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Accounting for intraspecific variation to quantify niche dynamics along the invasion routes of *Drosophila suzukii*

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Abstract

Biological invasions are one of the main threats to biodiversity worldwide, and understanding the mechanisms allowing invasive species to colonize their new environments is critical to the management of invasive populations. One particular aspect of invasion biology is to define the environmental conditions within which invasive species can persist (*i.e.* their ecological niche) to get insights on the potential role of adaptation in successful invasions, as well as to predict future invasion. Here, we use multiple correlative species distribution models and metrics of niche expansion and stability to investigate the worldwide invasion of the spotted-wing drosophila, *Drosophila suzukii*. By modeling the climatic niche of *D. suzukii* from occurrence data in its native and invasive ranges, we tested if a shift in the realized niche has occurred during invasion. Furthermore, we use recent population genetics work on the invasion history of the species to test whether invasive populations have preferentially invaded areas with climatic conditions more similar to the ones in their precise area of origin. Overall, our results show that *D. suzukii* displays a wide climatic niche and suggest that the species' success in the invaded ranges may result from the absence of environmental challenges upon colonization. Furthermore, we show that the use of different geographical backgrounds can impact the outputs of niche comparisons and advice using complementary methods in the study of niche dynamics during biological invasions.

Introduction

Adaptive evolution can facilitate biological invasions (Reznick & Ghalambor, 2001; C. E. Lee, 2002; Lambrinos, 2004; Wares, 2005; Prentis *et al.*, 2008) but some invasive species may not always face adaptive challenges in the invaded range. In such case, similar environmental conditions between introduced and native ranges can allow invaders to persist in an area from which they were historically out of reach (Facon *et al.*, 2006; Estoup *et al.*, 2016). This suggests that a change in the dispersal ability of a species – or in the case of invasive species, dispersal means (Nathan, 2006) – could explain its successful introduction in a newly available area if the environmental conditions match the ones from the source area (Facon *et al.*, 2006; Hayes & Barry, 2008). Investigating the degree of environmental differentiation between native and invaded ranges can thus shed light on the processes involved in successful invasions. Namely, absence of differentiation between native and invaded environments would suggest that invasive populations did not face adaptive challenges upon colonization whereas the identification of a niche shift (Guisan *et al.*, 2014) would in turn hint towards other mechanisms at play in the new range (Hill *et al.*, 2013).

Species distribution models (SDMs) are predictive statistical models which combine species spatial occurrences data to their environmental characteristics (Elith & Leathwick, 2009). As such, they represent a tool to estimate the climatic envelope of species or populations in their current range (i.e. their realized niche; Hutchinson, 1991). The contribution of niche theory to the study of biological invasions is particularly relevant to characterize invasive species' niches across their distribution, assess the amplitude of environmental changes undergone during invasions (Broennimann *et al.*, 2007; Medley, 2010; R. Tingley *et al.*, 2014) or predict future invasions (e.g. Lozier & Mills, 2011). To this end, a classical approach is to project SDMs calibrated on the native range in other areas, either invaded or not (Broennimann & Guisan, 2008). However, some invasions may require a finer niche modeling approach than SDM projections based on coarse resolution presence data from the entire native range. For instance, different populations within a large native geographic distribution can have different realized niches (Peterson & Holt, 2003). In such case, SDMs calibrated on each populations' environments rather than on the entire species' distribution might be more accurate in predicting environmental suitability elsewhere. In a recent study, Godefroid *et al.* (2015) used SDMs in several species of the genus *Dendroctonus*, characterized by divergent niche requirements. Their results suggest that classical models based on species' entire range calibration tend to under- or overestimate the potential range of the species when compared to a global prediction from lineage-based projections. Consequently, if only a limited proportion of the native distribution served as a source for the invasion, or, if multiple sources with divergent niche requirements are present in the native distribution, intraspecific niche differentiation could be overlooked and therefore bias niche projection on uncolonized areas (Godefroid *et al.*, 2015; Lecocq *et al.*, 2016). Finally, the presence of bridgehead populations (i.e.

where primary invasive populations act as source(s) for subsequent invasions, Lombaert *et al.*, 2010) should be taken into account when predicting future colonization. As these populations may have experienced niche shift in the invasive range, they have the potential to further colonize areas where environmental conditions are not suitable for ancestral populations. Predictive models should thus be calibrated not only on the historical native range, but also on the invasive range (Broennimann & Guisan, 2008; Medley, 2010).

Such a complex invasion scenario can be found in the worldwide spread of the spotted-wing *Drosophila suzukii* (Matsumura, 1931). This drosophilid species native from south-eastern Asia has started to colonize Europe and the United States in 2008 (Hauser, 2011; Calabria *et al.*, 2012) and is now widely distributed across the globe, with the latest occurrences in the Southern hemisphere reported in Brazil (Deprá *et al.*, 2014). *D. suzukii* is a major pest for stone fruits and berries crops, causing considerable damage for the fruit production economy in the infested cultures (J. C. Lee *et al.*, 2011). Whereas the colonization history of *D. suzukii* is now well documented (Adrion *et al.*, 2014; Fraimout *et al.*, 2017) its remarkable ability to invade such a diverse array of environments remains puzzling. At the ecological level, *D. suzukii* is known to persist in a rather unoccupied niche within the *Drosophila* genus. Its preference for ripe fruits and unique ability to oviposit through hard fruit skin (Atallah *et al.*, 2014; Karageorgi *et al.*, 2017) suggest that the spread of the species should not be prevented by resource competition with closely related species (but see Dancau *et al.*, 2017; Rombaut *et al.*, 2017; Shaw *et al.*, 2017). Furthermore, the wide range of host plants used by *D. suzukii* points toward a rather generalist status of the species (J. C. Lee *et al.*, 2011; Poyet *et al.*, 2014). The species' very large distribution in its native range (Kimura, 2004; Asplen *et al.*, 2015) suggest that Asian populations experience a wide array of bio-climatic variation. Thus, native *D. suzukii* may represent either a pool of wide-tolerant populations or discrete units which may have evolved within differentiated niche among Asian localities. Consequently, the global spread of *D. suzukii* – initiated by multiple differentiated genetic and geographic sources (Fraimout *et al.*, 2017) – may have been facilitated by its climatic tolerance regardless of the source populations, or initiated by specialized propagules having colonized areas with similar environmental conditions. So far, several studies have investigated the role of environmental variables in the spread of *D. suzukii* at regional scales within the different invaded ranges (e.g. Gutierrez *et al.*, 2016; Langille *et al.*, 2016) but few have considered the invasion history at a global scale to explain the remarkable success of this recent invasion.

Here we used an ensemble of SDMs associated with knowledge on the invasion history of *D. suzukii* to examine species-environment relationships along its invasion routes and address three specific questions: 1) What is the realized niche of *D. suzukii* in its native and invasive range? 2) Can we observe niche shifts between ancestral and invasive populations? 3) Do invasive populations show more similarity in their realized niche than with their most probable geographical sources? Given the efficiency of the

species to have colonized such a broad range of environments is a relatively short time (i.e. less than ten years, Asplen *et al.*, 2015) we predict that high similarity between native and invasive niches could explain the success of *D. suzukii*'s invasion. Conversely, we expect that models predicting low environmental suitability in areas where the species is known to occur, would suggest a shift in the species' niche, and that invasion success in such case may involve other factors invoking local adaptations. Overall, by addressing the three aforementioned questions we test the hypotheses that i) *D. suzukii* might in fact be a generalist species, having colonized environments which were historically out of reach and ii) accounting for the invasion history of the species can bias the outputs of niche comparisons.

Material & Methods

Occurrence data

We gathered a total of 344 presence data of *D. suzukii* from its native range in south-eastern Asia and in its invasive range where *D. suzukii* is consistently invasive through years in continental USA, Hawaii, Europe and the Southern hemisphere distributions (Brazil and the French island La Réunion) from published occurrence records, databases, and personal observations from the field (Fig. S1). To avoid any potential geographic sampling bias within continent, we applied a "systematic sampling" by enforcing a minimum distance of 50 km among nearby presences (Fourcade *et al.*, 2014).

For continental USA occurrences, the EDDMapS county checklist (2016, www.eddmaps.org) provided a thorough record of the species. We thus adapted our modeling approach to the specificity and potential bias of this area (see "split" method from Fourcade *et al.* 2014) and specifically used from these data a downscaling strategy known as "envelope approach" (Bombi & D'Amen, 2012). We randomly sampled 150 locations within the surface covered by counties where *D. suzukii* have been recorded and used these points as pseudo-presences. The number of pseudo-presences is thus similar to the number of presences used to model the invaded distribution in Europe. This approach allowed us to model the species distribution by taking advantage of the good coverage of the data at the county level and preventing the bias in space and time that can occur in occurrences records in USA from unbalanced search efforts.

Geographic backgrounds: accounting for invasion history

The worldwide invasion history of *D. suzukii* has been described in details in Fraimout *et al.* (2017). Briefly, it is characterized by two initial main routes of invasion from Asia to western USA (Hauser, 2011) and southern Europe (Calabria *et al.*, 2012). Subsequently, spread within USA was initiated by western USA propagules dispersing to eastern USA. Furthermore, genetic data revealed the existence of gene flow from eastern USA to Europe.

To test if presence in the invasive range could be better predicted knowing the invasion history of the species, the analyses were performed using two sets of geographic extents. First, we used broad-scale continental backgrounds defining the native area in south-eastern Asia (hereafter “Asia”), and both major invaded areas in USA and Europe (see colored boxes, Fig. S1). Second, we assigned occurrences to more precise geographical units corresponding to the genetic groups of *D. sukuzii* described in Fraimout *et al.* (2017): Asia, Hawaii, western USA, eastern USA, Brazil, La Réunion and Europe (see colored occurrence points, Fig. S1). *D. sukuzii* populations have initially invaded southern Europe and western USA (Hauser, 2011; Calabria *et al.*, 2012), most likely from continental Asian areas (see Fig.1 in Fraimout *et al.* 2017). Thus – and although they represent a single genetic cluster – we refined the geographical background to focus on the occurrences in continental Asia by excluding Japan in the geographical extent (Fig. S1). This allowed us to perform comparisons along the invasion routes of *D. sukuzii* between geographical areas of known history. First, we followed the two initial routes of invasion by comparing the native area (Asia and continental Asia) to western USA and Europe independently. Second, we followed the spread of *D. sukuzii* in USA by comparing western to eastern USA. Finally, given the possibility of gene flow between USA and Europe, we performed comparisons between eastern USA and Europe. Unfortunately, the small record of presences in the most recent colonization in Brazil and the relative small areas that represent the two islands (Hawaii and La Réunion) prevented us from including them in the comparative analyses of niche modeling and niche overlap.

Environmental data and representation in the climatic space

The selection of the environmental predictors for niche modeling is a source of uncertainty in model predictions that can be reduced with sound statistical methods and ecological knowledge of the target species (Barbet-Massin *et al.*, 2014; Petitpierre *et al.*, 2017). A low number of predictive variables reduces the issues of model overfitting (*i.e.*, when predictors are exceeding the number of occurrences) and multicollinearity (*i.e.*, when the predictive variables are highly correlated, Heikkinen *et al.*, 2006). Therefore, we focused on eight climatic variables to encompass the mean trends, the variability, and the extremes of temperature and precipitation at a given location: (1) mean annual temperature, (2) mean annual precipitation, (3) temperature seasonality, (4) precipitation seasonality, (5) temperature of the coldest month and (6) of the warmest month, (7) precipitation of the driest month and (8) of the wettest month. Similar sets of variables have proved their efficiency in applying SDMs to ectotherms organisms (Tingley *et al.*, 2016) and particularly invasive insects (Hill *et al.*, 2017) and are expected to be relevant for *Drosophila* species distributions (Kellermann *et al.*, 2012). This set of predictors provided three more advantages. First, it makes the comparison possible with niche modelling of other taxa and with other insects (Hill *et al.*, 2017). Second,

Petitpierre *et al.* (2017) showed in a recent article that these eight climatic variables yield a high transferability of SDMs at macroclimatic scale when they projected the climatic niche of invasive plants in different environments. We extracted these climatic variables from the Worldclim Global Climate data on the current climate (version 1, 1960-1990; Hijmans *et al.*, 2005) at a 10 arc-minute resolution (ca. 18.5 km × 18.5 km) to explore the climatic space of *D. suzukii*'s distribution.

In order to get a visual representation of the positions of the occurrences in the climatic space, we performed a principal component analysis (PCA) on the climatic predictors using the “FactoMineR” library (Husson *et al.*, 2017) in R.

Ecological niche modeling

We first modeled the distribution of *D. suzukii* at a global scale (*i.e.* from its native and invasive distributions) following Beaumont *et al.* (2009). This approach seems particularly suitable to model distribution of invasive species as it provides more accurate assessment of the potential invasive distribution at that stage of the invasion, where expanding populations are not expected to be at equilibrium with the climate (Beaumont *et al.*, 2009). Then, to evaluate the capacity of the models to predict the presence of the invasive populations from the presence records of the ancestral population, we modeled separately the native niche of *D. suzukii* (Asia), its invasive niche in USA, and its invasive niche in Europe. We then projected the native modeled niche on the invasive range (in the USA and in Europe). Conversely, the native range was also projected from the two invasive ranges, separately. All models were calibrated either using continental scale (*i.e.*, Europe, USA) or intra-continental scale using the genetic groups and the geographical backgrounds described above.

We performed an ensemble of eight modeling techniques, all implemented in the biomod2 package (Thuiller *et al.*, 2014) in R: (1) generalized linear models (GLM), (2) generalized boosted models (GBM), (3) generalized additive model (GAM), (4) flexible discriminant analysis (FDA), (5) classification tree analysis (CTA), (6) artificial neural networks (ANN), (7) random forests (RF) and (8) multivariate adaptive regression splines (MARS). Because our datasets do not provide true absences, we generated 10 sets of 1000 artificial absence records (pseudo-absences) by randomly sampling from the grid cells of each study area (Barbet-Massin *et al.*, 2012). We replicated ten times the splitting of the data into a random subset including 70% of the data for calibration and one second subset with the remaining for evaluation by cross-validation. We used the true skill statistic (TSS) to evaluate the predictive performance of each modeling technique (Allouche *et al.*, 2006). To account for the inter-model variability in predictive performance, and because they have been shown to provide the best predictive performance, we chose consensus methods (Araujo & New, 2007; Marmion *et al.*, 2009) by averaging the predictions of models from the eight

modeling techniques (and across GCMs to get the consensus distribution in the future), removing models with a TSS below the quality threshold of 0.5 (Marmion *et al.*, 2009). We calculated the average values and standard deviation of TSS across pseudo-absences and data-splitting runs to evaluate the ensemble model.

Finally, we computed Multivariate Environmental Similarity Surfaces (MESS) to determine the extent of the environmental differences between model training in one range and model projections in another (Elith & Leathwick, 2009). MESS output values (climatic similarity) were then reported at the presence records in the range where the model is projected.

Quantifying niche shifts between ranges

In addition to the crossed projections from niche modeling, we measured the niche overlap between native and invasive ranges. We used Broennimann *et al.*'s framework (2012), which provides a quantification of the niche similarity between two taxa that occurred in different geographic regions by correcting for bias related to the availability of environmental space. For each geographical background, we performed a PCA calibrated on the entire environmental space of the study area (hereafter called PCA-env). We used the same eight climatic predictors than we selected for ecological niche modeling. The scores of the occurrences on the first two axes of PCA-env were projected onto a 100×100 grid, and a smoothed density of occurrences in environmental space was calculated using a kernel density function to compare ecological niches independently of sampling effort and of the spatial resolution of the environmental grid (Broennimann *et al.*, 2012).

To quantify the similarities in climatic requirements between ranges, we calculated Schoener's D (Schoener, 1968, reviewed in Warren *et al.*, 2008), a measure of niche overlap which varies from 0 (no overlap) to 1 (complete overlap). We then performed statistical tests of niche equivalency and similarity (Warren *et al.*, 2008; Broennimann *et al.*, 2014). We tested the hypothesis of niche equivalency by comparing the niche overlap calculated on the observed datasets and with the overlaps calculated on 1000 sets of simulated datasets. Simulated datasets were built from a random sample of the same number of occurrences than the observed dataset of each range. We performed a two-way test of equivalency to determine whether the niche overlap is more or less equivalent than random. Then, we calculated the overlap between one range and the randomly shifted density of occurrences of another range, and vice versa. This process was repeated 1000 times. We then performed a two-way test of niche similarity to determine whether niches are more similar than expected at random. The null hypothesis (*i.e.*, niches are no more similar to one another than expected at random) was rejected if the observed overlap was greater than 95% of the simulated values of overlap.

Finally, we calculated three components of niche changes: niche expansion, niche stability, and niche unfilling (Guisan *et al.*, 2014). Niche expansion is the proportion of densities that occurred in climatic conditions only within the invaded niche (*i.e.* not found in the native one). Conversely, niche unfilling is the proportion of densities occurring in climatic conditions only within the native niche (Guisan *et al.*, 2014). Finally, niche stability refers to the proportion of densities in climatic conditions occurring in both native and invaded ranges. To take into account the availability of climates between ranges when quantifying niche changes, we calculated the niche overlap within the most common environments shared between the two ranges by removing marginal climates (Guisan *et al.* 2014). We calculated the niche metrics at the intersection of backgrounds reduced with different percentiles of density overlap (75th, 85th, 90th, 95th, and 100th) to test if the scores of niche metrics are consistent across the different environmental extents. All niche metrics have been calculated using the *ecospat* library in R (Broennimann *et al.*, 2014).

Results

Variation in D. suzukii presence data for climatic variables

We visualized the distributions of the occurrence data and their associated environmental variables in the climatic space by performing a PCA on the dataset (Fig. 1). The two first axes explained a moderate amount of variation in the data (48.87%). Occurrences were discriminated along the first axis (25.57%) on average from an increasing gradient of precipitation with a decreasing seasonality and a decline of the maximum temperatures during the warmest month. The second axis discriminated the occurrences from the latitudinal gradient and an average increase in temperature seasonality and in minimum temperature during the coldest month.

Projections of the niche of D. suzukii across biogeographical regions

The ensemble modeling of the worldwide current distribution of *D. suzukii* obtained a high evaluation score (TSS = 0.821 ± 0.047 ; mean $\pm$ SD; Fig. 2). Models computed from the backgrounds in Asia (TSS = 0.753 ± 0.05 , Fig. 3), continental Asia (TSS = 0.759 ± 0.052 , Fig. S4), or from the two invasive ranges (USA: TSS = 0.842 ± 0.067 , Europe: TSS = 0.856 ± 0.076 , Fig. 3) showed a high predictive performance. Models calibrated on the native range were projected across both invasive ranges (Fig. 3). These projections yielded environmental suitabilities on average higher or equal to 0.50 in central and western Europe and included all the described invasive range of *D. suzukii*. In USA, projections from the native model yielded climatic suitability on average superior to 0.65 but only in eastern USA. All models were reciprocally projected on each other (Fig. 3). Asia, USA, and Europe mostly displayed analog or sub-analog climate (Table 1, Fig

S2). The MESS analysis identified non-analog climate conditions in Northern Europe and the Alps when compared with the Asian native range and the invaded range in USA (Fig. S2). Similarly, some regions at the margin of the invasive range in western USA were non-analog to the native range (Fig. S2). As expected, the occurrences in each invasive range were better predicted with the reference model (e.g. when European records were used to model European distribution). However, model calibrated on USA yielded fairly high environmental suitability in different parts of Europe whereas the reciprocal projection of the European model in USA did not yield environmental suitability values superior to 0.3.

Measures of broad-scale niche changes

We first investigated niche changes at a broad geographical scale between Asia and USA, Asia and Europe, and USA and Europe to account for the global invasion of *D. sukukii*. The environmental space available in the invasive ranges in USA and Europe were both widely included in the environmental space available in Asia (Fig. 4). The niche overlaps between Asia and the invasive ranges were low ($D = 0.33$ and $D = 0.3$ in USA and in Europe, respectively, Fig. 4, Table 1). We also found a low overlap between USA and Europe ($D = 0.2$, Fig. 5, Table 1). This classification of the values of Schoener's D followed the suggestion of Rödder and Engler (2011) to facilitate interpretation of the results: no overlap or very limited overlap for D comprise between 0 and 0.2, low overlap between 0.2 and 0.4 and moderate overlap between 0.4 and 0.6. These overlaps were more equivalent than random and were more similar than expected by chance (Table 1).

The values of the niche dynamic metrics were similar across percentiles (Fig S3). We report the results for the 75th percentiles here and the results for the other percentiles in Fig. S3. *D. sukukii* had high niche stability from the native range to its two main invaded ranges (97% and 100 % from Asia into USA and Europe, respectively), and almost no niche expansion (Table 1). We identified niche unfilling from Asia to USA (18%) and from Asia to Europe (36%, Table 1). We found no signal of expansion from USA to Europe but substantial niche unfilling (43%, Table 1).

Measures of niche changes along the invasion routes

We first investigated niche changes following the two initial invasion routes of *D. sukukii* from Asia to western USA and Europe. We found no signal of niche expansion into western USA when considering native distributions in all Asia or continental Asia (Fig. 4, Table 1). Both comparisons revealed high niche stability (100%) and evidence for niche unfilling (39% and 20% from Asia and continental Asia to western USA, respectively). Measures of niche changes from continental Asia to Europe revealed lower niche

stability (70%, Table 1) and higher niche expansion (30%) and niche unfilling (51%) relative to comparisons from all Asia to Europe. Western USA and Europe displayed more analog or sub-analog conditions when compared with Asia than when compared with continental Asia only (Table 1).

We then proceeded along the invasion routes across USA by measuring niche changes from western to eastern USA (Fig. 5, Table 1). The climatic conditions used by *D. suzukii* in western USA were almost not used in eastern USA (86% of niche unfilling, Table 1, Fig. 5). Consequently, we report a 64% niche expansion from western to eastern USA, associated with low niche stability (i.e. 36%), low niche overlap and mostly non-analog climate, Table 1). Finally, measurements of niche changes from eastern USA to Europe indicated a 54% niche expansion with moderate niche stability (54%), 29% niche unfilling, and mostly non-analog climate (Table 1). Niche overlaps between these two regions were not more similar than expected by chance (Table 1).

Generally, presences in the invasive ranges were better predicted when the models were calibrated on the whole south-eastern Asia than on continental Asia only (i.e. when we restricted the geographic extent to fit with the invasion history, Fig. S4). Moreover, all the measures of niche overlaps between the native ranges and the invasive ranges (in North America and Europe) were very limited when considering continental Asia only (Table 1). These niche overlaps were more equivalent than random. The niche overlap was more similar than expected by chance when density in USA were randomly shifted ($P < 0.05$, Table 1).

Discussion

In the present paper we aimed at assessing the realized niche of *D. suzukii* in its native and invasive range and sought to identify niche dynamics and potential niche shifts along its dispersion at a worldwide scale using multiple SDMs and niche metrics.

The generation of niche-based distribution models is subject to several uncertainties which need to be acknowledged prior to the interpretation of results. First, they inherently rely on the occurrence points used for calibration. Because our dataset incorporates occurrences from a wide distribution, it should encompass a sufficient amount of environmental variation to calibrate the models and predict invasive ranges. Second, a challenge in the generation of niche-based distributions from presence data is the lack of consideration for possible biotic interactions. Indeed, absence of occurrence of a species in a geographical area may be the result of out-competition by a conspecific, presence of predators, or other patterns of biotic interactions (Soberon & Peterson, 2005; Hirzel & Le Lay, 2008). It is thus primordial to consider that absence of distribution records may not be due solely to unsuitable environmental conditions. In the case of *D. suzukii* one of its main ecological characteristic is the evolution of its ovipositing behavior from an ancestral 'Drosophila-like' decaying substrate, to a wide variety of ripening stone fruit and berries (Asplen

et al., 2015; Keesey et al., 2015; Karageorgi et al., 2017). This specialization in egg-laying behavior opened
 a new niche for the species which remains unoccupied by other drosophilid species (Poyet et al., 2015).
 Therefore, *D. suzukii* should not have direct competitors within drosophilid species (but see Dancau et al.
 2017, Shaw et al. 2017, Rombaut et al. 2017), nor known predators, which relaxes the weight of potential
 biotic interactions in the calibration accuracy of the our models. However, it has been shown that the
 observed or modeled range of the plant host could improve distribution models of species in interaction
 (Barbet-Massin & Jiguet, 2011). In the case of *D. suzukii*, the host plants specifically used by the species
 could then be used as an environmental variable in the model. However, *D. suzukii* specifically lays on
 ripening stonefruits and berries as strawberries, raspberries or grapes. The information on this type of crops
 is not available in land use data at global scale yet, but could be successfully used on smaller spatial extent.
 Considering this, it is also important to account for the effect of the targeted crops on *D. suzukii*'s
 distribution. Indeed, artificial environments such as those formed by agricultural crops – where temperature
 and humidity levels can be adjusted – may provide the species with some refuge (Tochen et al., 2016).
 Hence, the occurrence of natural populations of *D. suzukii* in areas where climatic conditions are not
 predicted to be suitable could be explained by the presence of such human altered habitats. However,
 previous field study suggest that *D. suzukii* in the wild makes use of natural habitats surrounding agricultural
 lands (Kenis et al., 2016; Klick et al., 2016). Thus we argue that our climatic descriptors are still relevant
 to explain the species distribution in most of its range. Lastly, the presence of non-analog climates – i.e.
 different combinations of environmental conditions – between regions may bias outputs of model
 projections by underestimating areas of environmental suitability in the projected region (Schwartz, 2012).
 Here, the worldwide geographic scale of our study system implied to evaluate niche dynamics between areas
 with non-analog climates. Although the presence of non-analog climates should not ultimately prevent the
 use of model projections and niche metrics, one must treat the resulting values with caution and avoid over
 interpretation (Fitzpatrick & Hargrove, 2009). Taking all the above points into consideration we propose
 several axes of discussion for our results, which can add to our understanding of the global invasion of *D.*
suzukii.

Model projections at a global scale revealed high environmental suitabilities in all current invasive
 distribution of *D. suzukii* we could project onto (namely Europe, USA, and Brazil) suggesting a fair
 relevance of the selected climatic variables. The global model represents the realized niche of the species
 and provides a present-day snapshot at the current stage of the invasion (Fig. 2). As for other Asian invasive
 insects (e.g. *Halyomorpha halys*, Zhu et al. (2012); *Vespa velutina*, Arca et al. (2015); *Harmonia axyridis*,
 Poutsma et al. (2008)), and as expected from its broad distribution in Asia (Asplen et al., 2015), the realized
 native niche of *D. suzukii* is large, and encompasses a wide array of climates. This result is compatible with

our first hypothesis suggesting that the large ancestral niche of *D. sukukii* would provide the species with high potential to colonize several areas without necessarily facing environmental challenges. To further explore this hypothesis we specifically investigated the niche dynamics of *D. sukukii* following its invasion history both spatially (i.e. in areas with recorded *D. sukukii* invasions) and temporarily (i.e. following the sequence of invasion from one area to another).

We did not detect signal of niche expansion from Asia to the two initially invaded ranges in USA and Europe but rather high levels of niche stability between these regions. This suggests that the first invasive *D. sukukii* propagules encountered similar climates as in their native range upon colonization of USA and Europe. More precisely, MESS analyses between Asia, Europe and USA revealed that the two first historical outbreaks of *D. sukukii* in northern California and southern Europe most likely occurred in areas with analog climates to the native area (Fig. S3). First records of *D. sukukii* in these two regions occurred almost simultaneously (Hauser, 2011; Calabria *et al.*, 2012), and evidences to explain the biological mechanisms underlying these successful introductions are still lacking. Although invasive populations may have independently adapted locally at these introduction points, our results provide a more parsimonious alternative by suggesting that *D. sukukii* did not face adaptive challenges – at least in regard to climatic conditions – during the first stages of invasion.

One of our main objectives was also to estimate the effect of incorporating information about the species invasion history in SDMs outputs and measurements of niche differentiation. Overall, reducing the native range of *D. sukukii* to its most probable area of origin in continental Asia did not yield higher suitabilities – rather lower suitabilities – of presence in the invasive European or North American ranges based on SDMs projections (Fig. S4). However, the invaded ranges were within non-analog conditions which might explain that model calibrated on the continental Asian native range poorly predicted the presence into the novel climates of invasive ranges (Fig S4). Additionally, whereas niche metrics scores and MESS analysis further confirmed the high level of niche stability between Asia and western USA, and confirmed the availability of analog climates, we found contrasting results in niche differentiation between Asia and Europe when using the continental Asian background only. Specifically, we observed a 30% niche expansion from continental Asia to Europe which was not previously detected using the broad-scale Asian background. This suggests that the reduction in spatial extent used for model calibration reduced the part of available and analog climates between ranges, making it difficult to forecast the invaded range from continental Asia only. Alternatively this could also suggest that invasive populations do not completely share climatic requirements with this particular part of the native range.

Accounting for the invasion history of *D. sukukii* by refining geographical backgrounds to western and eastern USA also revealed distinctive results compared with the use of broad-scale continental

backgrounds. In western USA, model projections seemed to indicate poor environmental suitability, whichever background used for model calibration (Fig. 3). However, climates in this region are analog to the native Asian range (Fig. S2) and we found high niche stability between Asia and western USA (Table 1, Fig. 3). It is possible that the model projection failed to predict suitable areas in this region because occurrence points in western USA may represent marginal populations within the native area.

Furthermore reducing backgrounds to western and eastern USA allowed us to get insight on the niche dynamics of the species across USA which was previously inaccessible from the analysis of the entire USA background. Specifically we obtained high scores of niche expansion along the invasion routes across USA likely driven by non-analog climates. From a climatic point of view, these results suggest that *D. suzukii* experienced a large variation in precipitation levels between these particular regions, with higher mean annual precipitation (Fig. S5) and seasonality (Fig. 5) along this invasion route. Precipitation and humidity levels are expected to have an effect on the distribution of *D. suzukii* (dos Santos et al., 2017), but a previous laboratory and field study suggest that higher levels of humidity should promote rather than constrain the species activity (Tochen et al., 2016). From our results we can thus infer that propagules from western USA expanded their niche towards more favorable climate in eastern USA. Population genetics data on the invasion history of *D. suzukii* suggests unilateral gene flow from eastern USA to the northern part of Europe (Fraimout et al., 2017). We detected non-analog climates, and therefore a potential niche expansion from eastern USA to Europe, whereas no expansion was previously detected when considering the complete territory of the USA as source for the invasive populations in Europe, because, overall, USA and Europe share similar climates (Fig. 4, Fig S2). Furthermore, eastern USA and European climatic envelopes were not entirely differentiated by ordination in the two first axes of the PCA (see Fig. 1 for graphic representation on PC1 and PC2). It is thus possible that the expansion we observe might in fact be driven by the drier climates in southern regions of Europe – possibly explaining expansion towards lower mean precipitation (Fig. S5) – where introduction of *D. suzukii* from eastern USA most likely did not occur. As gene flow most likely occurred in northern Europe, similar niche dynamics analyses at a smaller geographic scale – i.e. focused on northern European climates – would be worth to validate our results.

Finally, our study raises some critical points on the use of SDMs for the study of biological invasions. Specifically, whereas the west coast of USA and the state of California particularly, did not yield high suitability values whichever the native niche used for model projections, measures of niche metrics indicated a high level of niche stability, analog climates, and no signal of niche expansion in this particular region. Such differences between methods have been previously reported also in Drosophilidae for the invasive *Zaprionus indianus*. In that case, whereas a niche shift had been reported from ancestral African niche to cooler climates in elevated regions in invaded region of India (Da Mata et al., 2010), Hill et al.

(2017) conversely showed high environmental stability between the two regions using the niche shift metrics also used in the present study. Thus, interpretation of model-based projection might lead to misleading conclusions when climates in native and invaded ranges differ – e.g. in our case a niche shift in western USA – and our study emphasizes the complementary aspects of these methods for niche comparisons.

Concluding remarks

Our analysis revealed several points of interest in the understanding of the worldwide invasion of *D. suzukii*: i) In addition to its wide trophic niche (Poyet *et al.*, 2015) *D. suzukii* also displays a broad climatic niche inherent from its large native range in south-eastern Asia, and as a result our models calibrated at global scale predicted high environmental suitabilities in most of the invasive ranges. This result points towards a generalist status for *D. suzukii* (at least for climatic conditions) that could explain its successful introduction in areas which may have been historically constrained by a lack of migration means. ii) Overall, our results showed relative niche stability between the native and the two primarily invaded ranges in Europe in USA, and are compatible with the hypothesis that *D. suzukii* did not face climatic – and possibly adaptive – challenges upon colonization of these areas. iii) Whereas targeting geographical background specifically involved in the invasion process can help capturing detailed niche dynamics in invaded ranges – e.g. here between western and eastern USA – restricting the native range only to the most likely source of invasion may result in failure to predict invasive distributions. Accounting for invasion history in SDMs applied to biological invasion should thus be treated cautiously (Zhu *et al.* 2017). Furthermore we encourage the use of complementary methods such as SDMs and niche metrics in the analyses of niche dynamics during biological invasions along with the analysis of niche analogy that informs the reliability of niche scores and niche projections (Guisan *et al.* 2014). iv) Finally, although *D. suzukii* has widely colonized most continents of the world, the significant amounts of niche unfilling in USA and in Europe (> 10%, see Hill *et al.* 2017) suggest that the species is not in climatic equilibrium and have the potential to spread further within these two areas.

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Figure legends

Table 1: Measures of niche overlap, expansion, stability and unfilling between regions.

Figure 1. Principal components analysis calibrated on the worldwide presence data of *D. sukukii* (left panel) and its associated climatic variables (right panel).

Figure 2. Ensemble modeling of the worldwide current distribution of *D. sukukii*

Figure 3. Reciprocal model projection between the Asian native range and both invasive ranges in Europe and USA.

Figure 4. Niche dynamics between the Asian native range and both invasive ranges in Europe and USA.

Figure 5. Niche dynamics along the invasive routes of *D. sukukii* in USA and Europe.

Table. 1. Measures of niche overlap, expansion, stability and unfilling between regions.

Schoener's D measures the niche overlap from 0 to 1. The equivalency test reports if the observed niche overlap is more equivalent ("greater") or less equivalent ("lower") than niche overlaps calculated between randomly simulated datasets. The p-values of the two-way test of niche similarity are presented. In the first test ("obs. 1 / sim. 2"), the density of occurrences in the region 1 was compared with the randomly shifted density of occurrences in the region 2. In the second test ("sim.1 / obs. 2"), the density of occurrences in the region 2 is compared with the randomly shifted density of occurrences in the region 1. The statistical significance of the equivalency and similarity tests is coded as follows: * for $P < 0.05$, ** for $P < 0.01$, *** for $P < 0.001$, and NS when non-significant. For each niche comparison, the table presents the median, the standard deviation, and the range of the MESS values at each presence record describing the niche 2. Climate conditions are considered as non-analog below -20, sub-analog climate conditions in the range [-20, -10], and analog above -10 (following Mateo *et al.* 2014). The scores of three niche shifts metrics are also presented: niche expansion, niche stability, and niche unfilling.

niche 1	niche 2	MESS median $\pm$ sd [min, max]	D	equivalency test	similarity test (p values)		niche shifts metrics		
					obs. 1 / sim. 2	sim.1 / obs. 2	expansion	stability	unfilling
Asia	USA	-6 $\pm$ 12 [-23, 30]	0.33	greater***	0.032*	0.011*	0.03	0.97	0.18
Asia	western USA	-7 $\pm$ 7 [-15, 20]	0.2	NS	0.290	0.013*	0	1	0.39
Asia	eastern USA	-1 $\pm$ 17 [-23, 30]	0.28	greater***	0.086	0.027*	0.02	0.98	0.82
Asia	Europe	-4 $\pm$ 8 [-14, 32]	0.3	greater***	0.093	0.009**	0	1	0.36
USA	Europe	24 $\pm$ 16 [-21, 57]	0.2	lower*	0.077	0.023*	0	1	0.43
western USA	Europe	-41 $\pm$ 32 [-173, 46]	0.32	NS	0.039*	0.097	0.39	0.61	0.6
eastern USA	Europe	-22 $\pm$ 30 [-160, 30]	0.35	NS	0.120	0.057	0.54	0.46	0.29
western USA	eastern USA	-96 $\pm$ 31 [-154, -31]	0.17	NS	0.096	0.168	0.64	0.36	0.86
continental Asia	USA	-1 $\pm$ 19 [-26, 39]	0.18	greater***	0.074	0.012*	0.17	0.83	0.25
continental Asia	western USA	-27 $\pm$ 31 [-98, 39]	0.3	greater***	0.054	0.009**	0.03	0.97	0.2
continental Asia	Europe	-18 $\pm$ 19 [-113, 27]	0.12	greater***	0.262	0.059	0.3	0.7	0.51

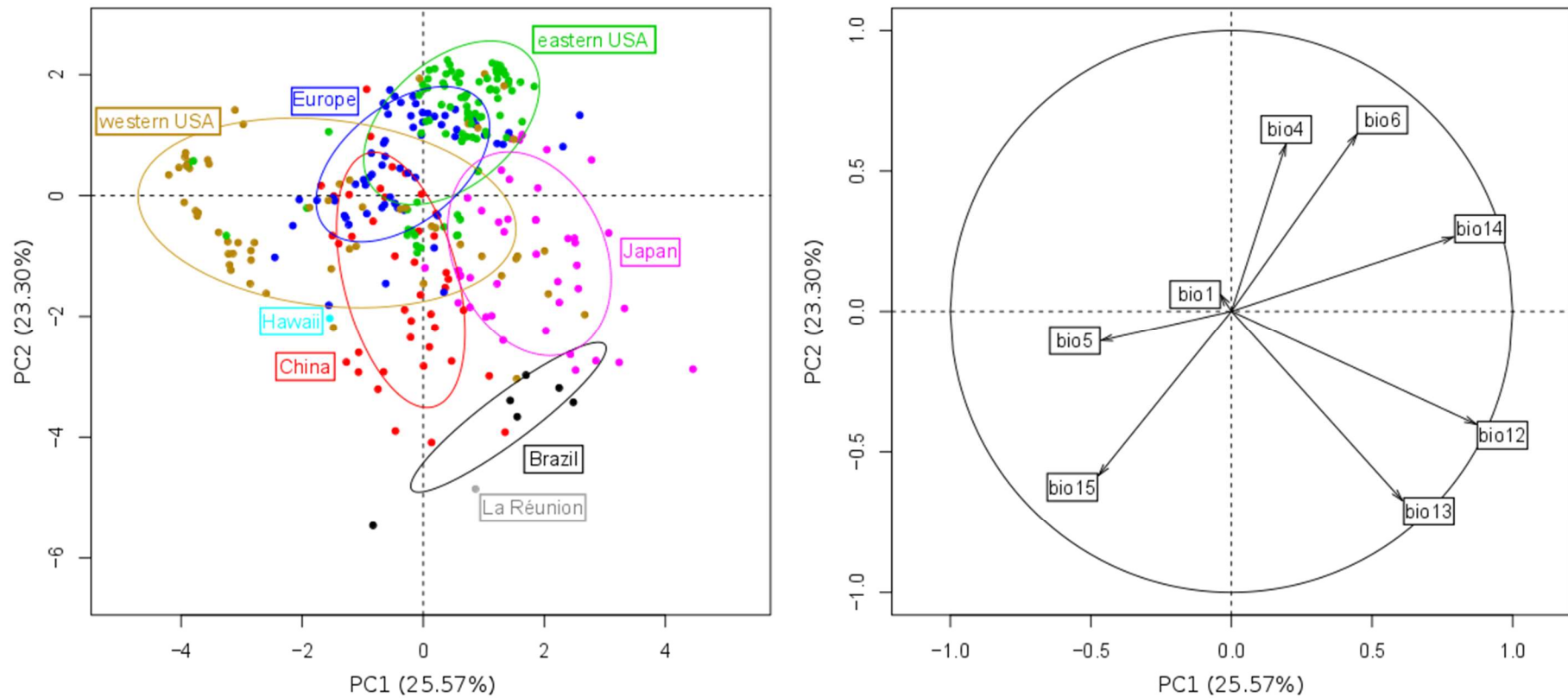


Fig. 1.

Principal components analysis calibrated on the worldwide presence data of *D. sukuzii* (left panel) and its associated climatic variables (right panel).

Points represent each presence in the current native and invasive range of *D. sukuzii*. Climatic variables were extracted from the Worldclim Global Climate database (www.worldclim.org) and were coded as follows: bio1 = mean annual temperature; bio4 = temperature seasonality; bio5 = maximum temperature of the warmest month; bio6: minimum temperature of the coldest month; bio12 = annual precipitation; bio13 = precipitation of the wettest month; bio14 = precipitation of the driest month; bio15 = precipitation seasonality.

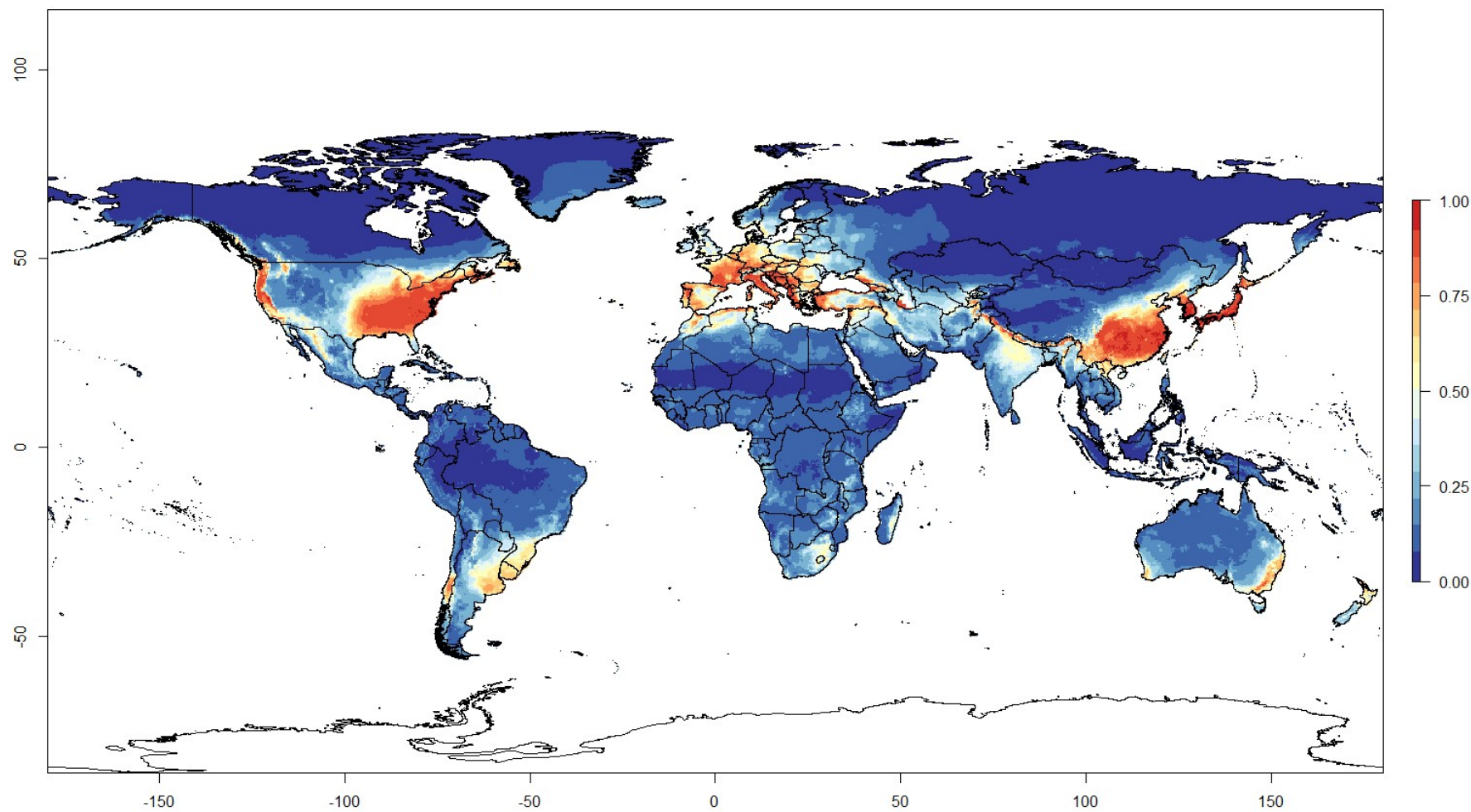


Fig. 2. Ensemble modeling of the worldwide current distribution of *D. sukuii*

Models were calibrated on all 344 presence data from *D. sukuii* worldwide distribution and projected back globally. Color scale represents the environmental suitability from low (blue) to high (red).

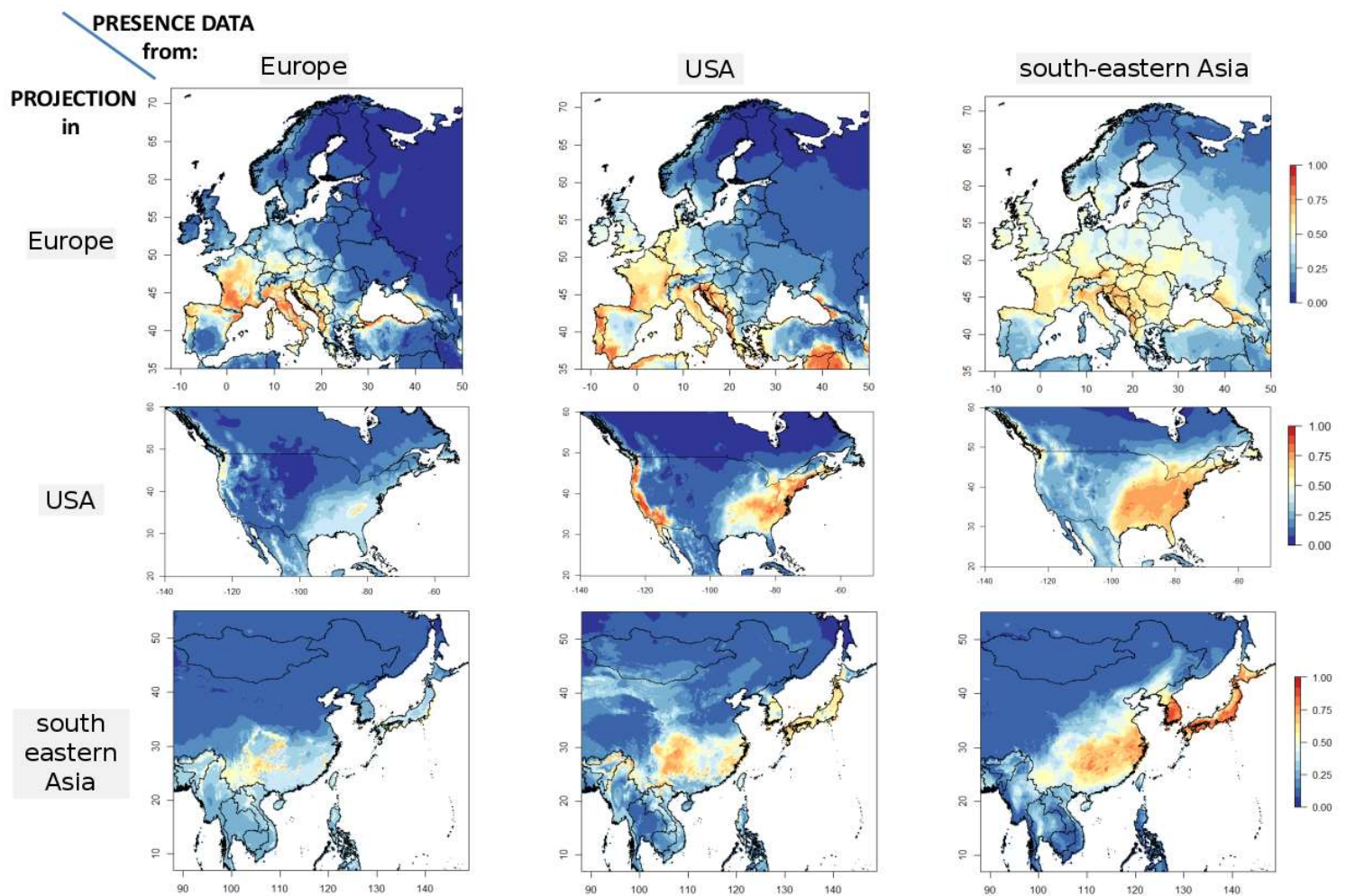


Fig. 3. Reciprocal model projection between the Asian native range and both invasive ranges in Europe and USA.

Models were calibrated on the presence data from each of the focal ranges of *D. sukii* (across) either Asia, USA or Europe, and reciprocally projected onto (down) each other. Color scale represents the environmental suitability from low (blue) to high (red).

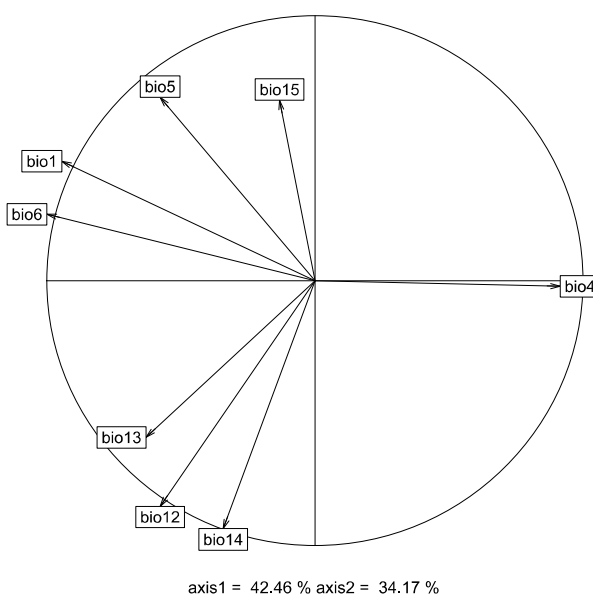
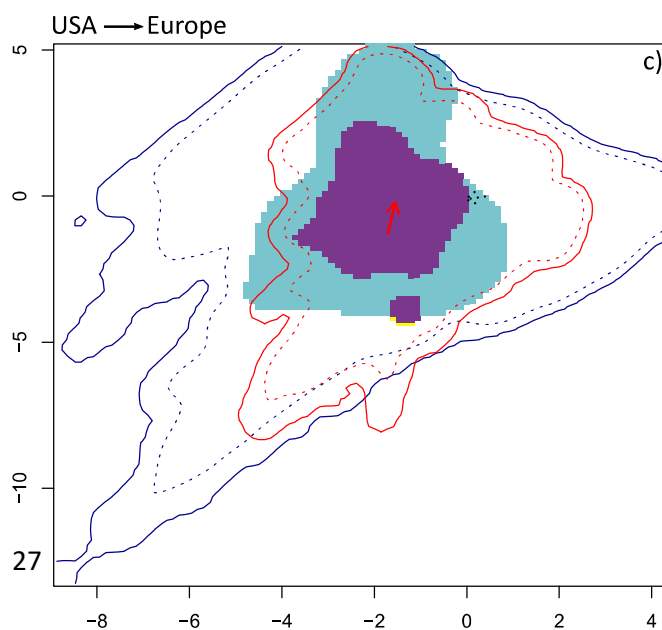
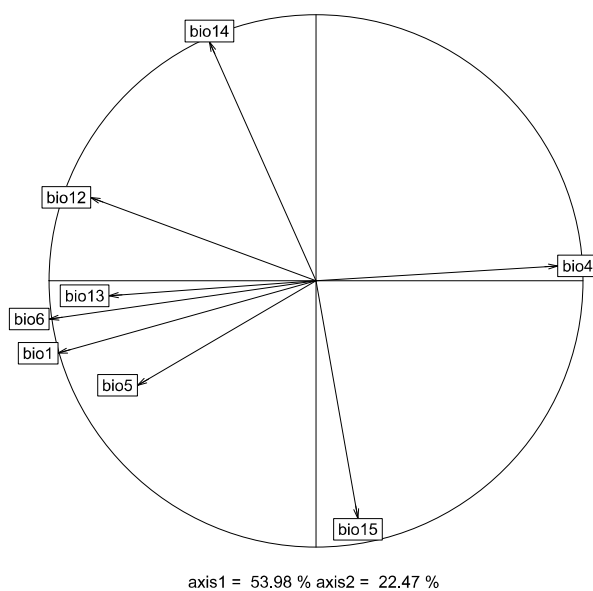
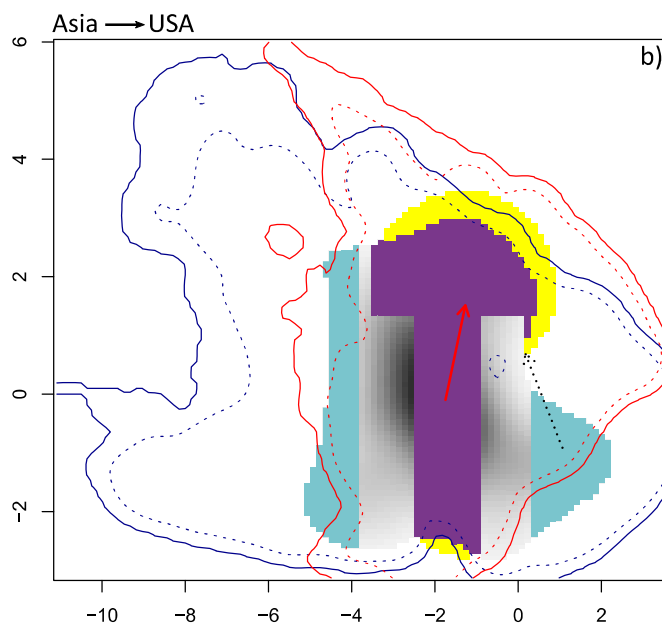
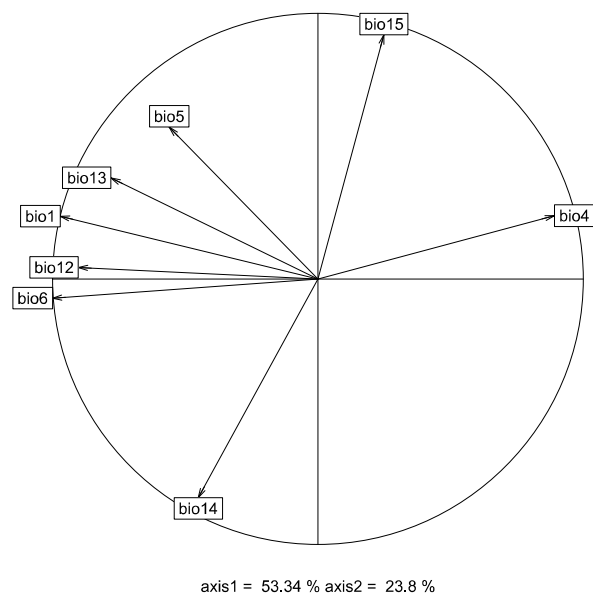
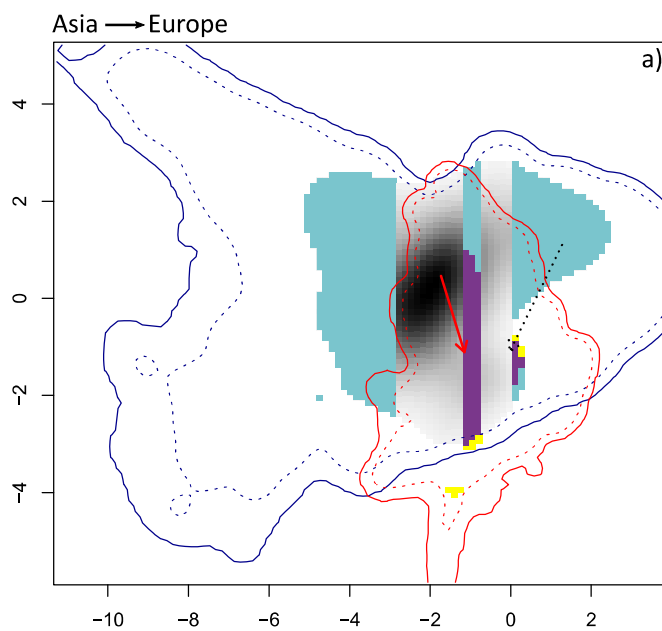
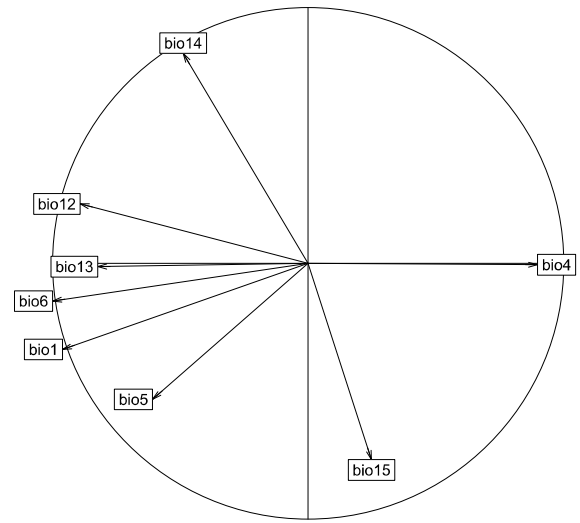
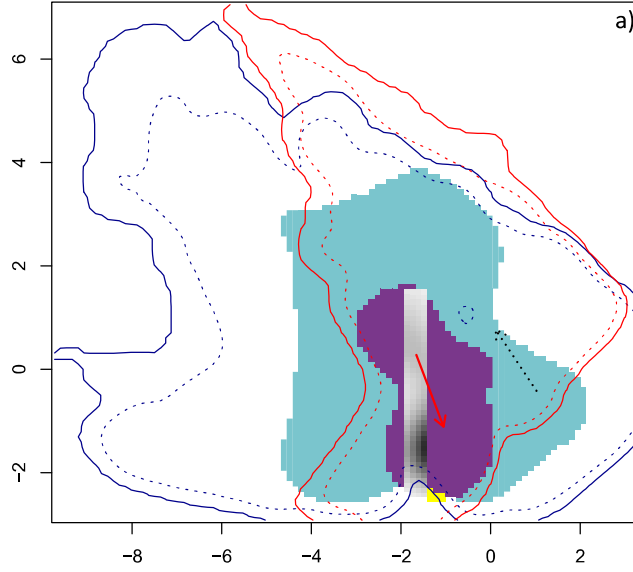


Fig. 4. Niche dynamics between the Asian native range and both invasive ranges in Europe and USA.

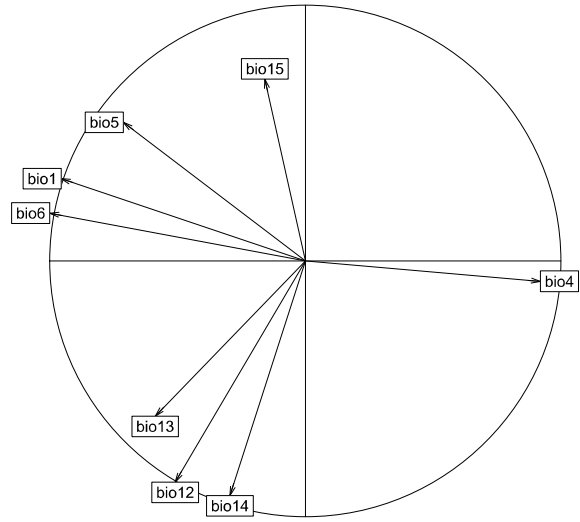
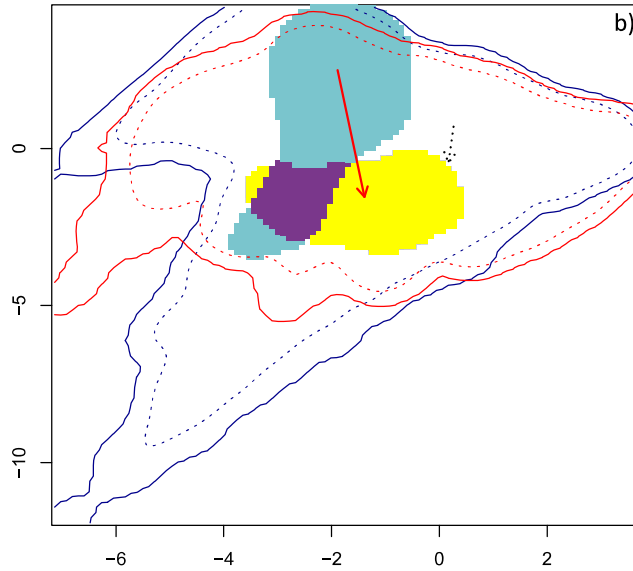
Principal components analyses were calibrated on environmental background (PCA-env) to compare the use of the environmental space from one region 1 (in blue) to one region 2 (in red). Solid and dotted lines correspond to 100% and 50% of the available environment space, respectively. We compared the use of the environmental space between the native range in Asia and USA (a), and Europe (b), and between the two invasive ranges, USA and Europe (c). The niche overlap is partitioned into three components: niche stability (in purple), the niche expansion (in yellow), and niche unfilling (in blue). The black dashed arrow indicates the change in the centroid of the climatic conditions from the region 1 to the region 2 and the red arrow the change in the centroid of the occurrences density of the population from the region 1 to the region 2. Correlation circles in the left column show the contribution of each environmental variable to the two first axes of the principal components analysis. Environmental variables are the mean annual temperature (bio1), mean annual precipitation (bio12), temperature seasonality (bio4), precipitation seasonality (bio15), temperature of the coldest month (bio6) and of the warmest month (bio5), precipitation of the driest month (bio14) and of the wettest month (bio13).

Asia → western USA



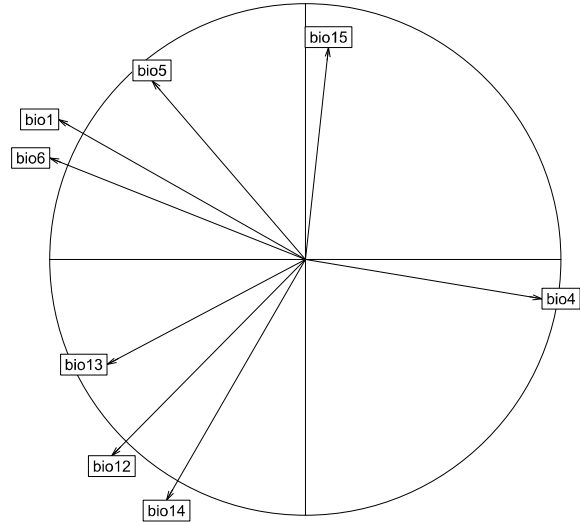
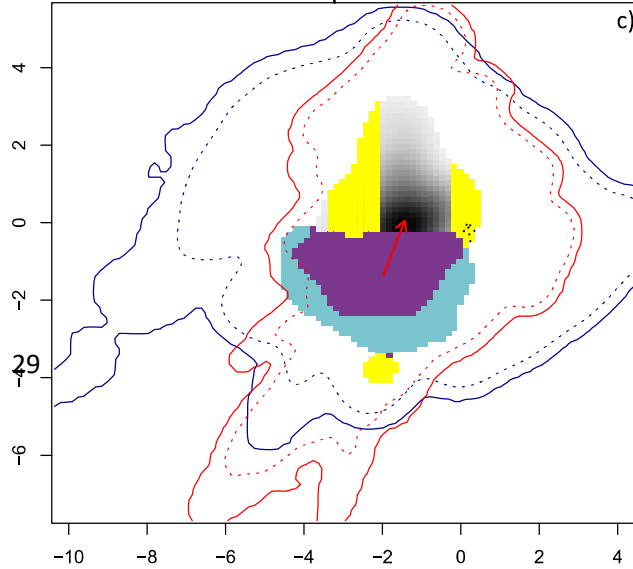
axis1 = 55.66 % axis2 = 19.81 %

western USA → eastern USA



axis1 = 46.6 % axis2 = 33.92 %

eastern USA → Europe



axis1 = 44.98 % axis2 = 32.07 %

Fig. 5. Niche dynamics along the invasive routes of *D. sukuzii* in USA and Europe.

Principal components analyses were calibrated on environmental background (PCA-env) to compare the use of the environmental space from one region 1 (in blue) to one region 2 (in red). Solid and dotted lines correspond to 100% and 50% of the available environment space, respectively. We compared the use of the environmental space (a) between Asia and western USA (b) western USA and eastern USA, and (c) eastern USA and Europe.

The niche overlap is partitioned into three components: niche stability (in purple), the niche expansion (in yellow), and niche unfilling (in blue). The black dashed arrow indicates the change in the centroid of the climatic conditions from the region 1 to the region 2 and the red arrow the change in the centroid of the occurrences density of the population from the region 1 to the region 2. Correlation circles in the left column show the contribution of each environmental variable to the two first axes of the principal components analysis. Environmental variables are the mean annual temperature (bio1), mean annual precipitation (bio12), temperature seasonality (bio4), 4) precipitation seasonality (bio15), temperature of the coldest month (bio6) and of the warmest month (bio5), precipitation of the driest month (bio14) and of the wettest month (bio13).

Supplementary material to the manuscript: Climatic niche modeling along the invasion routes of *Drosophila suzukii*

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Key words: ecological niche modeling, *Drosophila suzukii*, invasion routes, niche conservatism, niche overlap

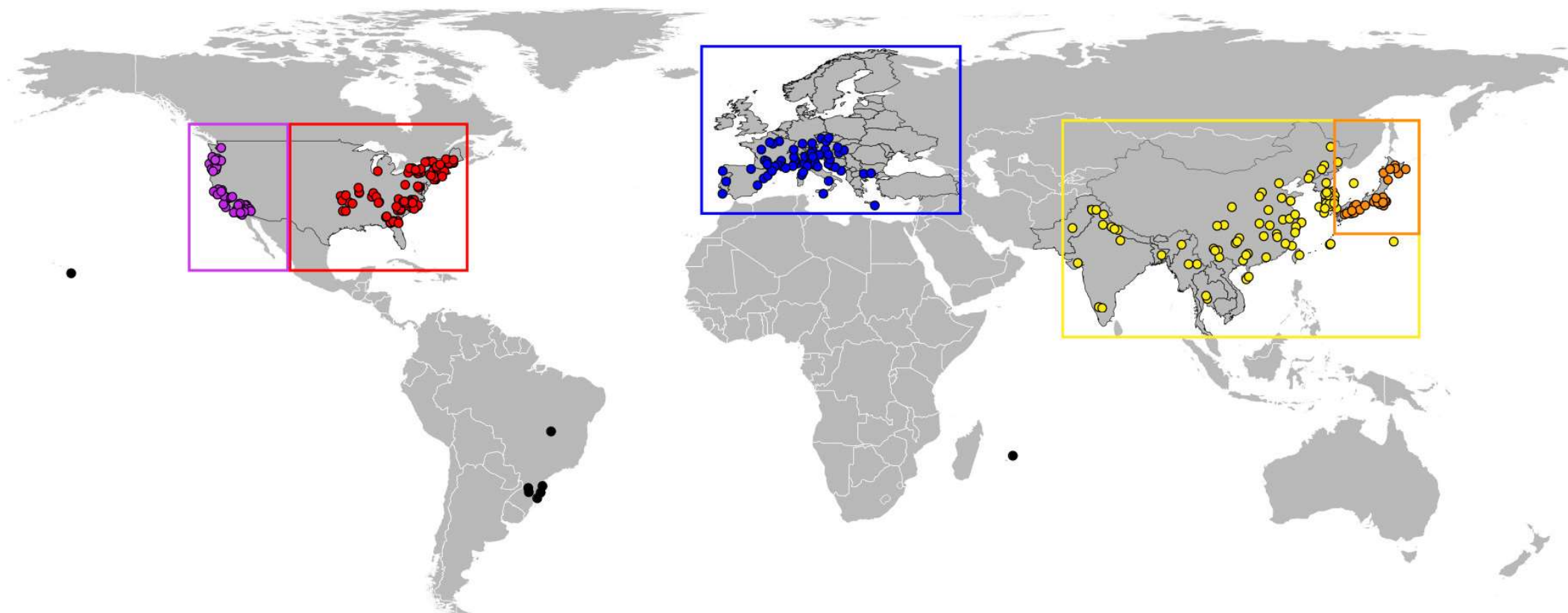


Fig. S1. Map of occurrences data & geographical backgrounds. The 344 occurrence points are represented by filled circles on the map. Colored boxes correspond to the geographical backgrounds used in the analyses: Yellow = continental Asia; orange = Japan; yellow + orange = Asia; blue = Europe; purple = western USA; red = eastern USA; purple + red = USA

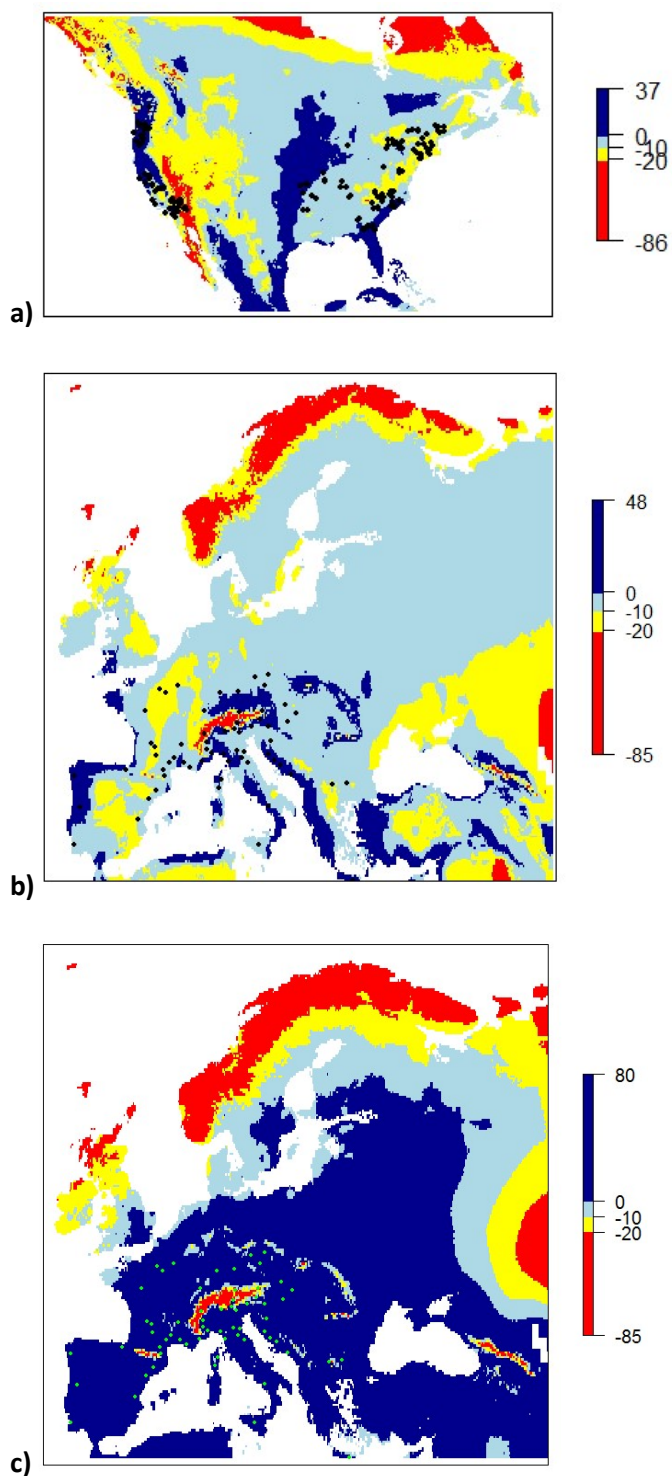


Fig. S2. Multivariate environmental similarity surfaces (MESS) between the native range and the invasive ranges in USA (a) and in Europe (b), and between USA and Europe (c).

A pixel with a positive value indicates that it falls within the range of environmental values present in the native range, while a pixel with a negative value indicates that at least one variable has a value that is outside of the range of environmental values present in the native range (Mateo et al. 2014). Following Mateo et al. 2014, we defined sub-analog climate conditions in the range $[-20, -10]$, non-analog below -20 and analog above -10 . Points indicates the presence records.

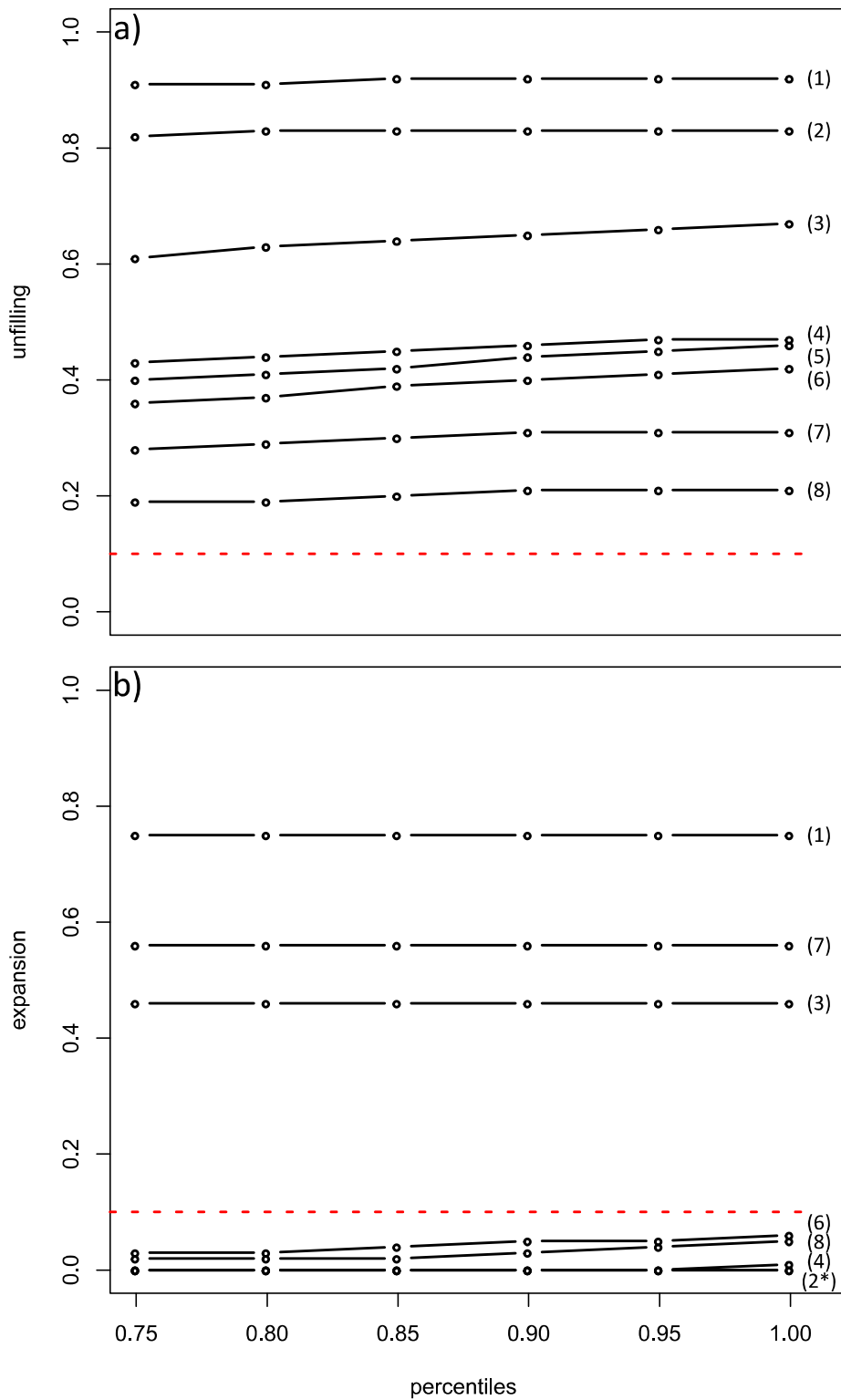


Fig. S3. Scores of the niche metrics across the different percentiles (75th, 80th, 85th, 90th, 95th, and 100th). The red dashed line indicates the 10% threshold above which the niche unfilling (a) and niche expansion (b) are considered to be relevant. Numbers in brackets correspond to the different projections from which the metrics were calculated: (1) western USA → eastern USA; (2) Asia → eastern USA; (3) western USA → Europe; (4) USA → Europe; (5) Asia → western USA; (6) Asia → Europe; (7) eastern USA → Europe; (8) Asia → USA. On panel b) the asterisk (*) indicates merged curves between projections (2) and (5).

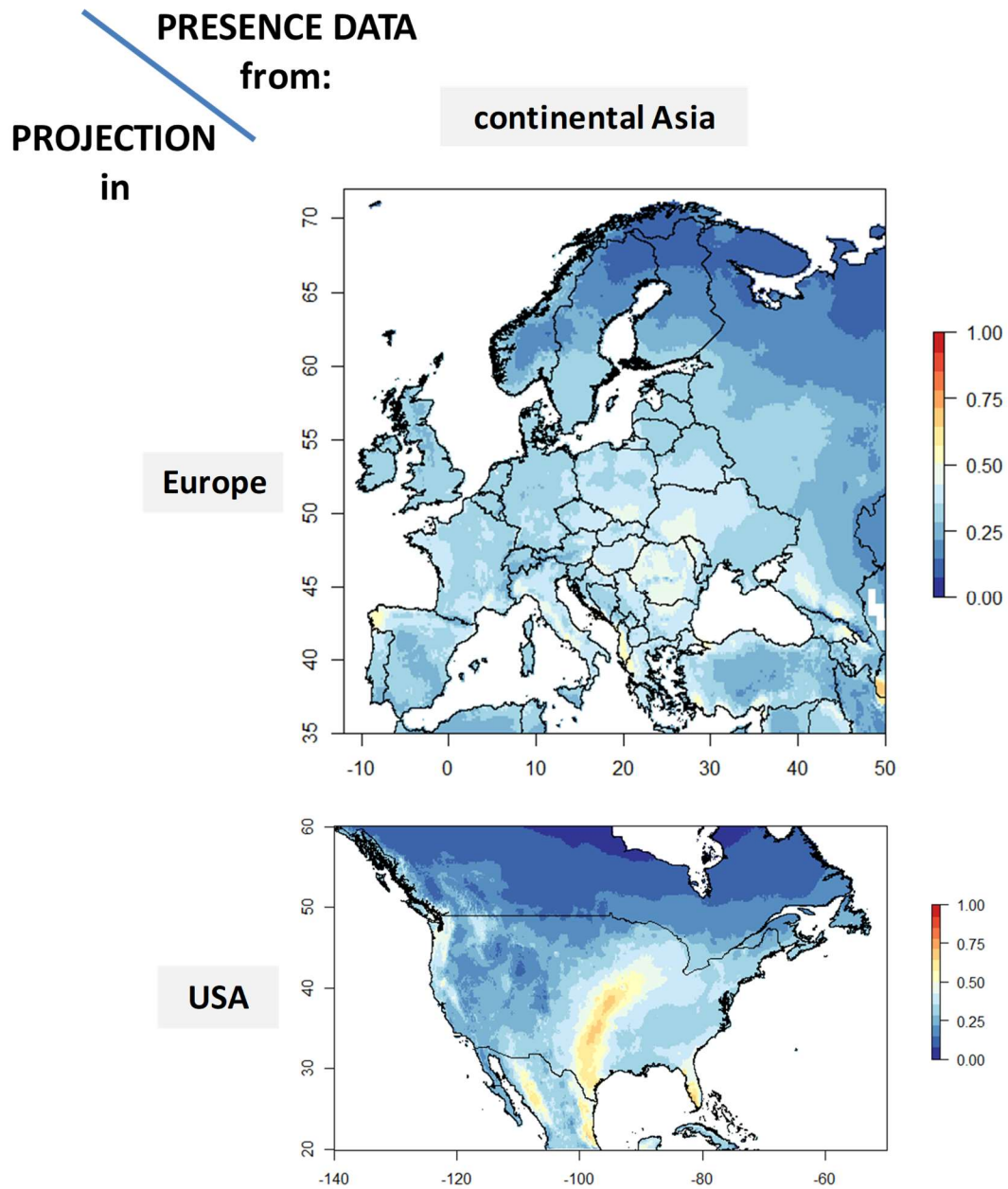


Fig. S4. Model projection from continental Asian native range to both invasive ranges in Europe and USA.
Models were calibrated on the presence data of *D. suzukii* in continental Asia projected the invasive ranges.

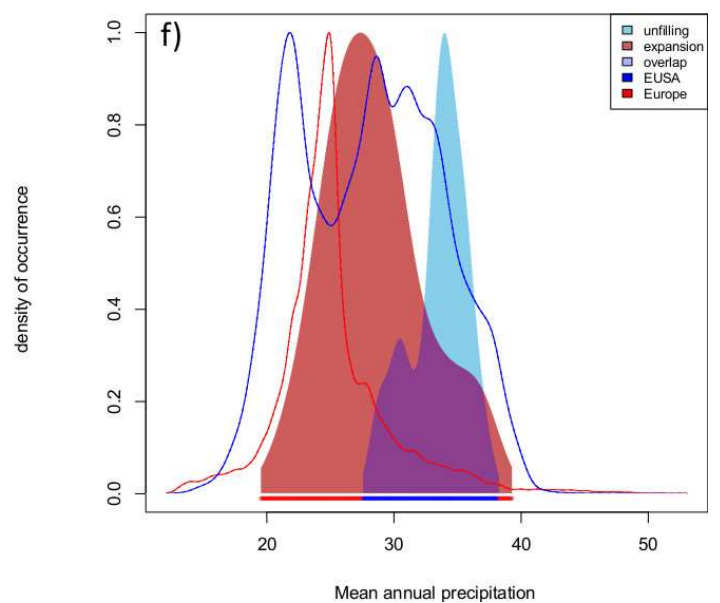
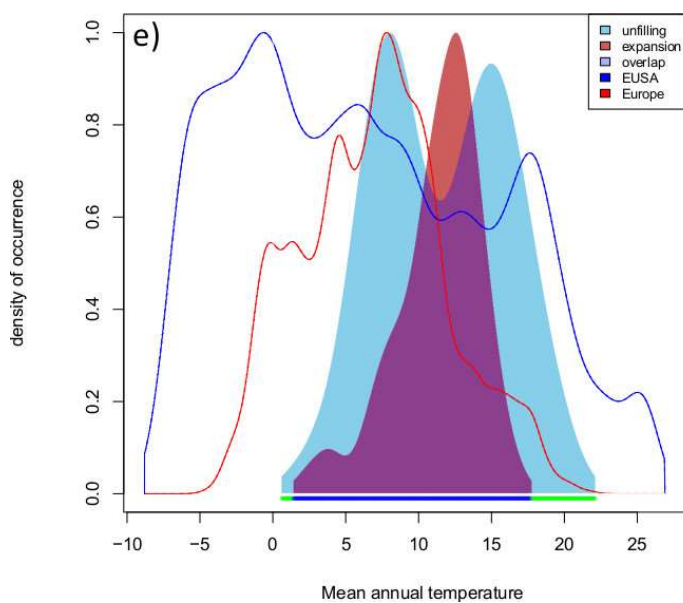
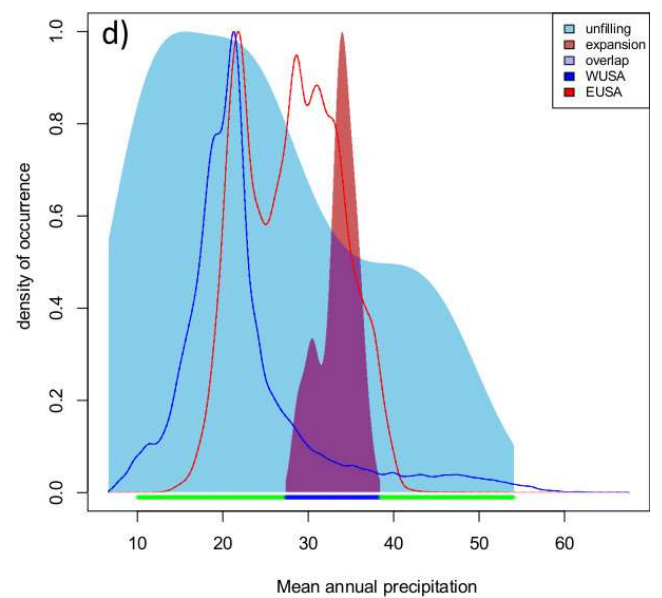
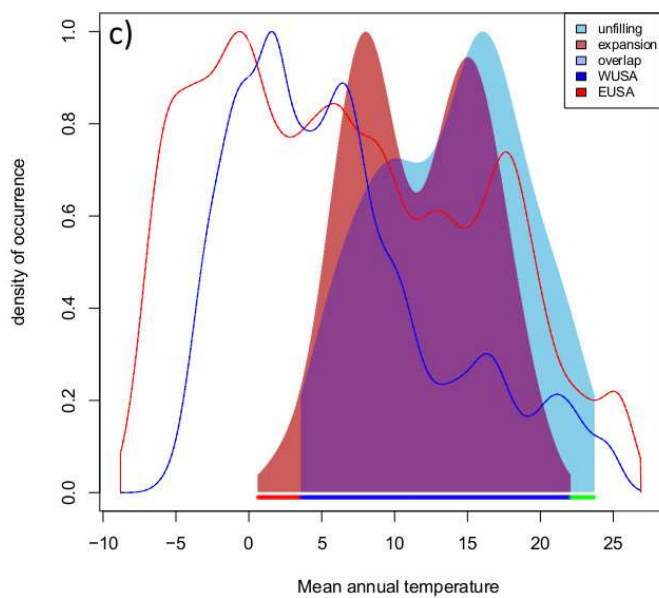
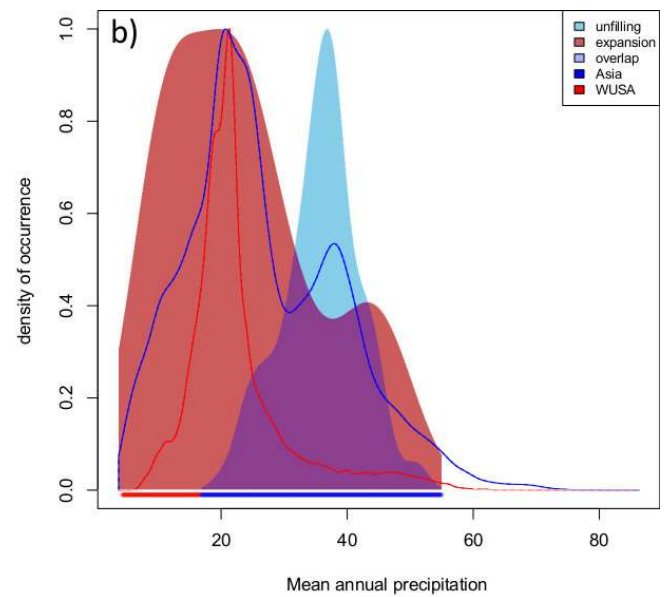
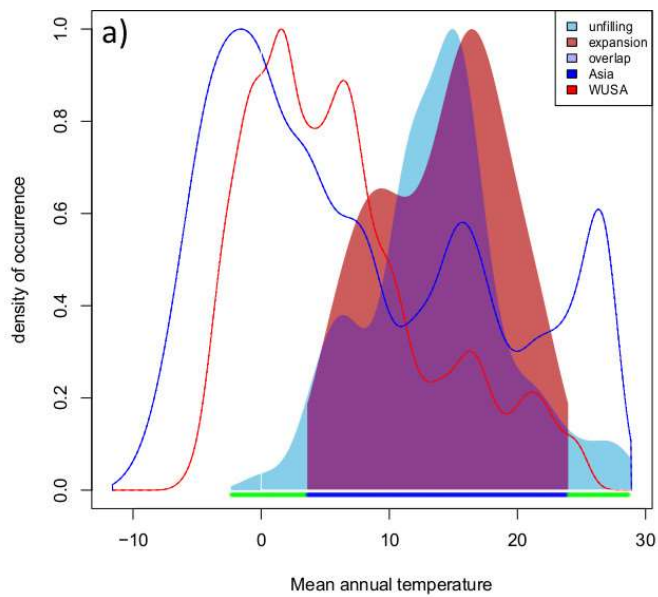


Fig. S5. Diagrams of niche dynamics along the invasion routes of *D. sukuzii* in USA and Europe

Each plot represents the available environment available in region 1 (blue line) and in region 2 (red line) and the distribution of the density of occurrences along the mean annual temperature (panels a,c,e) or the mean annual precipitation (panels b,d,f) into three components: niche stability (purple filled curves), niche expansion (red filled curves), and niche unfilling (light blue filled curves). Niche dynamics are represented for the following pairs of projections: Asia → western USA (top row); western USA → eastern USA (middle row); eastern USA → Europe (bottom row).