

Supplementary material (version 2)

The Human Release Hypothesis for biological invasions: human activity as a determinant of the abundance of invasive plant species

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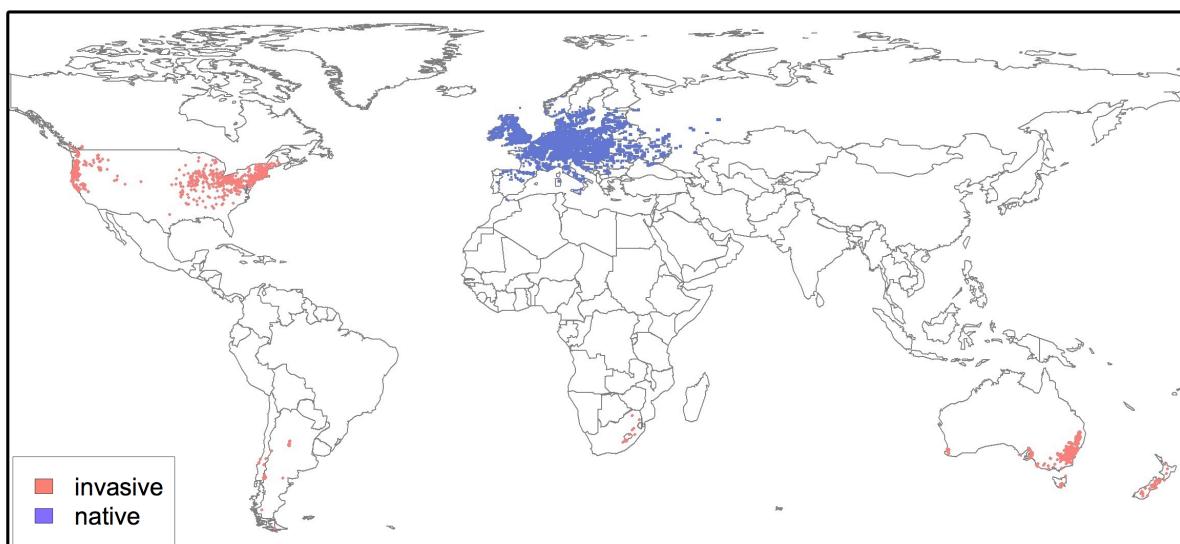


Figure S1. *Rosa rubiginosa* (sweetbriar rose) occurrences used in our MAXENT model.

Occurrences were taken from existing literature (see Appendix 2 in Supplementary material) and our field observations; blue = native occurrences; pink = invasive occurrences. For the final MAXENT model we included a randomly reduced dataset until data points were evenly distributed and no spatial autocorrelation was detected in the model residuals.

Appendix 1

Methods used for climatic envelopes and for niche equivalency test

Sweetbriar rose (*Rosa rubiginosa* L.) occurrences were taken from the literature (see Appendix 2 in Supplementary material) as well as from personal observations. In total, we collated 1425 occurrence records from the invasive range (Australia, New Zealand, North America, South America, South Africa) and 12132 occurrences from the native range (Europe, Asia, North Africa; see Figure S1 in Supplementary material and dataset 1). However, we did not include all native occurrences into our final MAXENT model because of a strong spatial autocorrelation in the model residuals. Therefore, we randomly reduced the native occurrences until data points were evenly distributed based on the Moran's I coefficient; this point was reached when the dataset was reduced to 3033 native occurrences. As a priori assumption we defined the global range of our study species which would later serve as background for pseudo-absences. Nine bioclimatic variables were chosen from the WorldClim Global Climate Data-set¹ to define the global range of our study species: annual mean temperature (bioclim 1), isothermality (bioclim 3), temperature seasonality (bioclim 4), mean temperature of warmest quarter (bioclim 10), mean temperature of coldest quarter (bioclim 11), annual precipitation (bioclim 12), precipitation seasonality (bioclim 15), precipitation of the wettest quarter (bioclim 16), and precipitation of the driest quarter (bioclim 17). We followed the approach from VanderWal et al. (2009)² choosing the spatial extent that would provide the most accurate results and biologically meaningful fit. Therefore, we chose those bioclimatic variables that sufficiently outlined the potential global range of this species based on the total occurrences with the ArcGis® software and excluded redundant variables and monthly values. According to these criteria bioclimatic variables that highlighted almost the entire world as a potential habitat were neglected. All nine bioclimatic variables were added into one composite raster file, which was converted into a polygon representing the area with *R. rubiginosa* occurrences. Out of this area all bioclimatic variables were extracted to define the climatic envelope using the MAXENT (Maximum Entropy modelling for species geographic distributions) software (Vers. 3.3.3k)^{3,4}. We chose five bioclimatic variables that contributed useful information by themselves: annual mean temperature (bioclim 1), mean diurnal range (bioclim 2), temperature annual range (bioclim 7), mean temperature of warmest quarter (bioclim 10), annual precipitation (bioclim 12), and precipitation seasonality (bioclim 15); and checked for collinearity with a correlation matrix.

Within the MAXENT software we selected a 20 % test percentage out of our dataset, 100 replicates (Bootstrap), and fade by clamping to mitigate clamping issues. Our climatic model based on the invasive occurrences had a high discrimination performance with an average test AUC of 0.90. Our climatic envelope model based on the native occurrences performed slightly less well with an average test AUC of 0.87. In both models, we detected no spatial autocorrelation in the residuals.

A threshold rule was applied to convert continuous suitability surfaces into binary outputs only showing areas that are suitable for modelled groups. We selected the threshold ‘maximum training sensitivity plus specificity logistic threshold’ which focuses on the correct classification of presences and background points⁵.

Moreover, we quantified the degree of niche overlap between the invasive and native niche by using the Schoener’s D index^{6,7} from the R (v. 2.15) package ‘phyloclim’ (v. 0.9.2) which was recently shown to outperform other metrics when assessing niche overlaps⁸. Schoener’s D indicates the degree of accordance between two niches based on climate envelope model outputs and ranges from 0 = no overlap to 1 = full overlap. In a one-tailed test, Schoener’s D is compared to the percentiles of null distributions obtained from pseudo-replicated climate envelope models where localities from invasive and native populations are pooled and randomly partitioned. We set 100 as the factor for pseudo-replication which has been shown to be sufficient to reject the null hypothesis with high confidence^{7,9}. The derived Schoener’s D of 0.31 ($p<0.0001$) verified the pattern observed in the map, that is, invasive and native populations occupied different climatic niches.

As complementary direct approach we compared how the native and invasive sites differ in their climatic attributes using a principal component analysis (PCA)¹⁰. We chose 15 out of 19 bioclimatic variables from the WorldClim Global data-set: annual mean temperature (bioclim 1), mean diurnal range (bioclim2), isothermality (bioclim 3), temperature seasonality (bioclim 4), temperature annual range (bioclim 7), mean temperature of wettest quarter (bioclim 8), mean temperature of driest quarter (bioclim 9), mean temperature of warmest quarter (bioclim 10), mean temperature of coldest quarter (bioclim 11), annual precipitation (bioclim 12), precipitation seasonality (bioclim 15), precipitation of the wettest quarter (bioclim 16), and precipitation of the driest quarter (bioclim 17), precipitation of warmest quarter (bioclim 18),

precipitation of coldest quarter (bioclim 19); thereby including all bioclimatic variables but the monthly values. The dataset analysed by the PCA (Figure S4) included all invasive occurrences ($N = 1425$), all native occurrences ($N = 12132$) and as absences we included the background pixel derived by our MAXENT model ($N= 8660$). In a next step niche equivalency (Schoener's D index) and niche similarities (Schoener's D index) were calculated based on the scores of the first two axes of the PCA for the native and invasive occurrences and the available background climate respectively (package = ecospat v. 1.0)¹¹. To this end the ordination scores were used to create a grid (resolution 100 cells) with occurrence densities. Equivalency and similarity tests were then run in 100 iterations.

With the PCA we detected a slightly stronger overlap ($D = 0.53$, $p>0.05$) than with the MAXENT predictions. Notably, invasive occurrence densities show a broader spread in the available climatic space than native occurrence densities (Figure S4), which supports our hypothesis that other than climatic constraints are governing the spread of invasive sweetbriar populations. The test of similarity revealed that the ranges were not more similar to each other than to a random range ($p<0.05$), thus, niche similarity can be rejected.

References Appendix 1

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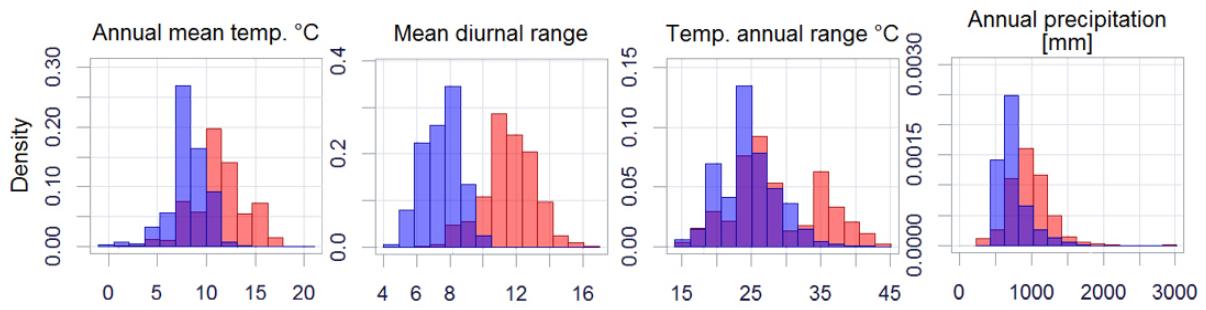


Figure S2. Histograms of the annual mean temperature [°C], mean diurnal range, temperature annual range and annual precipitation [mm] for all *Rosa rubiginosa* sites.

The annual mean temperature, mean diurnal range, temperature annual range and annual precipitation were the most important predictors contributing each more than 10% to the MAXENT models. The histograms show the density (frequency standardized to 100) of native (blue) and invasive (pink) occurrences for each parameter value (overlap in purple).

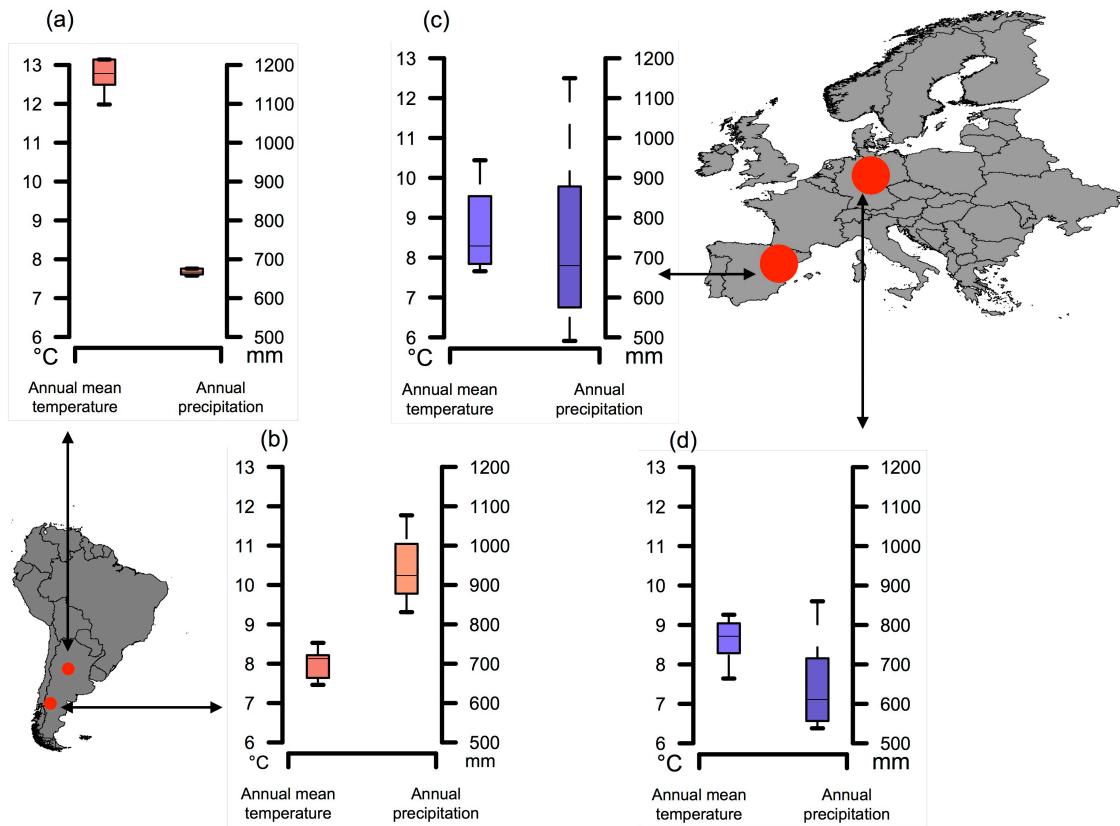


Figure S3. Annual mean temperature [°C] and annual precipitation [mm] for selected invasive (pink) and native (blue) populations of *Rosa rubiginosa* (sweetbriar rose). In the invasive range populations are located in Central (a, N=6) and Southern Argentina (b, N=7). In the native range populations are located in Spain (c, N=7) and Germany (d, N=11). Annual mean temperature and annual precipitation vary greatly within the invasive range and also within the native range. Smaller population sizes in the native range (mostly less than 10 individuals compared to hundreds of individuals in the invasive range) therefore are not explained by these two climatic variables.

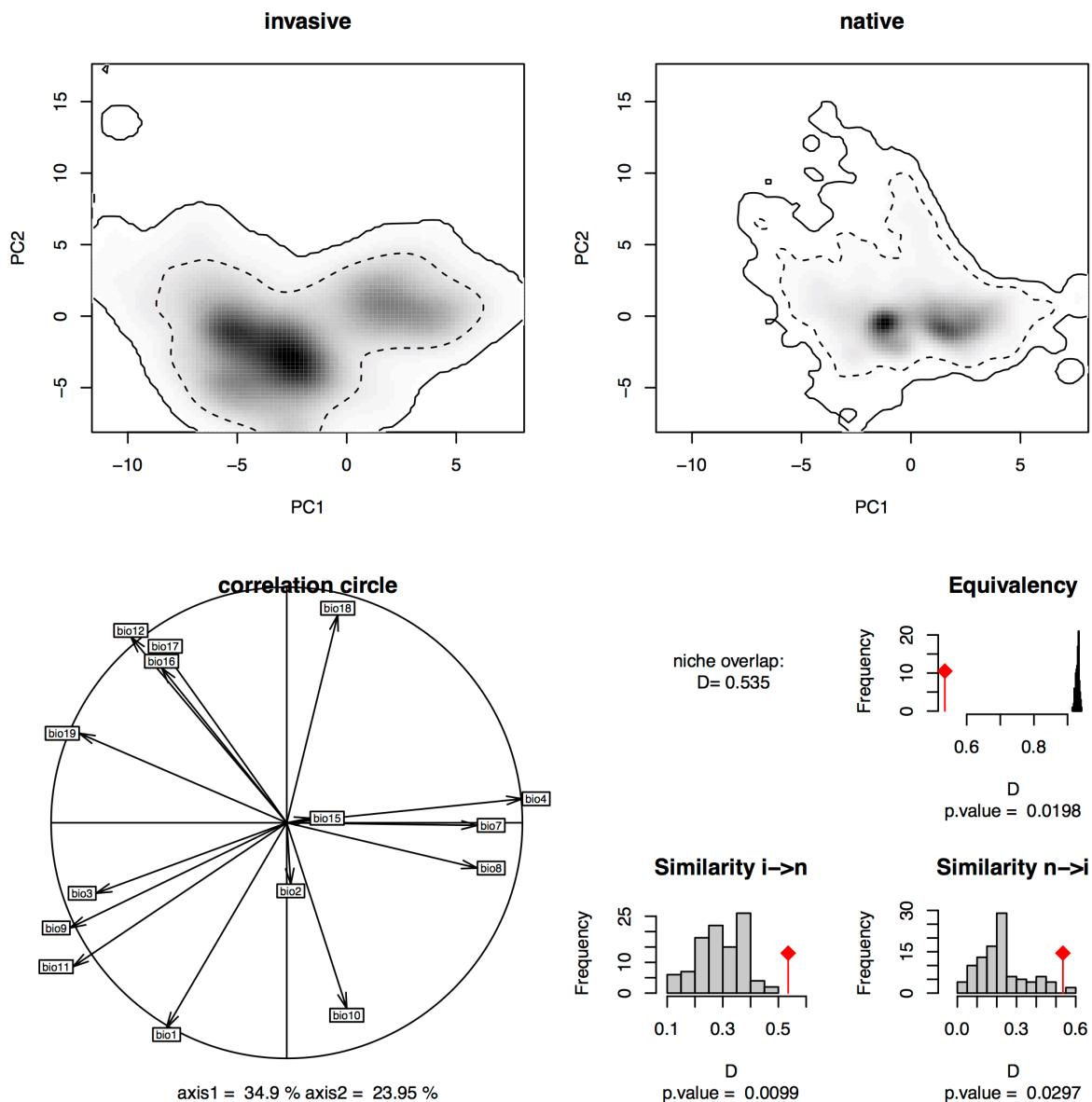


Figure S4. Principal component analysis (PCA) of total dataset (1425 invasive sites, 12132 native sites, 8660 background pixel) with bioclimatic variables as predictors.

The upper two plots represent the niche of the sweetbriar rose based on invasive occurrences (left) and native occurrences (right). Grey shadings represent the density of the occurrences by cell. The first axis explained 34.9% of the variance and the second axis 23.95%. Histograms show the observed niche overlap D between the two ranges (bars with a diamond) and simulated niche overlap (grey bars) on which tests of niche equivalency ($D=0.53$, $p<0.05$), climatic similarity of the invasive (i) to the native (n) range and of the native to the invasive range were calculated from 100 iterations ($p<0.05$).

Appendix 2

List of plant distribution data sources for *Rosa rubiginosa* L. used by E. W. to compile the geographic distribution in the native and introduced areas. The sources are arranged by continents. All web based data sources were accessed in December 2012.

North America

1. AKEPIC. *Alaska Exotic Plant Information Clearinghouse Database*. Available at:
<http://aknhp.uaa.alaska.edu/maps/akepic/>
2. CalWeedMapper. *California Invasive Plant Council*. Available at:
<http://calweedmapper.calflora.org/>
3. EDDMapS. *Early Detection and Distribution Mapping System*. Available at:
<http://www.eddmaps.org/>
4. E-Flora BC. *Electronic Atlas of the Plants of British Columbia [eflora.bc.ca]*. Available at: <http://www.geog.ubc.ca/biodiversity/eflora/index.shtml>
5. IPAMS. *Invasive Plant Atlas of the MidSouth*. Available at: <http://gri.msstate.edu/ipams>
6. IPANE. *Invasive Plant Atlas of New England* Available at: <http://nbii-nin.ciesin.columbia.edu/ipane/>
7. Jepson eFlora. *Rosa rubiginosa, Jepson Flora Project*. Available at:
<http://ucjeps.berkeley.edu/IJM.html>
8. NCU Flora. *Flora of the Southeastern United States*. Available at:
<http://herbarium.unc.edu/seflora/firstviewer.htm>
9. NMBCC. *New Mexico Biodiversity Collections Consortium Gateway to New Mexico Biodiversity*. Available at: <http://NMBiodiversity.org>
10. PNW Herbaria. *Consortium of Pacific Northwest Herbaria*. Available at:
<http://www.pnwherbaria.org>
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<http://sbsc.wr.usgs.gov/research/projects/swepic/swemp/swempA.asp>

Europe

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