecious weed native to North America and Mexico, and was accidentally introduced to many parts of the world, including Asia, South America, Australia and Europe. Both in its native and introduced ranges, *A. artemisiifolia* is causing great damage to the society due to its highly allergenic pollen, and because it grows as a weed in many crops, where it is hard to control (Wan et al, 2005; Essl et al, 2015). In China, pollen aller-

gens have been found in 2–3% of the human population, where *A. artemisiifolia* occurs and resulting health cost have been estimated to 1.4 billion CHY per year (Zhou et al, 2015). *Ambrosia artemisiifolia* was established in Japan more than 100 years ago, and became widely distributed throughout the Japanese islands by 1950s (Fukano & Yahara, 2012). In China, *A. artemisiifolia* has been reported since the 1930s and has been considered as a harmful weed in various crops since 1997 (Wan et al, 1993). Besides being linked to agricultural land, *A. artemisiifolia* is also widely distributed along linear transport structures, such as railways, roads and rivers both in China (Wan et al, 1993) and Japan (Hisauchi, 1950). The ability of *A. artemisiifolia* to grow side branches after partial control by cutting and herbicides and its high proliferation rate renders its management challenging (Wan et al, 2005; Essl et al, 2015). Herbicides and mechanical control (i.e. uprooting, cutting and ploughing) treatments are well suited for the short-term management of small emerging populations (Essl et al, 2015). In crop situations, herbicides for biomass reduction of *A. artemisiifolia* are available; 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 biological control. This option has proven to be most successful against *A. artemisiifolia* in China by using *Ophraella communa* LeSage (Coleoptera: Chrysomelidae) and *Epiblema strenuana* Walker (Lepidoptera: Tortricidae) (Zhou et al, 2011b). Both species are native to North America. *Ophraella communa* is an oligophagous leaf beetle with *A. artemisiifolia* as its preferred host plant (LeSage, 1986; Futuyma & McCafferty, 1990; Palmer & Goeden, 1991). In East Asia, it was accidentally introduced and first discovered in Chiba Prefecture (eastern Japan) in 1996, from where it rapidly spread across the main Japanese islands (Yamazaki et al, 2000; Moriya & Shiyake, 2001). In China it was first recorded in 1999 (Zhou et al, 2014). Under favorable environmental conditions, *O. communa* can reach 4–7 generations per year, which allows it to build up high local densities during the second half of the *A. artemisiifolia* growing season. This beetle can cause complete defoliation and death of *A. artemisiifolia* under both experimental and field conditions (Palmer & Goeden, 1991; Zhou et al, 2014). It is currently used as the most efficient and successful biological control agent against *A. artemisiifolia* in China and is also reported to cause heavy damage to *A. artemisiifolia* in Japan (Yamazaki et al, 2000; Fukano & Doi, 2013). Earlier studies indicated that *O. communa* is mainly adapted to subtropical conditions (Zhou et al, 2010). Recent studies in China attempted to select for *O.*

*communa* strains that can occur and reach higher numbers of generations at higher latitudes where temperatures during the coldest months of the year are significantly lower (Zhou et al, 2011a, 2013). In Japan and South Korea, the beetle so far has not yet been deliberately redistributed (Winston et al, 2014).

*Epiblema strenuana* is a stem mining and gall-inducing moth producing fusiform galls mainly on lateral branches of mature *Ambrosia* plants, with 3–4 generations per year under favorable conditions (Ma et al, 2008). It has been reported to complete 2–3 generations in Northern China and 4–5 generations in Central China (Zhou et al, 2014). It was deliberately introduced from Mexico to Australia in 1982 against *Parthenium hysterophorus* L., and later became established and subsequently also widely distributed on *A. artemisiifolia* (McFadyen, 1992). The moth was deliberately introduced from Australia to China in 1990 to control *A. artemisiifolia*, released in 1993 after additional host specificity tests and subsequently became widely established in southern China (Wan et al, 2005).

First mass releases of these two biological control agent were made in 1993 in Yueyang, Hunan, where they controlled more than 2,000 km<sup>2</sup> of *A. artemisiifolia* infestations in Hunan Province in 1999 and subsequently also spread to Hubei and Jiangxi provinces (Li et al, 1999). In southern China, *O. communa* and *E. strenuana* coexist in many areas invaded by *A. artemisiifolia* and are recommended to be used together to successfully control *A. artemisiifolia* in China (Zhou et al, 2014).

Sun et al (2017) recently constructed, for the first time, species distribution models based on worldwide occurrences and important bioclimatic variables simultaneously for a plant invader and its biological control candidates in view of selecting candidates that potentially cover a large range of the target invader. Their study was performed for *A. artemisiifolia* and six biological control candidates in view of assessing their suitability to control *A. artemisiifolia* in Europe. The main objective of the present investigation is to predict the overlap of suitable *A. artemisiifolia* areas by the two biological control agents in East Asia (EA) both for current and future climatic conditions. More specifically, we asked (1) what percentage of the suitable *A. artemisiifolia* range in EA is also suitable for the two agents; (2) which part of the suitable *A. artemisiifolia* area in EA is likely to remain uncovered by these two agents; and (3) for which abiotic conditions to select for in order to develop climatically adapted strains for particular regions, where *A. artemisiifolia* is presently unlikely to be covered. Besides SDMs, we also performed Principal Component Analyses (PCA) of both the North American and East Asian climatic niche of *A. artemisiifolia* and of the available occurrences of two biological control agents.

## Materials & Methods

### *Species occurrences and bioclimatic data*

We collected all available occurrence data from the literature for *A. artemisiifolia* and the two biological control agents *O. communa* and *E. strenuana* worldwide. Geo-referenced occurrence records of the three species were downloaded from online resources: the Global Biodiversity Information Facility online database (GBIF; <http://www.gbif.org>), the Southwest Environmental Information Network (SEINet; <http://swbiodiversity.org>), the Barcode of Life Data Systems (BOLD; <http://www.boldsystems.org/>), and the Berkeley Ecoinformatics Engine (Ecoengine; <https://ecoengine.berkeley.edu/>). The many additional sources for occurrences of *A. artemisiifolia* and the two insect species are given in the Supporting Information of Sun et al (2017).

We used WORLDCLIM climate data available at <http://www.worldclim.org> (developed by Hijmans et al, 2005) with 19 variables (Appendix 1) at 5 minutes spatial resolution (~10 km close to the equator) to derive a set of meaningful predictors that are considered critical to the plant or insect physiological functions for development and survival of each of our species. We chose important variables for each species under the current climatic condition and four future scenarios based on Sun et al (2017). For the four ‘future’ scenario projections for the 2050 time slice (averages for 2041–2060), we adopted two general circulation models (GCMs: 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) and downloaded from <http://www.worldclim.org> at a spatial resolution of 5 minutes. For all the ‘future’ scenarios, we used the same 19 bioclimatic variables as for the ‘current’ scenario, and these were extracted for each projection, i.e. HadGEM2-AO, rcp26 (HD-26); HadGEM2-AO, rcp85 (HD-85); IPSL-CM5A-LR, rcp26 (IP-26); IPSL-CM5A-LR, rcp85 (IP-85) (Appendix 1).

### *Species distribution modelling*

Based on worldwide occurrences and important bioclimatic variables, we modelled the current and future (according to the four climate change scenarios) potential habitats in the introduced East Asian range for each species, using the Biomod2 framework (Thuiller et al, 2013). A combination of different modelling techniques to adjust for the inherent uncertainty of these models was suggested to find the optimal solution from an ensemble of predictions (Araújo & New, 2007). For 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 (ROC) curve and the true skill statistic (TSS) (Pearce & Ferrier, 2000). More details on the modeling approach are given in Sun et al (2017). 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.

### Bioclimatic niche analyses

Niche overlap between *A. artemisiifolia* in the native North American (NA) and the invaded East Asian (EA) 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*. We then used PCA-env in *Ecospat* to run niche equivalency and similarity tests, which were shown to consistently out-perform other ordination metrics of niche overlap variables (Broennimann et al, 2012; Cola et al, 2016). 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 directions (NA ↔ EA) using 100 repetitions (Broennimann et al, 2012).

All analyses were performed using R statistical software, version 3.3.2 (R Development Core Team 2016).

## Results

### Model performance

Area under the curve (AUC) evaluates the discriminatory power of model predictions that ranged from 0.70 to 0.99 across the three species and four model types in our models. More than 95% of AUC values were larger than 0.8 (AUC of 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; Table 1). Specifically, GBM and RF were generally equally predictive and both tended to be more predictive than GLM

and MaxEnt; *A. artemisiifolia* and *O. communa* had a higher AUC than *E. strenuana* (Appendix 2). In general, given the high AUC values achieved in all analyses, our models thus yielded acceptable AUC values and provided useful information for an analysis of climate suitability of the studied target invasive plant species *A. artemisiifolia* and the two biological control agents through modelling of the species distributions. Those highly accurate predictions exhibit potential distributions very close to the observed ones. The high AUC values also suggest that it is possible to obtain reasonable distribution predictions in a specifically introduced area using the data worldwide, i.e. from both native range and other introduced ranges.

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

	<i>Ambrosia artemisiifolia</i>	<i>Ophraella communa</i>	<i>Epiblema strenuana</i>
<b>Current climate scenario</b>			
GLM	0.88±0.002	0.88±0.004	0.84±0.01
GBM	0.89±0.002	0.90±0.003	0.89±0.006
RF	0.89±0.003	0.91±0.003	0.89±0.006
MaxEnt	0.87±0.003	0.83±0.004	0.83±0.009
<b>HD-26 Future climate scenario: HD-26</b>			
GLM	0.87±0.003	0.87±0.002	0.83±0.01
GBM	0.89±0.002	0.90±0.002	0.90±0.006
RF	0.90±0.002	0.91±0.002	0.91±0.006
MaxEnt	0.86±0.003	0.83±0.003	0.80±0.01
<b>HD-85 Future climate scenario: HD-85</b>			
GLM	0.88±0.003	0.88±0.002	0.84±0.008
GBM	0.90±0.003	0.92±0.001	0.86±0.008
RF	0.89±0.003	0.92±0.001	0.86±0.009
MaxEnt	0.88±0.003	0.84±0.003	0.78±0.01
<b>IP-26 Future climate scenario: IP-26</b>			
GLM	0.89±0.003	0.87±0.002	0.87±0.01
GBM	0.90±0.002	0.90±0.002	0.91±0.008
RF	0.91±0.002	0.91±0.001	0.91±0.008
MaxEnt	0.89±0.003	0.85±0.002	0.82±0.009
<b>IP-85 Future climate scenario: IP-85</b>			
GLM	0.87±0.003	0.87±0.002	0.88±0.008
GBM	0.89±0.003	0.90±0.002	0.91±0.006
RF	0.91±0.003	0.91±0.002	0.91±0.006
MaxEnt	0.87±0.003	0.84±0.003	0.88±0.008

GLM, Generalized linear model; GBM, Generalized boosting model; R, Random forest model; MaxEnt, Maximum entropy.

### Geographical overlap between suitable areas for *A. artemisiifolia* and those for the two insect species

Within 100 years after the introduction of *A. artemisiifolia* into EA, its range now extends from north-east to south-east of China, Korea and most islands of Japan (Appendix 3), which well corresponds to the latitudinal limits of the distribution in North America (Sun et al, 2017). Under climate change, *A. artemisiifolia* is predicted to expand its range in China towards south-west and further north-east, while only very little in Korea and Japan, in total by only 2% (Fig. 1).

Model predictions based on current and four future climate scenarios indicate a larger overlap of *O. communa* than that of *E. strenuana* with the suitable area for *A. artemisiifolia* in EA, with *O. communa* being more widely distributed in the South of China and in Japan (Fig. 1). However, both *O. communa* (from 40.3% to 21.6%) and *E. strenuana* (from 29.8% to 20.3%) show a reduced overlap under future as compared to their current climatic scenarios, and this is especially pronounced for *O. communa*. Under climate

change, *O. communa* is predicted to be less suitable in southern and western China, especially in the provinces of Chongqing, Guizhou, Guangxi, Guangdong and Fujian, while *E. strenuana* is predicted to be less suitable in the Chinese provinces of Sichuan, Henan, Anhui and Jiangsu, as well as in Japan (Fig. 1). Hence, under current climatic scenarios, a total of 42.9% of the area suitable for *A. artemisiifolia* is predicted to be also climatically suitable for at least one of the two biological control agents, but only 29.8% overlap is predicted under future climatic scenarios (Appendix 4). The predictions of the suitable area of each of three species under current and future climate scenarios are presented in Appendix 3 and 5.

### Bioclimatic niche analysis

For niche detection, we analyzed *A. artemisiifolia* occurrences in North America and East Asia using PCA-env. The first two PCs explained 86.9% of the variation in the data (PC1 = 74.28%, PC2 = 12.62%; Fig. 2). The introduced EA niche exhibits a large niche

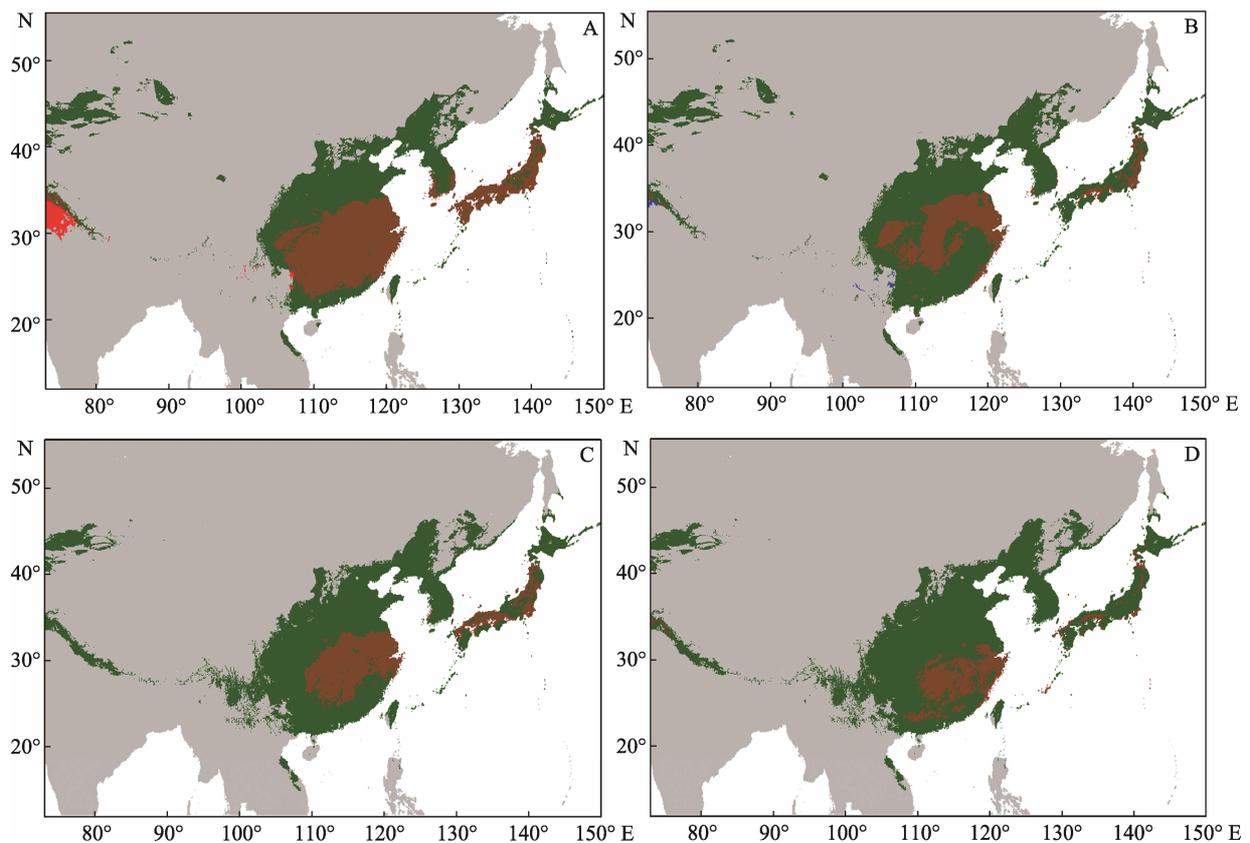


Fig. 1 Geographical predictions of *Ambrosia artemisiifolia* and two biological control insects for East Asia, under present and future climatic scenarios. The climatic suitability indicates the optimal threshold of the percentage of models predicting each species. Dark green in all figures, *A. artemisiifolia*, under current climatic conditions: (A) Red, *Ophraella communa*; sienna, overlap 40.3%; (B) Blue, *Epiblema strenuana*; sienna, overlap 21.6%. Under future climatic scenarios: (C) Red, *Ophraella communa*; sienna, overlap 29.8%; (D) Blue, *Epiblema strenuana*; sienna, overlap 20.3%. Models calibrated in East Asia only.

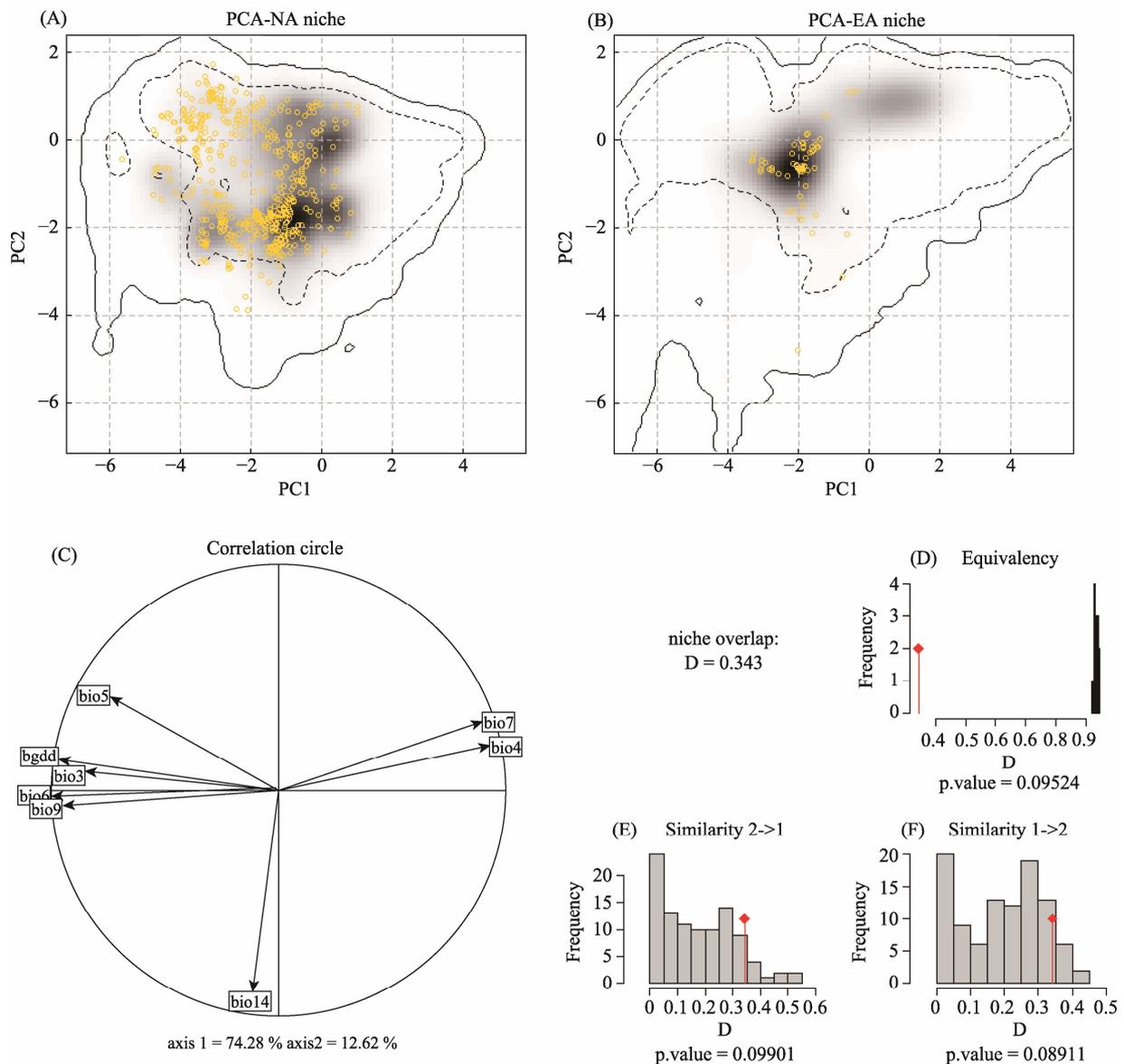


Fig. 2 Niche of *Ambrosia artemisiifolia* in climatic space using principal component analysis (PCA-env). Panels (A) and (B) represent the niche of the species along the two first axes of the PCA for the native North American (NA) and introduced East Asian (EA) range, respectively. Gray shading shows the density of the occurrences of the species by the cell. The solid contour lines illustrate 100 percent of the available environment, and dashed lines indicate the 50 percent of the most common background environment. Yellow circles in (A) and (B) give the occurrences of two insect species in NA and in EA. The contribution of the climatic variables of the two axes of the PCA and the percentage of inertia explained by the two axes is given in (C). Histograms (D–F) show the observed niche overlap  $D$  between the two ranges (bars and a diamond) and simulated niche overlaps (gray bars) on which tests of niche equivalency (D), niche similarity of EA and NA (E), and niche similarity of NA to EA (F) are calculated from 100 iterations, with the significance level of the tests.

unfilling compared to the native NA niche along the x-axis towards cooler summers and higher temperature seasonality (Fig. 2A–C). In addition, Fig. 2B also shows a small niche shift towards decreased precipitation of the driest month in EA. Niche equivalency and both way niche similarity are rejected between the NA and EA niche ( $P > 0.09$ ), indicating that *A. artemisiifolia* has undergone a significant alteration of its enviro-

mental niche during the invasion process (Fig. 2 D–F). Occurrences of the two agents very well cover the niche of *A. artemisiifolia* in NA, but this is not yet the case for the cooler and dryer niche in EA (Fig. 2A, B).

## Discussion

In view of predicting the effect of global climate

change on the biological control program of *A. artemisiifolia* in East Asia, we modelled simultaneously the distributions of the plant invader and two of its biological control agents both under current and future climatic conditions.

### *Predicted species distributions*

The niche unfilling by *A. artemisiifolia* in EA was towards cooler and increased temperature seasonality areas, confirming earlier finding by Petitpierre et al (2012) and Sun et al (2017) for the introduced range of *A. artemisiifolia* in Europe. The predicted distribution maps further suggest more than half of the suitable area of *A. artemisiifolia* in EA to be presently unsuitable for the two biological control agents, which is considerably smaller compared to the situation in NA, where the suitable range of the two insect species was found to cover ca. 70% of the suitable *A. artemisiifolia* habitats (Sun et al, 2017). These unsuitable areas in EA are located in Northern and Central China, most of Korea and Northern Japan (Fig. 1). The low suitability prediction in South Korea may be due to the lack of occurrences in our models. The realized niche in EA shows that the niche uncovered by the two agents is mainly in the cooler and drier areas with increased temperature seasonality, which is in line with our geographic predictions.

Using the mean of the four future bioclimatic scenarios well represents the predicted future overlap between the plant and the insects in EA, although there is some species-specific variation. The spatial overlap of the suitable area for *A. artemisiifolia* and its two agents is further reduced by climate change (42.9% vs. 29.8%, for current and future climate, respectively). Especially the cover of *O. communa* on the suitable area of *A. artemisiifolia* drops from 40.3% to 29.8%, which however is in line with the prediction for Europe (Sun et al, 2017). A possible explanation for this reduced biological control opportunity in EA under climate change is that future warmer summers, later autumn frosts and increased temperature seasonality will allow north- and west-ward spread of *A. artemisiifolia*, but not of the two insect species, as the invasive plant species and its biological control agents do not necessarily react in a similar manner to climate change (Schweiger et al, 2008; Barriopedro et al, 2011; Björkman & Niemelä, 2015).

### *Management implications*

We found that a large part of the geographic range of *A. artemisiifolia* in western and northern China, Korea and northern Japan will not be suitable for the two biological control agents. Our analysis also indicates the *O. communa* is not suitable for Korea, and *E.*

*strenuana* is not suitable for most areas in Japan and Korea. Besides the possibility to explore on introducing additional biological control agents to cover these gaps (cf. Gerber et al, 2013), specific strains of the two study species could be selected for to cover the present and future *A. artemisiifolia* range in EA presently unsuitable for these insects. For this, our niche analysis clearly indicates the abiotic conditions to select for in order to develop adapted strains for these areas, which would include selecting for lower summer temperatures and increased temperature seasonality. For this, genetic variation in relevant performance traits will be crucial, but, so far, measures of genetic variation in functional traits have rarely been studied in biological control agents (Roderick et al, 2012). Previous research with *O. communa* reported genetic variation in relevant performance traits, such as for flight activity (Tanaka, 2009) and photoperiod response to environmental conditions (Tanaka et al, 2015). Similarly, Zhou et al (2013) selected strains of *O. communa* adapted to cold temperatures by cold acclimation in the previous generation to facilitate their range expansion towards northern China and thus to track their host-plants into colder climate and to build-up higher densities through an increased number of generations in these areas. Specific selection regimes during commercial mass productions could thus greatly speed up the development of strains adapted to the yet uncovered *A. artemisiifolia* area in EA.

We acknowledge that studies on the demographic interactions between the invasive alien plant and its biological control 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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## Supplementary Material

Appendix 1 List of all 19 predictors available in WORLDCLIM bioclimatic data set and growth degree days (GDD)  
<http://www.biodiversity-science.net/fileup/PDF/2017096-1.pdf>

Appendix 2 Differences in discrimination ability (AUC) across all levels

<http://www.biodiversity-science.net/fileup/PDF/2017096-2.pdf>

Appendix 3 Geographic continece predictions of *Ambrosia artemisiifolia* and its two biological control agents, *Ophraella communa* and *Epibleama strenuana* under present climatic scenarios in East Asia with occurrences presented.

<http://www.biodiversity-science.net/fileup/PDF/2017096-3.pdf>

Appendix 4 Geographic predictions of overlap of *Ambrosia artemisiifolia* and its two biological control agents *Ophraella communa* and *Epiblema strenuana* under present and future climatic scenarios in East Asia.

<http://www.biodiversity-science.net/fileup/PDF/2017096-4.pdf>

Appendix 5 Mean and standard deviation of geographic predictions of *Ambrosia artemisiifolia* and its two biological control agents *Ophraella communa* and *Epiblema strenuana* under four future climatic scenarios in East Asia.

<http://www.biodiversity-science.net/fileup/PDF/2017096-5.pdf>