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LETTER

Improving International Trade Regulation by Considering Intraspecific Variation for Invasion Risk Assessment of Commercially Traded Species: The *Bombus terrestris* Case

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Abstract

International trade of species facilitates the establishment of nonnative organisms. Highlighting areas potentially suitable for invasive species (risk areas) allows for effective importation regulations to prevent the spread of and the potential damage caused by such species. Species distribution models (SDMs) are commonly used to predict risk areas but they usually disregard intraspecific differentiation and corresponding differences in climatic requirements. We used *Bombus terrestris* as an example of a commonly traded species and developed SDMs at the species- and subspecies-level to assess the value of subspecific information for risk area predictions. We show that species-level models are less efficient than subspecies-based SDMs and that risk areas differ considerably between subspecies. Therefore, the invasive potential of a species can depend on the subspecies imported and the particular climatic condition of the target area. This paves the way to novel policy-relevant guidelines to legislate for smart regulations instead of complete import interdictions.

Introduction

Globalization of trade of many species as food, game, pets, or beneficial organisms for pest control and pollination facilitates the establishment of nonnative organisms (Perrings *et al*. 2010). There are numerous examples of invasive organisms resulting from such trade (Lowry *et al*. 2012). These biological invasions are a major contributor to ecosystem function disruption, biota homogenization, and species endangerment across the world (Mack *et al*. 2000). The international trade of bumblebees exemplifies a contradiction between benefits and problems raised by trading nonnative species (Velthuis & van Doorn 2006). Bumblebees were first introduced to improve pollination of agricultural crops in New Zealand around 1900 (Velthuis & van Doorn 2006). Since the 1980s, bumblebee hives are massively produced for pollination in greenhouses where a colony lasts about few months and then dies. Thus, more than two million colonies of the most often traded bumblebee, *Bombus terrestris*, are produced each year to supply the constant demand. They are shipped throughout the world leading frequently to accidental escapes (Velthuis & van Doorn 2006). *Bombus terrestris* is of West-Palearctic origin but accidental escapes from greenhouses and deliberate releases for pollination of agricultural fields fostered establishments in Japan, Chile, Argentina, New Zealand, and Tasmania (Inari *et al*. 2005; Schmid-Hempel *et al*. 2007; Goulson 2010; Murray *et al*. 2013), leading to dramatic effects on native species (Dafni & Shmida 1996; review in Lecocq *et al*. 2015b).

Given the important advantages of many traded species for human livelihood, health or economy, a complete interdiction of international species trade is not feasible. Therefore, efficient invasive species management strategies are needed. Effective strategies require the prediction of “risk areas” where suitable environmental conditions

Table 1 Subspecies of *Bombus terrestris* and their specific use and introduction history

Subspecies	Specific features	Traded	Nonnative establishments
B. t. africanus	Aestivation	Not traded	–
B. t. audax	Overwintering	Traded (populations from UK and from New Zealand).	New Zealand (1885 and 1906), Tasmania (1992), Chile
B. t. calabricus	Aestivation	Not traded	–
B. t. canariensis	Aestivation	Traded. Used in Canary Island	–
B. t. dalmatinus	Large colonies, Aestivation and/or overwintering depending on the population, Short hairs	Traded. Currently the most traded subspecies because of its superior characteristics from the commercial point of view (largest colonies with large size of workers, high pollination efficiency, and highest rearing success)	Japan (1996), South of Israel (expansion from the North since 1930 and agricultural use since 1991)
B. t. lusitanicus	Aestivation	Currently not traded. Collected by producers in the early years of the commercialization (during the 1990s)	–
B. t. sassaricus	Aestivation	Traded. Used in Sardinia. In the past used in Western Europe.	–
B. t. terrestris	Overwintering	Traded.	–

Traded shows if the subspecies is or was traded according to reviews by Velthuis & van Doorn (2006) and Rasmont *et al*. (2008). Specific features displays known specific phenology or morphology potentially related to eco-climatic niche. Nonnative establishments details known establishment sites for subspecies according to reviews by Velthuis & van Doorn (2006) and Rasmont *et al*. (2008), but see the introduction for a description of the nonnative distribution at species level; years are years of introduction or of first observation. Subspecies considered in species distribution models are highlighted in bold.

allow successful establishment and further invasions now or in the future. Previous studies attempted to predict these potentially suitable areas through species distribution modeling (SDM; e.g. Marcer *et al*. 2012; Verbruggen *et al*. 2013). However, such studies usually model the species of concern as a unity and disregard intraspecific differentiation and potential niche divergence and corresponding individualistic responses of the subunits (Pearman *et al*. 2010; D'Amen *et al*. 2013). SDMs have also been developed for *B. terrestris* at the species level (Kadoya & Washitani 2010; Rasmont *et al*. 2015) but in fact breeding and international trade concerns several subspecies with unique characteristics and distributions (Velthuis & van Doorn 2006; Table 1). *Bombus terrestris* subspecies differ in morphology, genetic, foraging efficiency, behavior, colony size, but also in hair length, diapause condition, and phenology (reviews in Velthuis & van Doorn 2006; Rasmont *et al*. 2008; Lecocq *et al*. 2015a). These specific features, especially the last ones, and their distribution in very different regions (Rasmont *et al*. 2008) make it most likely that their climatic requirements differ considerably. Therefore, the invasive potential of *B. terrestris* could depend on the particular subspecies imported and the climatic conditions in the target area.

In this paper, we used *B. terrestris* as an example to investigate the consequences of subspecific differentiation on risk area predictions for internationally traded species. Based on their native distribution, we used SDMs to predict current and future suitable areas for each *B. terrestris* subspecies that actually are or could be used for international trade. We ultimately aimed to assess the usefulness of subspecies-based invasive risk assessment to provide guidance in improving the regulations of nonnative species imports.

Methods

Studied taxa and occurrence database

We focused on *B. terrestris* subspecies that currently are or were used for international trade (Velthuis & van Doorn 2006): *B. terrestris audax*, *B. terrestris dalmatinus*, and *B. terrestris terrestris*, and those likely to be bred and traded in the future because of their excellent characteristics and positive appraisal by breeders (personal communication): *B. terrestris africanus* and *B. terrestris lusitanicus* (Table 1). We excluded subspecies with limited geographic range because of their limited native distribution and consequent unsuitability for SDMs at the chosen resolution, i.e., a 30 arcmin resolution (Table 1).

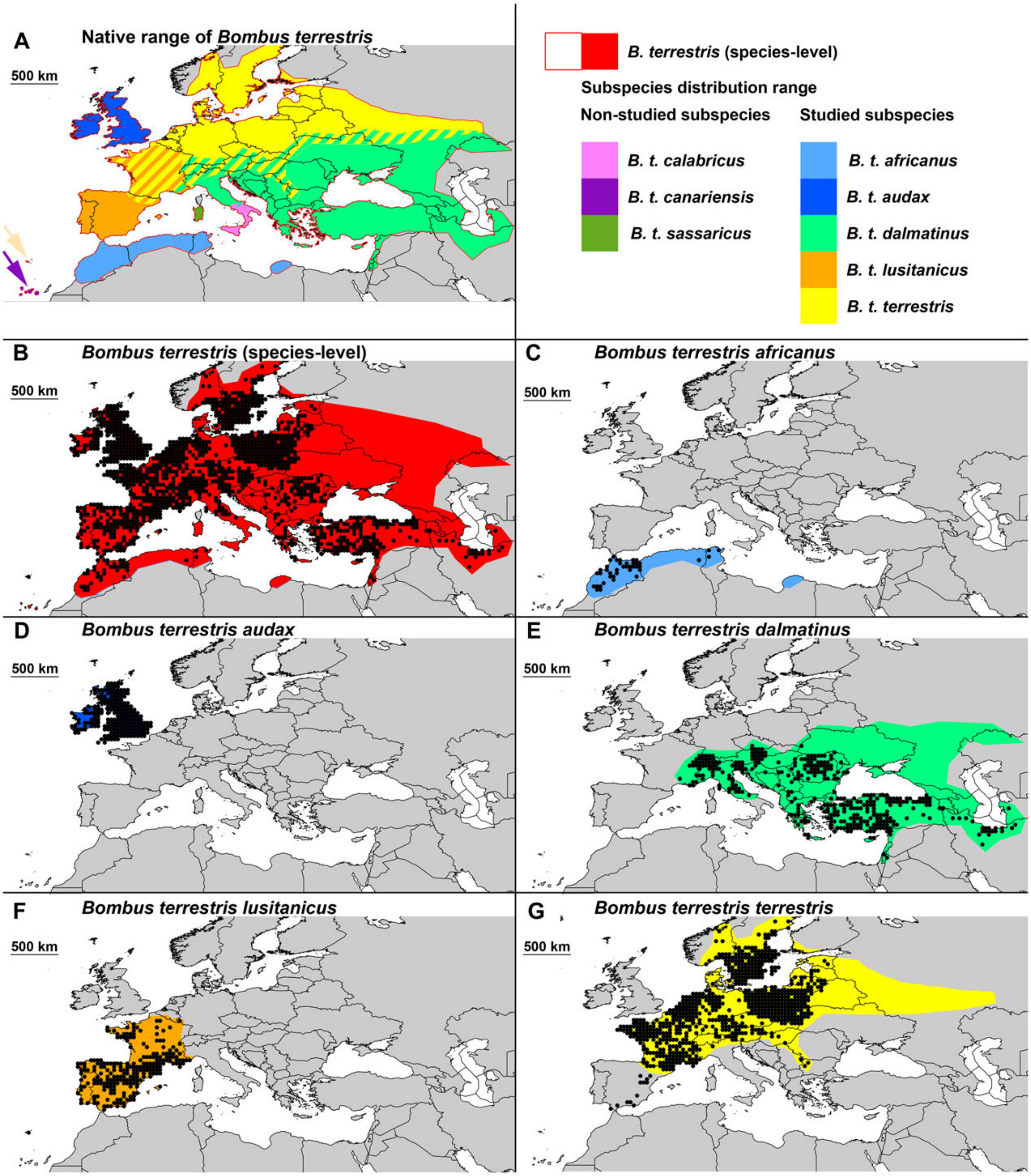

Figure 1 Native distribution range of *Bombus terrestris* and observation points used for species and subspecies distribution models (only the West-Palearctic distribution of *B. terrestris* subspecies are displayed). (A) Native distribution ranges of *Bombus terrestris* and its subspecies according to Rasmont *et al*. (2008, 2015). (B–G) Observation points aggregated at a 30 arcmin grid for the species-level (B; observation points are the sum of observation points of studied subspecies) and for the subspecies-levels (C–G).

Table 2 Relative contributions of each chosen bioclimatic variable in distribution models for *Bombus terrestris*

Subspecies	Annual mean temperature	Temperature seasonality	Maximum temperature of the warmest month	Precipitation of the wettest month	Precipitation seasonality
B. terrestris (species-level)	**57.15**	16.36	13.52	5.31	7.66
B. terrestris africanus	31.2	6.24	**55.4**	1.67	5.51
B. terrestris audax	2.23	**86.2**	8.79	0.17	2.58
B. terrestris dalmatinus	3.88	25.7	**44.1**	21.14	5.14
B. terrestris lusitanicus	**40.9**	28.9	13.3	4.28	12.64
B. terrestris terrestris	20.2	13.2	**46.7**	6.16	13.75

Most important bioclimatic variables are highlighted in bold.

The occurrence data of *B. terrestris* in their native range were extracted from the database *Base de données fauniques Gembloux-Mons* (BDFGM; Rasmont *et al.* 2015). For one third of the data points used, taxonomic information was originally provided at the subspecies level (all corresponding specimens are stored in entomological collections and quality control was based on morphological characters according to Rasmont *et al.* 2008). For the remaining two thirds of the data points used we had no access to the relevant specimens or they have not been stored but we assigned subspecies status when only one subspecies is present in the relevant area according to Rasmont *et al.* (2008). All other observations in the BDFGM, i.e. without subspecies information but coming from areas where more than one subspecies are possible, were not considered. For the SDMs, we used the entire species range except for Russia, Belorussia, Kazakhstan, and Ukraine (i.e. ignored in the models) because of the low sampling intensity in these countries. We calibrated our models with 1,287 observations for *B. terrestris africanus*, 11,411 observations for *B. terrestris audax*, 6,061 observations for *B. terrestris dalmatinus*, 2,098 observations for *B. terrestris lusitanicus*, and 13,803 observations for *B. terrestris terrestris* (Figure 1). We aggregated the data to presence/absences at a 30 arcmin grid to account for potential differences in local sampling effort and to obtain reliable absence data. To further increase the robustness of absence data, we considered only those empty grid cells as absences where other bumblebee species (about 70 species) were observed between 1950 and 2014, according to the BDFGM database with 575,421 observation points in total. Observations without reliable subspecies status were not considered as absences but were ignored in the models.

Climatic data and species distribution models

We used 19 bioclimatic variables (see www.worldclim.org/bioclim) from WorldClim (Hijmans *et al.* 2005) at a 10 arcmin grid for the time period of 1950–2000. We aggregated the bioclimatic variables to the resolution of the bumblebee distribution data. In order to avoid statistical problems due to high levels of collinearity among the climate variables, we selected five relevant and least correlated variables ($r < 0.6$) bioclimatic variables (Table 2) by means of complete linkage cluster analysis based on a spearman correlation matrix (Table S1) in R 3.1.1 (R Development Core Team 2013).

In order to compare consequences of subspecific differentiation on risk area predictions, we developed SDMs at the species-level (sp-SDM; all the five here considered subspecies were analyzed together) and at the subspecies-level (ssp-SDM). Each SDM was developed using boosted regression trees (BRTs) (Elith *et al.* 2008). All BRT computations were performed in R (R-package gbm, Ridgeway *et al.* 2013) using a learning rate of 0.001, a tree complexity of three (lower complexities resulted in worse models while higher complexities performed similarly) and a bag fraction of 0.75. We assessed the relative importance of each climatic variable by their contribution to the results of the BRTs based on the number of times a variable was selected for binary splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all the individual trees (Friedman & Meulman 2003). Resulting occurrence probabilities from the sp-SDM and ssp-SDMs were transformed into presence/absence maps based on a threshold obtained by maximizing the true skill statistic (TSS) (Allouche *et al.* 2006). We evaluated each model using (i) 10-fold cross-validated area under the curve (AUC) of a receiver operating characteristic plot (Fielding & Bell 1997), (ii) sensitivity (the proportion of observed presences that are predicted as such), (iii) specificity (the proportion of observed absences that are predicted as such), and (iv) TSS (sensitivity + specificity – 1; ranging from –1, lowest predictive accuracy, to 1, highest predictive accuracy; TSS > 0.75 reflect an excellent model and TSS > 0.40 reflect a good model, Landis & Koch 1977). In order

Table 3 Evaluation of models for *Bombus terrestris*

Subspecies	AUC	Sensitivity	Specificity	TSS
B. terrestris (species-level)	0.85	0.82	0.82	0.64
B. terrestris africanus	0.96	0.97	0.98	0.95
B. terrestris audax	0.99	0.97	0.98	0.97
B. terrestris dalmatinus	0.92	0.86	0.89	0.75
B. terrestris lusitanicus	0.95	0.91	0.92	0.84
B. terrestris terrestris	0.92	0.90	0.88	0.78

AUC, 10-fold cross-validated area under the receiver operating characteristic curve. Sensitivity is the proportion of observed presences that are predicted as such. Specificity is the proportion of observed absences that are predicted as such. TSS is the true skill statistic.

to estimate potential impacts of climate change, we projected the SDMs for each subspecies to conditions in 2070 according to the different representative concentration pathways (RCPs; Moss *et al.*, 2008) under five global circulation models (GCMs; CCSM4, HadGEM2-AO, IPSL-CM5A-LR, MIROC-ESM, and NorESM1), and applied an ensemble approach to identify levels of agreement among the projections of the different GCMs (Araújo & New 2007).

Results

Overall, the prediction abilities of our models were good to excellent with AUC > 0.85 and TSS > 0.64 (Table 3). The relative contributions of each bioclimatic variable to the models differed between (i) subspecies and species-levels and (ii) among each subspecies (Table 2). For ssp-SDMs, the cross-validated AUCs, TSS, sensitivities, and specificities were high suggesting that models efficiently reflected the subspecies distribution (Table 3). These values were always higher for each ssp-SDM than for the species-level suggesting that independent subspecies models were more efficient than the sp-SDM (Table 3). Interestingly, the worldwide predicted suitable area was much larger for the sp-SDM compared to the combined results of all ssp-SDMs (for current climate and all RCP scenarios; Figures 2, S1, and S2). The sp-SDM predicted climatically suitable areas out of the natural range in Africa, Arabian Peninsula, Indian region, Australasia, south of North America, and South America (Figure 2). These climatically suitable areas remained similar in projections for 2070 regardless of the RCP scenario considered (Figure S1). Considering the ssp-SDMs, the globally predicted suitable areas differed considerably among the subspecies (Figures 2 and S1). Climatically suitable areas outside the natural range of the currently traded subspecies were mainly predicted in (i) south of South America, New Zealand, and Tasmania for *B. terrestris audax*, (ii) North America, North Africa, Central Asia, India, China, and Japan for *B. terrestris dalmatinus* and (iii) south of South America, New Zealand, southeast Australia, and Tasmania for *B. terrestris terrestris* (Figure 2). For the two other subspecies, suitable areas were mainly predicted in (i) the Iberian Peninsula, South Africa, Arabian Peninsula, north of Mexico, south of South America, and Australia for *B. terrestris africanus* and (ii) the Mediterranean Europe, South Africa, south of South America, Australia and New Zealand for *B. terrestris lusitanicus*. Generally, the total amount of climatically suitable areas across the globe remained constant under scenarios of future climate change across subspecies (but with a slight decrease of the current native range for all subspecies except for *B. terrestris africanus* and *B. terrestris dalmatinus*) (Figures 2 and S1).

Discussion

Species-level-based and subspecies-level-based predictions for traded species

Ignoring intraspecific differentiation could deeply affect model accuracy (Pearman *et al.* 2010; D'Amen *et al.* 2013). In the context of traded species, this can lead to (i) overestimating the species' invasive potential since individuals from any location in the native range are considered to tolerate all climatic conditions in the entire range of the species (i.e. disregarding local differentiation) or (ii) underestimating the species' invasive potential when outlying populations, that happen to be the populations that are used in the international trade because of their specific features, have little weight in the development of SDMs at the species level (i.e., considered as outliers). Considering each differentiated group of populations individually for modeling could overcome these limitations.

Internal model validation, in the sense of using data within the native range, indicated that the predictive abilities of our models were good to excellent (comparison with Landis & Koch 1977; Rasmont *et al.* 2015). Unfortunately, data on successful invasions outside the native range are too scarce or geographically imprecise impeding reliable external model validation. However, we provide a qualitative assessment of model predictions and reported invasions. The Sp-SDM agreed with some known nonnative occurrences but it (i) overestimated the risk some regions, e.g., suitable area prediction in Saharan region under current climate where species ecological requirements make actual establishments unlikely but also (ii) underestimated the invasive potential in other regions, e.g. very small areas predicted in Japan while *B. terrestris* is now naturalized there (Inari *et al.* 2005). In contrast, our ssp-SDMs (i) minimized predictions in most likely unsuitable areas (e.g., Sahara) and (ii) agreed well

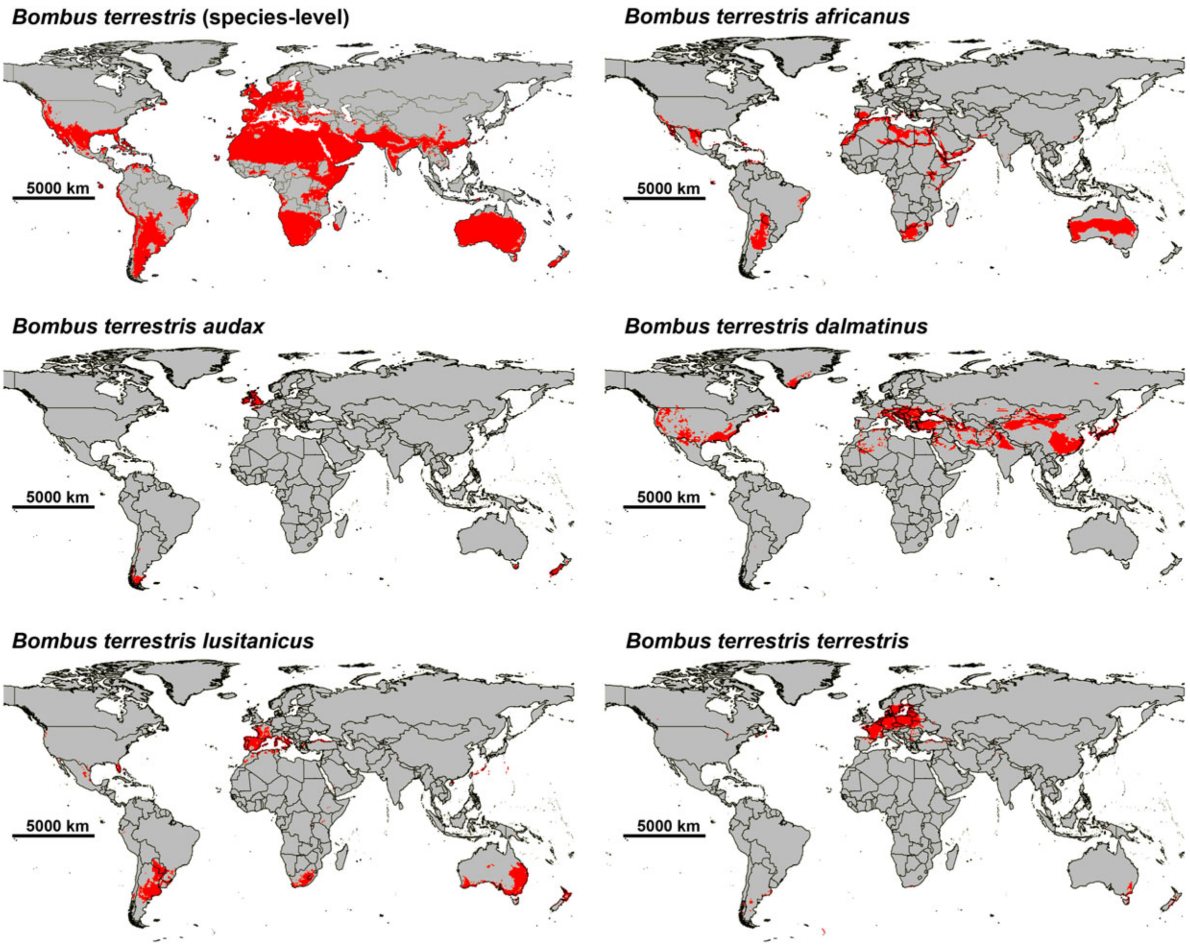

Figure 2 Current worldwide climatically suitable areas for marketed *Bombus terrestris* (species-level and subspecies). The climatically suitable areas are in red.

with the known instances where subspecies established outside their natural range. The *B. terrestris audax* SDM predicts climatically suitable areas in New Zealand and Tasmania (Figure 2), regions where the subspecies has been introduced and is now naturalized (Goulson *et al.* 2002; Goulson & Hanley 2004). Similarly, prediction of favorable condition for *B. terrestris dalmatinus* in Japan (Figure 2) are congruent with current observations in the wild (Inari *et al.* 2005). Taken together with the good performances of ssp-SDMs (Table 3), this suggests that predictions are more realistic when using the subspecies information. However, we cannot assess our predictions of favorable conditions for *B. terrestris audax* and *B. terrestris terrestris* in South America because a robust identification of subspecies occurring there is missing (Ruz & Herrera 2001; Schmid-Hempel *et al.* 2014) and in general it is hard to assess the accuracy of areas predicted as unsuitable since failed introductions are generally not well documented (Zenni & Nuñez 2013).

Risk area prediction and approach limitations

Assuming that subspecies-based models are more realistic, predictions of further potential invasions should be more efficient. We found considerable differences in the relative importance of the different climatic variables among the subspecies which suggests a certain level of niche differentiation. Such different climatic requirements are further supported by reported differences in preferred overwintering temperatures for the different subspecies (review in Rasmont *et al.* 2008). Corresponding to that, global predictions of climatically suitable areas differ considerably among the subspecies (Figure 2).Subspecies with the largest invasive potential (ssp. *africanus*, *lusitanicus*, and *dalmatinus*) are those adapted to Mediterranean, dry, and continental climates, while the invasive potential of subspecies from oceanic climates (ssp. *audax* and *terrestris*) is much smaller. Thus, risk area assessments at least depend on the traded subspecies and on the climatic conditions into which an alien species is released or escapes. A more accurate determination of such risk areas would require more realistic distribution models. Indeed, taxa distributions are constrained by several factors (e.g. Alexander & Edwards 2010). Some biotic interactions (e.g. food availability) could limit taxon distributions (e.g. Schweiger *et al*. 2008) and thus bias the assessment of climatically suitable areas leading to a higher uncertainty in the risk area assessment. However, using climate-based distribution models can still provide useful first-level information (although rough). Indeed, at larger scales the distributional range of many flying insects is mainly determined by climatic conditions rather than by biotic interactions (Schweiger *et al*. 2012) and the climatic conditions in the native and invaded range of a taxon are often very similar (Thuiller *et al*. 2005). Besides limitations of climate-based distribution models, special attention should be paid to the attribution of subspecies status whenever possible for long-term data storage and the further assessment of species with as yet undifferentiated subspecies by easily reachable diagnostic characters (e.g. Lecocq *et al*. 2015a) should be encouraged.

Toward a smart regulation of traded species: the example of *B. terrestris*

From a practical point of view, independent subspecies invasive risk assessment can allow more efficient international trade regulations which reconcile biological conservation and economic reality. Indeed, international trade regulation based on such risk assessments could allow trading particular subspecies into regions where it is unlikely that they can establish or survive in the wild rather than entirely banning a species important for local economy as is currently the case (Riley 2011). For such species with essential benefit for human livelihood and economy, smart regulations rather than a complete import interdict could be set up.

Currently, national and international regulations mainly prohibit imports of commercial *B. terrestris* despite their significant benefits for agricultural systems (Velthuis & van Doorn 2006). Our risk area comparison based on climatically suitable conditions for subspecies (Figures 2 and S1) provides useful information for setting up more pragmatic regulations (balanced between potential invasion limitation and crop pollination needs) taking into account differential invasive potential of marketed subspecies. In the Northern Hemisphere, import authorizations should be restricted to *B. terrestris audax* and *B. terrestris terrestris* because their climatically suitable areas are mainly restricted to their native range in this hemisphere. In the Southern Hemisphere, import interdicts should be applied to all subspecies except *B. terrestris dalmatinus* since it is the only subspecies without climatically suitable areas in these regions (Figure 2). For the currently nonmarketed subspecies (ssp *africanus* and *lusitanicus*), our models suggest that they have one of the largest invasive potential, especially in the Southern Hemisphere (Figure 2). Therefore, the commercialization attempts of these subspecies should be curbed to preserve native fauna and flora. These recommendations should be further elaborated to integrate other threats caused by exotic pollinator importations, especially the highly problematic pathogen spillover from commercially reared bumblebees to wild native species (Murray *et al*. 2013; Schmid-Hempel *et al*. 2014). Indeed, pathogen spillover remains likely during commercial translocations but preferred translocations to less or unsuitable climates might decrease the potential of pathogen spillover when naturalization of the alien bumblebee is impossible. Nevertheless, best management practices should always thus integrate measures that prevent the interaction between traded and native taxa as much as possible.

Conclusions and prospects

Our results strongly suggest that invasive risk assessment by SDMs can be improved by integrating information on intraspecific variation. Such a subspecies-based invasive risk assessment can provide more realistic guidelines to ultimately legislate for smart regulations and management that reconciles biological conservation and economic reality. Here applied to *B. terrestris* trade, such an approach should be extended to all traded organisms where a subspecific polymorphism is known and used by companies to select the best strain from a commercial point of view such as Australian parrots or rice (Song & Carter 1996; Low 2014). However, SDM-based invasive risk assessments should still be critically considered. First, SDMs generally assume that species do not adapt to new conditions while plasticity or adaptation could increase the invasive potential (e.g. Sexton *et al*. 2002). Second, since species distributions are not only shaped by climate, other subspecies-specific features, e.g., food requirements, should be considered to improve the assessment of invasive potential. Third, commercial imports can concern (i) specimens bred for several generations in nonnatural conditions to generate strains with specific ecological requirements (different from natural populations) or (ii) populations resulting from intersubspecific hybridization during the commercial breeding process (for bumblebees see Velthuis & van Doorn 2006). Artificial selection and hybridization can lead to genetic specificity and evolutionary novelty, resulting in changes in life history traits and ecological niche characteristics, and possibly in increased invasive potential (e.g., Facon *et al.* 2011). Further studies on plasticity and ecological characteristics of commercial strains would be needed for a more precise risk assessment.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Worldwide climatically suitable areas for *Bombus terrestris* (species-level and subspecies). The climatically suitable areas are in green. Current is the distribution of current climatically suitable areas. RCP2.6, RCP4.5, RCP6.0, and RCP8.5 are the predicted potential suitable climatic areas for 2070 according to representative concentration pathways (RCP) scenarios 2.6, 4.5, 6.0, and 8.5. The color scale indicates agreement (from one, yellow to five, red) among the five global circulation models (CCSM4, HadGEM2-AO, IPSL-CM5A-LR, MIROC-ESM, and NorESM1) in projections of climatically suitable area.

Figure S2. Comparison of worldwide climatically suitable areas predicted by SDMs developed at the species-level and at the subspecies-level. Brown colors indicate climatically suitable areas according to SDM based on the species-level. Pink colors indicate climatically suitable areas according to at least one SDM based on subspecies-level (for the future condition according to prediction by at least one global circulation model for one subspecies). Blue colors indicate climatically suitable areas according to SDM based on species-level or to at least one SDM based on subspecies-level. Current is the distribution of current climatically suitable areas. RCP2.6, RCP4.5, RCP6.0, and RCP8.5 are the predicted potential suitable climatic areas for 2070 according to representative concentration pathways (RCP) scenarios 2.6, 4.5, 6.0, and 8.5.

Table S1. Correlation between selected bioclimatic variables based on a spearman correlation matrix.

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