*Environmental Conservation* **40** (2): 167–181 © Foundation for Environmental Conservation 2012 doi:10.1017/S037689291200032X

# Predicting the distribution of invasive plants in the Ukrainian Carpathians under climatic change and intensification of anthropogenic disturbances: implications for biodiversity conservation

**THEMATIC SECTION**
Biodiversity Governance
in Central and Eastern
Europe

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Date submitted: 5 February 2012; Date accepted: 29 August 2012; First published online: 16 August 2012

## SUMMARY

**Biodiversity conservation in the Ukrainian Carpathians cannot be accomplished without a clear understanding of the factors negatively impacting habitats and species, and long-term projection of these impacts. One factor that may severely alter the ecosystems involved is the introduction and spread of invasive plant species, but the potential distribution and spatial aggregation of suitable habitats for several invaders have not been quantified. The Maxent approach was used to model the potential establishment within the entire mountain range of 11 alien invasive plant species based on stratified sampling and herbaria records and six variables representing climatic extremes, topography, and anthropogenic and natural disturbances. Predictions of habitat suitability were projected to two future change scenarios depicting increasing rates of climate warming and anthropogenic disturbances in 2050 and 2100. Under current climate and disturbance patterns, the models predicted suitable habitats for invasive species establishment to be aggregated in the south-west, east and north-east of the Ukrainian Carpathians, along major rivers and roads at altitudes of up to *c.* 700 m. Eight per cent of the total area within protected areas was predicted to be potentially susceptible to invasion by at least one species, with 13% of these susceptible habitats being suitable for all 11 species. Under the future change scenarios, suitable habitat ranges increased significantly in the entire study area and within regions of high conservation value. All species were projected to gain suitable habitats at higher altitudes along linear habitats and to potentially expand their ranges laterally from habitats predicted as suitable for current conditions along small rivers and roads. Under the scenario solely of increased average seasonal temperatures, suitable habitats for the establishment of at least one species within protected areas and a proposed ecological network increased by more than 15 percentage points by 2050 and by more than 30 percentage points by 2100 when compared with predictions for current conditions. Similar future patterns were discernible for the aggregation of suitable habitats for all 11 species. Incorporating increases in anthropogenic pressures into climatic-change projections led to a significantly greater projected expansion of suitable habitats for establishment as compared to scenarios considering only climatic changes. As the 11 species have already established viable populations within protected areas, further spread of at least one species is likely if conservation planning is not changed to include the management of invasive species in such areas.**

*Keywords*: biodiversity impacts, climate change, land-use change, Maxent, nature protection, plant invasion, species distribution modelling, Ukrainian Carpathians

## INTRODUCTION

Studies on plant invasion in temperate mountain regions have traditionally indicated a relatively lower invasion risk in these regions as climatic niche limits are approached with increasing altitude (Alexander *et al.* 2009), while human disturbances and propagule pressure decrease (Becker *et al.* 2005; Foxcroft *et al.* 2010; Haider *et al.* 2010, Haider & Kueffer 2011). High densities and long residence times of invasive alien plants in the lowlands are correlated with the spread of these species to higher altitudes (Alexander *et al.* 2009; Pyšek *et al.* 2011) and into protected areas, particularly those exposed to anthropogenic pressures (Pyšek *et al.* 2002). Several mechanisms may be responsible for this spread, including long-distance dispersal (Pyšek & Prach 1994), evolutionary adaptations (Becker *et al.* 2005; Alexander *et al.* 2009), low resistance of native communities (Levine *et al.* 2004), and/or shifts in propagule pressure (Colautti *et al.* 2006), anthropogenic disturbances and climatic regimes (Pauchard *et al.* 2009; Pyšek *et al.* 2010).

The Ukrainian Carpathian Mountains (hereafter, UA Carpathians) are a prime example of a temperate mountain range that is experiencing increased levels of invasion by

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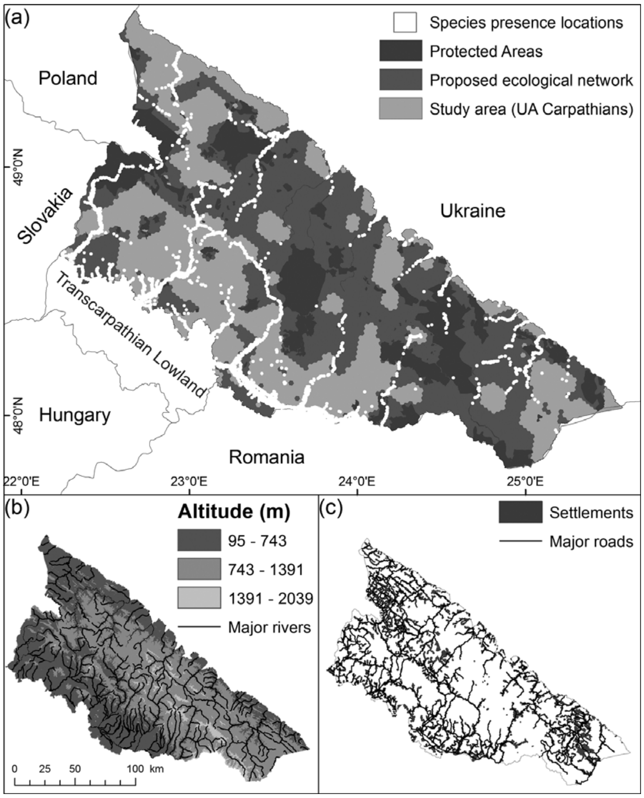

**Figure 1** (*a*) Protected areas/proposed ecological network, showing locations of all 11 invasive study species used for modelling, (*b*) altitude/hydrology, and (*c*) roads and settlements in the Ukrainian Carpathians.

alien plant species established for over a century in the adjacent lowlands and spreading to the interior of the mountains, including existing and proposed conservation areas (Protopopova & Shevera 1998; Protopopova *et al.* 2006). The UA Carpathians are rich in biodiversity (Tasienkevych 2008; Prots & Kagalo 2012), and over 200 000 ha of protected areas (PAs) have been established (Fig. 1*a*; Keeton & Crow 2009; Prots *et al.* 2010). The Carpathian Convention, established in 2003 to promote sustainable development in the Carpathian Ecoregion, gathered data on biodiversity, landscape features and human development to develop ecological networks in the Romanian, Serbian and UA Carpathians, with the aim to maintain and restore migration corridors between areas of high biodiversity value (Zingstra *et al.* 2009). In the UA Carpathians, the network has been designed to contain the minimum area of overall habitat required to protect predefined high-value conservation features (such as species or interconnected habitats, including PAs, and ecosystem processes) effectively, while being situated in regions that removed from centres of high anthropogenic pressure (Zingstra *et al.* 2009). Over 40% of the UA Carpathians are included in the proposed network, in addition to established PAs (Fig. 1*a*; Zingstra *et al.* 2009; Deodatus & Protsenko 2010).

Meanwhile, the spread of the invasives outside and inside PAs has been facilitated by anthropogenic disturbances to natural ecosystems, changes to land use in the post-Soviet era and agricultural mismanagement (Török *et al.* 2003; Keeton & Crow 2009; Prots & Drescher 2010; Baumann *et al.* 2011). Invasive plant species are found at high densities in close proximity to urban centres, major highways and riparian habitats in the Carpathian foothills and mountain valleys, and disperse into PAs along the frequently disturbed linear corridors, but human settlements and roads, and thus sources of propagule pressure and disturbance (particularly as development and agriculture are not properly regulated by authorities), can also be found within PAs and the ecological network (Fig. 1*c*). The entire mountain range is well connected through a vast network of roads and rivers (Nazarov *et al.* 2001; see Fig. 1*b*, *c*). Plant invasions are likely to intensify in the future, as average monthly temperatures and human infrastructure development in the UA Carpathians as a whole (such as urbanization, road construction and deforestation) and within PAs (foremost tourism) are projected to increase (Nazarov *et al.* 2001; Webster *et al.* 2001; Turnock 2002; Bartholy *et al.* 2011). An increase in average monthly temperatures may widen the suitable niche space of the invaders (Pauchard *et al.* 2009), while higher propagule pressure and more frequent anthropogenic disturbance regimes may contribute to the successful introduction and establishment of invasive plants and facilitate their spread, for example by removing natural vegetation and enriching soils (Price 2006; Pauchard *et al.* 2009).

However, despite increasing trends of plant invasion, the spatial features, future trends and biodiversity implications of the ongoing invasion process have not been considered sufficiently. Investigating this process is of particular importance because the establishment and subsequent spread of invasive plants in areas of high conservation value has been shown to have negatively affected biodiversity in other mountainous areas (Reinhart *et al.* 2001; Weaver *et al.* 2001; Muñoz & Cavieres 2008), and these impacts may be amplified in the wake of climate change and increases in anthropogenic pressures (Drake *et al.* 1997; Dukes & Mooney 1999; Dukes 2000; Nagel *et al.* 2004; Thuiller *et al.* 2007; Pauchard *et al.* 2009; Stohlgren *et al.* 2011).

In this paper, we use Maxent, a species distribution modelling software package designed to work with presence-only data (Elith *et al.* 2011), to predict future habitat suitability within the UA Carpathians for 11 widespread and potentially harmful (in terms of loss of local floral diversity; Botta-Dukàt & Balogh 2008) alien invasive plant species. The model uses six predictor variables, representing gradients in climate, topography and disturbance/propagule pressure to produce projections for future change scenarios, assuming seasonal temperature increases of $\leq 1.8\,^{\circ}$C and $\leq 3.8\,^{\circ}$C, and increases in anthropogenic disturbances of 10% and 30% for the years 2050 and 2100, respectively.

We hypothesized that, under current environmental conditions, conservation areas were susceptible to invasion by alien plants and that habitat suitability within these areas would increase dramatically in the future. Given that climate, topographic and anthropogenic predictors limit the distribution of suitable habitats for species establishment, we sought to assess the potential intensity (in terms of species and area) of invasion in areas of high conservation importance for both current predictor values and values modified to approximate future climate change and intensification of anthropogenic disturbance.

## METHODS

### Study area

The study area encompasses the entire range of the UA Carpathians (48°32′ N, 23°38′ E), which extend over an area of 24 000 km$^2$. The study area lies at an altitude of 95–2030 m, although 94% of the mountains are < 1200 m (Fig. 1*b*). The highest elevations are located in the southern parts of the UA Carpathians, while the south-west (bordering Romania), west (bordering the Transcarpathian Lowland of Ukraine) and north-west (bordering Poland) Carpathians are characterized by extensive valley systems and relatively gentle slopes. Precipitation of 500–1400 mm yr$^{-1}$ feeds a dense network of rivers (Fig 1*b*; Holubets *et al.* 1988). The July (warmest month) temperature varies from 20° C at the southern edge of the Carpathians and 18° C in the north to 6° C on the highest peaks (Herenchuk 1968; Kuemmerle *et al.* 2009). Winter temperatures range from –3° C to –10° C. The mountains are dominated by *Fagus sylvatica* and *Picea abies* forests, replaced by *Pinus mugo* and *Juniperus communis* in the subalpine and grasslands in the alpine belts (Herenchuk 1968; Kuemmerle *et al.* 2009).

### Study species

Using the Alien Plant Ranking System (APRS) developed by the Northern Prairie Wildlife Research Center (APRS Implementation Team 2000) and taking into account reports by regional experts (Botta-Dukàt & Balogh 2008), we determined the 11 potentially most harmful (to local biodiversity) alien invasive plant species to be *Acer negundo* L., *Ambrosia artemisiifolia* L., *Echinocystis lobata* (Michx.) Torr. & Grey, *Helianthus tuberosus* L., *Heracleum sosnowskyi* Manden, *Impatiens glandulifera* Royle, *Reynoutria japonica* Houtt., *Reynoutria* × *bohemica* Chrtek. & Chrtková, *Robinia pseudoacacia* L., *Solidago canadensis* L. and *Solidago gigantea* Aiton. All species, with the exception of *A. artemisiifolia* and *H. sosnowskyi*, were intentionally introduced to Central and Eastern Europe in the 18th and 19th centuries, eventually escaped controlled cultivation, and established self-replicating populations by the beginning of the 20th century (Botta-Dukàt & Balogh 2008). The species share similar physiological and life history traits (Appendix 1, Table S1, see supplementary material at Journals.cambridge.org/ENC; Walter *et al.* 2005; Weber & Jacobs 2005; Botta-Dukàt & Balogh 2008; Kabuce & Priede 2010). All species exhibit fast growth and relatively high reproductive rates. In addition, all species have wide ecological niches and successfully use water and anthropogenic vectors for long-distance dispersal. All the invasives, with the exception of *A. artemisiifolia*, *E. lobata* and *H. sosnowskyi*, reproduce vegetatively.

Combinations of these traits may contribute to competitive dominance of the invasives particularly in early successional habitats (Sakai *et al.* 2001; Pyšek & Richardson 2007), and populations of the species have been shown to negatively affect ecosystem composition and/or function in temperate invaded habitats outside the UA Carpathians (Botta-Dukàt & Balogh 2008). For example, *A. negundo* can spread rapidly in disturbed riparian habitats and is known to prevent regeneration of poplar and willow communities (Mędrzycki 2007). Meanwhile, dense stands of *I. glandulifera*, another invader of riparian habitats, tend to destabilize riverbanks as the shallow roots of the plants (10–15 cm) do not hold soil efficiently, thus altering abiotic conditions (Hejda & Pyšek 2006; Prots & Drescher 2010). It must be noted, however, that the impacts of invasive species are largely unquantified in the UA Carpathians and thus require further research.

### Data on species' presence

Several hundred presence records for each of the selected species (Table 1; Fig. 1*a*) were collected in the field, reviewed in the literature, and supplemented with reliable herbaria records from the University of Lviv (LW), the University of Uzhgorod (UU), the State Museum of Natural History in Lviv (LWS), and the University of Chernivtsi (CHER). Each of the species was modelled individually, with the exception of *Solidago* spp. and *Reynoutria* spp. The study species within each of these two genera are very similar in physiology and have overlapping niches in the study region (B. Prots, personal observation; see also Balogh 2008; Botta-Dukàt & Dancza 2008), and it is thus likely that mistakes exist in older datasets (literature data and field vegetation records) in identifying the genera as separate species. We therefore modelled these genera as one complex.

All data were available in a presence-only format. For each species/genus, the majority (> 80 %) of records originated from georeferenced (precision $\geq$ 10 m) field samples with an approximate mean distance between neighbouring locations of > 1000 m. Of these, 90 % were collected along major environmental gradients relevant to the current distribution of the species (that is, climate and location in relation to water and anthropogenic structures) in order to prevent sampling bias (see Phillips *et al.* 2009). The remaining samples consisted of locations identified in herbaria records and confirmed through field observation. Only locations where permanent populations have become established (occupying a sampling unit of 50 m$^2$ in consecutive years) were included in the modelling in order to minimize model inaccuracies due to casual opportunistic observations.

**Table 1** Maxent model results for 11 invasive plant species in the Ukrainian Carpathians - Model performance (AUC score) and relative importance of predictors (in per cent). Potentially highly invasive species, number of presence locations used for Maxent modeling, average model training and test AUCs, and permutation importance for the six predictor variables used for model fitting (in per cent; higher values indicate greater decrease in model performance if predictor is randomly permutated) are shown. Maxtwarm = 40-year average maximum temperature (°C) of the warmest month; mintcold = 40-year average minimum temperature (°C) of the coldest month; s_dist_sett_r - proximity (m) to roads and settlements; s_dist_water = proximity (m) to water bodies; slope = slope (°); sat = yearly sum of daily average active temperatures (°C) above 10° C.

| *Study species* | *No. of presence locations* | *Average training AUC* | *Average test AUC* | *Relative predictor importance (in %)* | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | *Maxtwarm* | *Mintcold* | *s_dist_sett_r* | *s_dist_water* | *Slope* | *Sat* |
| *Acer negundo* | 339 | 0.9699 | 0.9648 | 39.9679 | 0.7244 | 23.0268 | 5.7027 | 24.635 | 5.943 |
| *Ambrosia artemisiifolia* | 240 | 0.9711 | 0.9679 | 19.7075 | 0.5462 | 73.6679 | 1.1455 | 3.8306 | 1.102 |
| *Echinocystis lobata* | 367 | 0.9646 | 0.9599 | 31.9117 | 1.5186 | 20.4464 | 16.6179 | 24.819 | 4.686 |
| *Helianthus tuberosus* | 343 | 0.961 | 0.956 | 44.4308 | 1.3147 | 22.4974 | 11.6552 | 14.357 | 5.745 |
| *Heracleum sosnowskyi* | 563 | 0.9363 | 0.9288 | 1.9799 | 18.0262 | 46.4527 | 12.4737 | 15.387 | 5.681 |
| *Impatiens glandulifera* | 265 | 0.962 | 0.9564 | 29.4562 | 3.1003 | 39.8922 | 18.8685 | 6.5673 | 2.115 |
| *Reynoutria* spp. (*R. japonica*, *R. × bohemica*) | 581 | 0.9464 | 0.941 | 64.0463 | 3.4088 | 13.4029 | 6.6347 | 8.7031 | 3.804 |
| *Robinia pseudoacacia* | 365 | 0.9477 | 0.9411 | 37.5732 | 1.8994 | 47.7752 | 3.145 | 5.2493 | 4.358 |
| *Solidago* spp. (*S. canadensis*, *S. gigantea*) | 330 | 0.9634 | 0.9583 | 26.0037 | 1.6831 | 52.2463 | 0.9185 | 16.8975 | 2.2507 |

## Distribution modelling: Maxent

Maxent modelling is a general-purpose machine-learning method for making inferences from incomplete information. The application has specifically been developed for presence-only data because it does not make assumptions about absences and has been shown to outperform other presence-only modelling methods (Phillips *et al.* 2006; Dudik *et al.* 2007; Franklin 2009; Elith *et al.* 2011). Given a set of grid maps where each pixel represents a local value of a predictor variable and a set of coordinate points depicting species presence, Maxent estimates two probability distributions, one of predictor variables ($z$) over presence locations, $f_1(z)$, and another of predictor variables across randomly chosen background points from the entire study area, $f(z)$, and then determines the values for the response variable (here, suitability of pixels within the study area for the establishment of an invasive plant species) by finding the most uniform distribution of suitable areas given the constraint that the expected value of each predictor under this distribution matches its empirical average at the set of presence locations. The rules, or functions, of how the probability distributions are determined and matched in multivariate space are described by the features, or linear transformations, of potentially complex relationships between the density of predictors and presence/background locations (Elith *et al.* 2011).

For each of the nine species/genera, 10 000 random background points were extracted from the study area, representing potential habitat. Due to the geomorphology and presence of extensive river and road systems within the study area, it was assumed that significant geographical barriers to the potential distribution of the invasives do not exist. Along with the background points, 80 % of the presence records were used for model fitting and 20 % for testing. Because the performance of the models is influenced by the particular partitioning step the software assigns to the data, this effect was minimized by running a 5k cross-validation. This method randomly divides the occurrence data into five equal-sized folds, and models are created leaving out each fold in turn. The omitted fold is used for evaluation. A final model run was made for each species using all the presence records for model fitting in order to derive the most robust classification for visual interpretation (Hernandez *et al.* 2006).

The AUC (area under the curve) statistic obtained by the receiver operating curve (ROC) was used to evaluate the performance of models (Phillips *et al.* 2006; see also Evangelista *et al.* 2008). The ROC plots model sensitivity on the $y$ axis against (1 – specificity) on the $x$ axis for all possible thresholds. Sensitivity is the fraction of presence locations correctly predicted to overlay suitable habitat, and specificity is the fraction of background locations correctly predicted to overlay unsuitable habitat (Fielding & Bell 1997). An AUC value of 0.9 indicates that 90% of the time when a presence and background location are drawn at random, the first will have a higher predicted suitability value than the second. The statistical significance of the AUC can be determined by comparing the results with random predictions, which would have an AUC of 0.5. Guisan *et al.* (2007) proposed a classification scheme to assess the significance of AUC values above 0.5, where AUC $>$ 0.90 $=$ excellent, 0.90 $>$ AUC $>$ 0.80 $=$ good, 0.80 $>$ AUC $>$ 0.70 $=$ useful, and AUC $<$ 0.70 $=$ poor (see also Swets 1988; Jeschke & Strayer 2008). However, because the AUC does not consider the significance of predicted probability values (Lobo *et al.* 2007), a Wilcoxon ranked sum test implemented with the stats package in the R statistical software (R Development Core Team 2011) was applied for each model to test whether the suitability predictions over presence locations had a higher score than a set of background predictions randomly sampled from the study area (Phillips *et al.* 2006).

Maxent also provides a permutation test to assess the relative importance of predictor variables. After a model had been calibrated using model-specific measures of variable contribution (expressed as coefficients), each predictor was in turn randomly permutated at the training points (presences and background) and the decreases in model performance (AUC) were recorded. Permutation values were normalized over all predictors (Phillips 2010; Table 1).

## Predictor variables

Initially, 20 bioclimatic and three topographic variables were available for modelling. Of the 20 bioclimatic variables, 19 were retrieved as ESRI grids from the WorldClim global database at a resolution of 1 km (Hijmans *et al.* 2005). The bioclimatic data were regional averages of climatic grids generated by thin spline interpolation of average (1960–1990) monthly climate data from global weather stations. The 20th bioclimatic variable, sum of active temperatures (annual sum of average daily temperatures $>$ 10° C; see Herenchuk 1968; Prots & Kagalo 2012) was interpolated, using the topo-to-raster function in ArcMap 10, from an ecoregion map of the UA Carpathians (original scale 1:200 000) that displayed climatic regimes within topographic zones. The three topographic variables were derived from vector maps (original scale 1:200 000) on hydrology, roads and settlements (Fig. 1*b*, *c*) and from a digital elevation model (DEM; original resolution of 30 m). The vector maps and DEM were provided by the Geography Department of the University of Lviv (Jarvis *et al.* 2006; Hostert *et al.* 2008; Kruhlov 2008; Kuemmerle *et al.* 2009; Deodatus & Protsenko 2010). Layers relevant to propagule pressure and disturbance, such as proximity to water and to settlements and roads, were derived from the hydrology map and the combined map on roads and settlements using the simple (Euclidean) distance function in ArcMap 10. Slope was derived from the DEM.

In order to maintain the spatial accuracy of the DEM, all other variables were rasterized or resampled (in the case of the WorldClim datasets) to a resolution of 30 m using the cubic resampling function in ArcMap 10. The resampling did not improve the resolution of the climatic datasets and was performed solely in order to create raster layers of the same size without generalizing, and thus losing, some of the spatial information provided by the layer with the finest resolution (Yates *et al.* 2010). All layers were projected onto the UTM grid, zone 34 with WGS84 datum.

Initial models were run with all variables, and consistently showed that removing irrelevant predictor variables significantly improved the performance of the models. Predictor selection followed three steps.

(1) Initial model: a model was run including all available predictors and the AUC values on training and test data were recorded.
(2) Ecologically-based predictor selection: predictors that approximated (i) limiting factors controlling the ecophysiology of the species and (ii) natural or human-induced disturbances were preferentially selected. For example, because invasive plant species were reported to be limited by extreme temperature regimes (Botta-Dukàt & Balogh 2008) and because precipitation was not a limiting factor in the UA Carpathians (Herenchuk 1968), bioclimatic variables depicting seasonal maxima or minima were selected over annual temperature means and over precipitation in general. Models were rerun with the limited set of predictors, and AUC scores were compared with those derived from the initial model.
(3) Permutation-test based predictor selection: predictors with the lowest permutation importance ($<$ 2 %) in step (2) were removed. A final run was then made and AUC scores were compared with those in previous steps. The scores showed that elimination of irrelevant variables across species had improved the model.

The final predictors were thus: minimum temperature of coldest month (mintcold) as a proxy for susceptibility to frost, maximum temperature of warmest month (maxtwarm) as a proxy for susceptibility to drought, sum of active temperatures $>$ 10°C (sat) as a proxy for length of the growing season, proximity to water (s_dist_water) as a proxy for soil moisture and natural disturbances/propagule pressure, proximity to settlements and roads (s_dist_sett_r) as a proxy for anthropogenic disturbances/propagule pressure, and slope (slope) as a proxy for topographic preference (Table 1; Fig. S1, Appendix 1, see supplementary material at Journals.cambridge.org/ENC, for an example of a Maxent probability model fitted to the six predictors).

## Climatic and land-use projections

We applied two simple projection scenarios based on temperature shifts by 2050 and 2100 and high and low anthropogenic pressures. Climate projections assumed the A1B scenario developed by the IPCC Special Report on Emission Scenarios (SRES): an estimated increase in $CO_2$ concentration levels of 532 ppm and 717 ppm by 2050 and

2100, respectively. Based on this scenario, the European ENSEMBLES project developed a series of regional climate models for Hungary (for details see Bartholy *et al.* 2009, 2011). Their calculations extended into the UA Carpathians and were used to adjust the bioclimatic predictor variables according to the proposed 30-year average increases in temperature: 1.8° C and 3.8 ° C in winter and 1.5 ° C and 3.5 ° C in summer for the periods 2021–2050 and 2071–2100, respectively. Based on these increases, new values for the bioclimatic variables were created through simple addition of the mean increases for each pixel value. For example, 18 and 38 were added to all values of mintcold (in ° C × 10) to create the new set of mintcold predictors used for projections for 2050 and 2100, respectively.

In addition, two simple future settings of anthropogenic pressure were developed: (1) disturbances along roads and settlements will not increase above the current level due to low economic development; and (2) more land around settlements and roads will be disturbed due to high economic development (for models of land-use change in Europe, see Rounsevell *et al.* 2006; Kuemmerle *et al.* 2008). Low and high economic development could also be linked to stronger and weaker nature protection, respectively. The former disturbance setting determined the model projection scenario CL: changes in the climatic regimes for 2050 and 2100 were modelled without incorporating changes to the variables approximating anthropogenic disturbances/propagule pressure. The latter disturbance setting determined the model projection scenario CL&HED: climatic changes were combined with a net decrease in the distance to any given potential human disturbance point because there would be more such points and the impact of existing points may be greater (for a similar approach see Rouget & Richardson 2003). That is, for any pixel in the study area, the distance to roads and settlements that had been determined for current conditions decreased by 10 and 30 % by 2050 and 2100, respectively. A paired Wilcoxon signed-rank test (in R) was applied to test whether there was a significant range expansion across species under projections.

The four projections (CL and CL&HED by 2050 and 2100) developed for this study are purely illustrative and are primarily intended to portray general trends in the potential of the study species to profit from climate and land-use changes.

### Distribution of suitable habitat in protected areas and the ecological network

In order to quantify the impacts of invasion in PAs and the ecological network in terms of proportion of total area, or pixels, potentially suitable predictions for current distributions and future projections calibrated on all presence points were transformed into binary suitable (= 1) and unsuitable (= 0) values using an optimized threshold based on the ROC curve which maximized sensitivity plus specificity. This approach has been shown to perform well, but is sensitive to low prevalence of occurrence data, which is assumed to be the case here (Liu *et al.* 2005). Since information about prevalence could not be derived due to lack of absence data, the results must be considered as relatively conservative binary estimates. Comparisons between species were accomplished by overlaying the binary predictions. Areas that are suitable for one or more species within PAs, thus indicating the range of invasion risk and potential impacts on biodiversity, could then be quantified for current conditions. For future projections, the proposed ecological network was assumed to be a part of areas of high conservation value alongside current PAs.

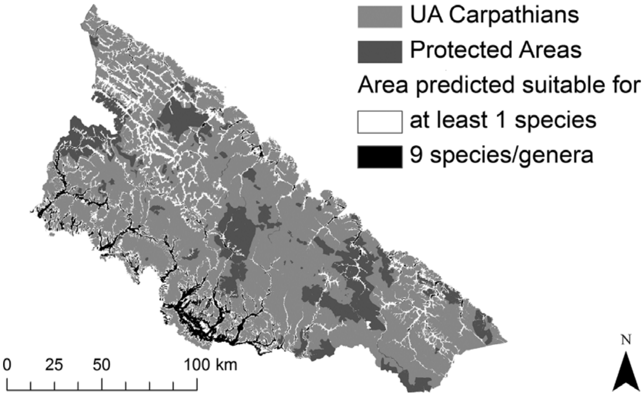

**Figure 2** Spatial distribution of suitable habitats for potential establishment of at least one or nine invasive plants/genera within the study area and within protected areas under current environmental conditions as determined by the Maxent models.

## RESULTS

With AUC values consistently > 0.9 (Table 1) for both training and test data, the predictive performance of the models was excellent. All predictions of habitat suitability were statistically significant ($W > 5\,000\,000$, $p < 0.001$). All predictor variables contributed significantly to model performance, but the relative importance of predictors varied across species and could be explained by species-specific niche preferences.

Binary predictions of habitat suitability clearly suggested a spatial aggregation of suitable habitats for establishment of the species within the study area (Fig. 2). Of the pixels predicted as suitable for the establishment of at least one species in PAs (8 % of the total number of pixels comprising the area within PAs), 13 % overlapped for all nine species (Fig. 2).

The spatial distribution of sites suitable for establishment of all nine species/genera showed a preference for major linear habitats along rivers and roads that are in close proximity to centres of high anthropogenic pressure in moist and warm lowlands (up to *c.* 700 m altitude), namely in the south-west (Upper Tysa Depression and Cirocha-Rika Low Mountains), west (Vyhorlat-Hutyn Volcanic Ridge) and, to a lesser degree, the east (Marginal Beskydy) and south-east (Marginal Gorgany) of the mountains (Fig. 3; Table 2). Suitability decreased at higher altitudes, and PAs at

**Table 2** Association between the prevalence of invasive plants (average number of all nine study species/genera per pixel) and mean values of maximum temperature of the warmest month (maxtwarm), distance to settlements and roads (s_dist_sett_r), and slope within each of the 33 geomorphologic regions in the Ukrainian Carpathians, listed in descending order by number of all nine study species/genera per pixel.

| Region | Nine species/pixel | Maxtwarm (C*10) | s_dist_sett_r (m) | Slope (degree) |
|---|---|---|---|---|
| 24. Upper Tysa Depression | 1.05 | 246.20 | 554.09 | 5.62 |
| 9. Cirocha-Rika Low Mountains | 0.17 | 237.49 | 797.99 | 10.58 |
| 15. Vyhorlat-Hutyn Volcanic Ridge | 0.13 | 235.16 | 1144.26 | 10.63 |
| 1. Marginal Beskydy | 0.05 | 218.84 | 800.13 | 8.79 |
| 10. Marginal Gorgany | 0.05 | 215.99 | 727.10 | 12.38 |
| 13. Latorytsia-Rika Verkhovyna | 0.04 | 213.28 | 481.15 | 12.88 |
| 20. Pokuttia-Bukovyna External Mountains | 0.04 | 220.18 | 1198.55 | 13.76 |
| 25. Rika-Apshytsia Cliff Mountains | 0.04 | 230.97 | 843.01 | 14.61 |
| 19. Brdo-Manchul Polonyny | 0.03 | 217.80 | 2140.58 | 19.57 |
| 29. Apshytsia-Kosivs'ka Low Mountains | 0.03 | 227.43 | 647.81 | 12.13 |
| 7. Ravka-Runa Polonyny | 0.02 | 210.61 | 1544.32 | 15.88 |
| 2. Dnister Beskydy | 0.02 | 211.68 | 742.89 | 10.58 |
| 8. Bukovets' Polonyny | 0.02 | 204.03 | 734.02 | 14.22 |
| 12. External Gorgany | 0.02 | 204.68 | 1628.24 | 15.71 |
| 27. Rakhiv Flysch Polonyny | $1.38 \times 10^{-2}$ | 200.30 | 2217.09 | 20.99 |
| 22. Hutsul Verkhovyna | $1.37 \times 10^{-2}$ | 207.60 | 838.60 | 12.25 |
| 4. External Beskydy | $1.17 \times 10^{-2}$ | 210.95 | 1143.55 | 13.54 |
| 16. Borzhava-Krasna Polonyny | $9.85 \times 10^{-3}$ | 204.33 | 2754.11 | 21.94 |
| 31. Rakhiv Crystalline Polonyny | $6.45 \times 10^{-3}$ | 206.06 | 2412.20 | 22.04 |
| 17. Internal Gorgany | $5.03 \times 10^{-3}$ | 189.49 | 2306.56 | 21.51 |
| 21. Pokuttia Gorgany | $3.57 \times 10^{-3}$ | 200.18 | 1253.38 | 18.69 |
| 5. Central Beskydy | $2.10 \times 10^{-3}$ | 199.53 | 2026.40 | 17.75 |
| 23. Svydivets' Polonyny | $7.61 \times 10^{-4}$ | 188.92 | 3066.20 | 19.08 |
| 28. Bukovyna Internal Mountains | $6.06 \times 10^{-4}$ | 204.50 | 1630.08 | 16.58 |
| 30. Hryniava Polonyny | $4.59 \times 10^{-4}$ | 196.64 | 1002.12 | 17.77 |
| 3. S'an-Stryi Verkhovyna | $3.95 \times 10^{-4}$ | 205.68 | 512.84 | 8.79 |
| 11. Beskydy Verkovyna | $2.80 \times 10^{-5}$ | 202.15 | 824.17 | 10.98 |
| 6. Internal Beskydy | $2.13 \times 10^{-5}$ | 197.77 | 1083.96 | 15.52 |
| 26. Chornohora Polonyny | $1.82 \times 10^{-5}$ | 183.36 | 2783.86 | 18.03 |
| 14. Central Gorgany | $6.60 \times 10^{-6}$ | 186.94 | 2800.98 | 19.62 |
| 18. Gorgany Verkhovyna | 0.00 | 191.30 | 2698.64 | 13.60 |
| 32. Chyvchyny Flysch Polonyny | 0.00 | 182.44 | 1637.59 | 18.50 |
| 33. Chyvchyny Crystalline Polonyny | 0.00 | 176.36 | 3339.36 | 15.28 |

altitudes > 700 m, characterized by relatively steeper slopes and exposed to fewer anthropogenic disturbances, were at lesser risk of being invaded. Furthermore, predictions did not extrapolate far beyond areas in which one or more of the study species were already established (compare Fig. 1 and Fig. 2).

Under the two scenarios, species may lose climatic and physical/environmental barriers that limit rapid spread today (Table 3). A strong and significant ($V = 0, p < 0.001$) increase in areas suitable for establishment across species was projected. The net gain of novel suitable habitats in the study area was significantly higher ($V = 0$, $p = 0.002$) under the scenario CL&HED than under the scenario CL for both 2050 and 2100. Decreasing the distance to points of anthropogenic pressure by 10% and 30% significantly increased the proportion of the total study area projected as suitable for species establishment (Table 3; Fig. 4). By 2100 (scenario CL&HED), all species were expected to find suitable habitat in at least 20% of conservation areas, and for some invasives significantly greater area became available (for example *R. pseudoacacia* = 43.3%, *H. tuberosus* = 30.0%).

The interior of the UA Carpathians and PAs and the proposed ecological network at higher altitudes became increasingly suitable under a warming climate (Fig. 4). The ecological network may become susceptible to invasion as it extends far beyond current PAs and encompasses areas in the south, west, east and south-east that already function as aggregation centres for a large number of invasives (Figs 3 and 4).

By 2050, when solely climatic changes are expected, 25 % of the total conservation area (PAs and ecological network) was projected to be suitable for at least one species, an increase by 17 percentage points compared with predictions for current conditions. Of this area, 25% became suitable for the establishment of all nine species/genera. Including high economic development and thus increased anthropogenic pressure increased the projected range of establishment of at

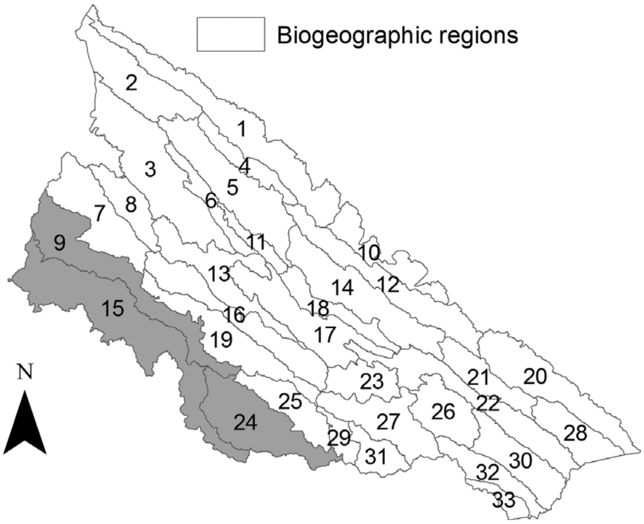

**Figure 3** Biogeographic regions within the Ukrainian Carpathians (see Table 2). Regions shaded grey contain the highest proportion of the nine invasive plant species/genera per pixel.

least one species slightly to 26%, but did not produce greater aggregation of suitable habitats for all nine species/genera (Fig. 4*b*). The majority of potential habitat.gained was in linear areas in the interior of the mountain range (namely in climatic zones that are currently unsuitable for the establishment of permanent populations). In areas that are highly suitable for invasion today, future projections suggested a lateral spread of species away from major linear habitats and along small waterways (Fig. 4*a*, *b*). Projections for 2100 demonstrated a continuation of this trend (Fig. 4*c*, *d*).

By 2100, suitable habitats had developed far into the interior of the mountain range, further increasing invasion risk in the central Carpathians and the south (for example in parts of Chyvchyny Crystalline Polonyny; see Table 2). Modelling climate change alone, 44 % of the total conservation area was projected to be suitable for at least one species, and 29 % of these areas were suitable for all nine species/genera. Under the assumption of high economic development by 2100, 47 % of ecologically valuable habitats were projected to be at risk of establishment of at least one species; of these at-risk habitats, 31% were suitable for all nine study species/genera (Fig. 4*d*). Major watersheds and roads in virtually all PAs and ecological networks were suitable for all nine species/genera; individual species may extend their ranges much further and invade a large number of smaller linear habitats. If current trends continue, by 2100 (under both scenarios), only the most remote parts of PAs at high elevations (such as parts of biogeographic regions Chornohora Polonyny and Internal Gorgany; see Fig. 3) were projected to remain free of invasion.

A comparison between the average habitat suitability gain across species within conservation areas (PAs/ecological network) and the study area as a whole revealed that a relatively greater gain in novel habitats was projected within conservation areas for the future change scenarios

**Table 3** Current modelled and future projected suitable habitats for invasive species within the Ukrainian Carpathians. Proportions of 30 × 30 m grid cells that contain suitable habitats in the entire study area (SA) and within protected areas (PA) are given for current predictions and future scenarios (CL = climate change; HED = high economic development). All projected models showed significant increases ($p < 0.001$) in suitable habitats for establishment of invasive species compared to predicted current suitable habitats.

| *Species* | *Area* | *Scenario* | | | | |
|---|---|---|---|---|---|---|
| | | *Current* | *2050 CL* | *2050 CL&HED* | *2100 CL* | *2100 CL&HED* |
| *Acer negundo* | SA | 0.076 | 0.166 | 0.171 | 0.240 | 0.277 |
| | PA | 0.02 | 0.136 | 0.224 | 0.213 | 0.249 |
| *Ambrosia artemisiifolia* | SA | 0.098 | 0.167 | 0.175 | 0.236 | 0.280 |
| | PA | 0.024 | 0.121 | 0.127 | 0.194 | 0.233 |
| *Echinocystis lobata* | SA | 0.091 | 0.153 | 0.157 | 0.218 | 0.246 |
| | PA | 0.029 | 0.118 | 0.121 | 0.184 | 0.209 |
| *Helianthus tuberosus* | SA | 0.107 | 0.185 | 0.191 | 0.304 | 0.350 |
| | PA | 0.04 | 0.143 | 0.148 | 0.258 | 0.3 |
| *Heracleum sosnowskyi* | SA | 0.152 | 0.247 | 0.256 | 0.315 | 0.358 |
| | PA | 0.06 | 0.196 | 0.203 | 0.257 | 0.296 |
| *Impatiens glandulifera* | SA | 0.115 | 0.153 | 0.158 | 0.218 | 0.249 |
| | PA | 0.052 | 0.117 | 0.121 | 0.181 | 0.209 |
| *Reynoutria* spp. (*R. japonica*, *R.* × *bohemica*) | SA | 0.113 | 0.170 | 0.175 | 0.290 | 0.330 |
| | PA | 0.044 | 0.126 | 0.129 | 0.249 | 0.285 |
| *Robinia pseudoacacia* | SA | 0.135 | 0.276 | 0.282 | 0.491 | 0.525 |
| | PA | 0.044 | 0.193 | 0.197 | 0.406 | 0.433 |
| *Solidago* spp. (*S. canadensis*, *S. gigantea*) | SA | 0.083 | 0.145 | 0.151 | 0.258 | 0.304 |
| | PA | 0.025 | 0.1 | 0.103 | 0.21 | 0.25 |

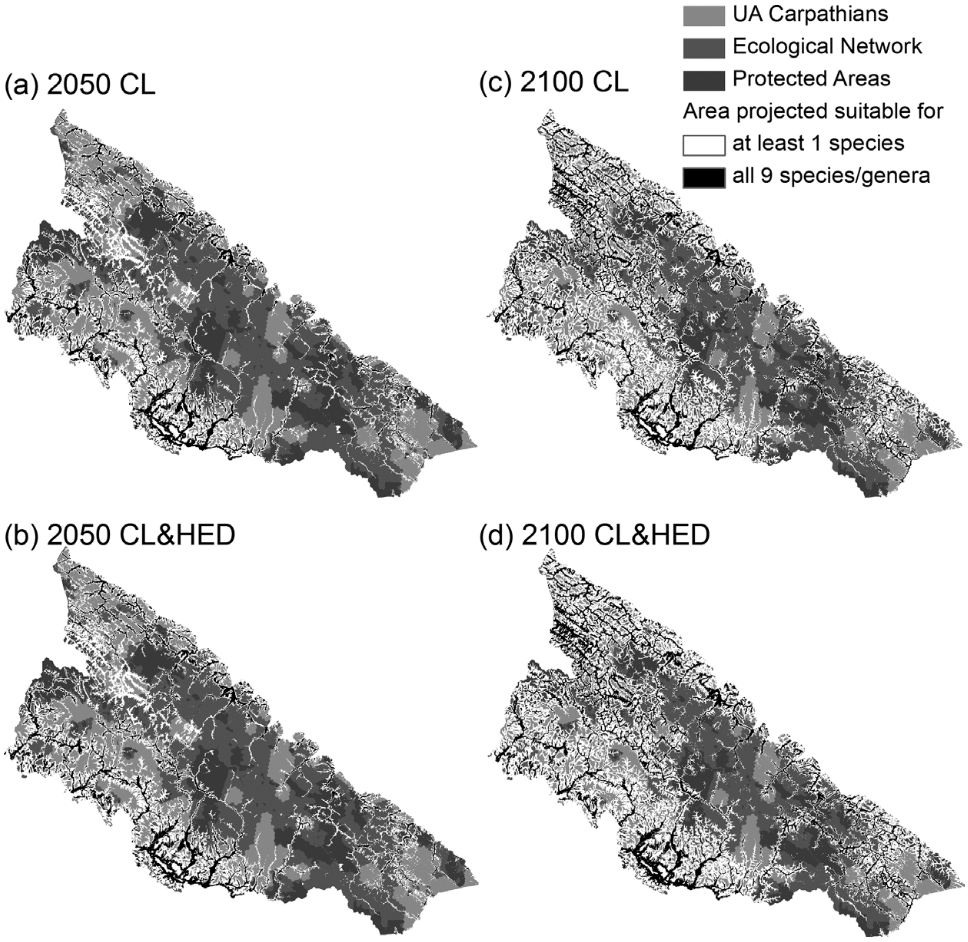

**Figure 4** Projected spatial distribution of suitable habitats for establishment of at least one or nine invasive plant species/genera by (*a*, *b*) 2050 and (*c*, *d*) 2100 within the study area and within protected areas and ecological network assuming (*a*, *c*) climate change (CL) and (*b*, *d*) climate change and high economic development (CL&HED).

(Fig. 5), although, for each species, relatively more pixels were projected to be suitable in the study area compared to conservation areas (Table 3). By 2100, under scenario CL&HED, conservation areas gained 24 % in potentially suitable habitats, as opposed to 22 % in the whole study area. For the same scenario meanwhile, 27 % of the area within conservation areas was on average projected to be suitable, five percentage points less than within the entire study area. A close examination of the spatial patterns of projected potential invasion revealed that the design of ecological networks at low to medium elevations (namely in regions of extensive projected gain in suitable habitats) was responsible for the relatively greater increases in potential invasion risk within conservation areas (compare Figs 1 and 4).

## DISCUSSION

The habitat suitability modelling suggests a potentially great expansion of the 11 alien invasive plant species in the Ukrainian Carpathians, reaching the subalpine line and occurring along virtually all major linear and/or frequently disturbed habitats in the mountains over the next 100 years. The consistently high permutation importance given to predictors depicting disturbances and the spatial patterns of potential migration into the interior of the UA Carpathians along rivers and roads emphasize the importance of these linear habitats for the establishment of propagating populations of invasives (Prots & Drescher 2010; Tickner *et al.* 2011). Although fewer sites are predicted/projected to be at risk of invasion by all nine study species/genera in protected areas (PAs), all PAs are at an increasing risk of being invaded by at least one species. In particular, habitat suitability is projected to increase dramatically at low and medium altitudes by 2050 and 2100, while the ecological network connecting PAs is proposed to cover many of these high-suitability areas.

A crucial step in designing the ecological network was to divide the mountain range into units (approximately 815 × 815 m) of low (0) to high (50) potential to meet conservation targets (Zingstra *et al.* 2009). Potential invasibility is generally concentrated in units of low conservation value (low potential to meet targets), which correspond to areas outside of PAs and the proposed ecological network; these were assigned conservation values of > 10 (Zingstra *et al.* 2009). At the same time, units of highest priority for conservation (value 50) are also relatively more exposed to invasives (Fig. 6).

Under current conditions, almost 40 % of these units are predicted to contain suitable habitat for at least one study species and over 15 % for all nine species/genera (Fig. 6). These 'high-conservation-high-potential-invasibility' units occur particularly along freshwater habitats at low altitudes

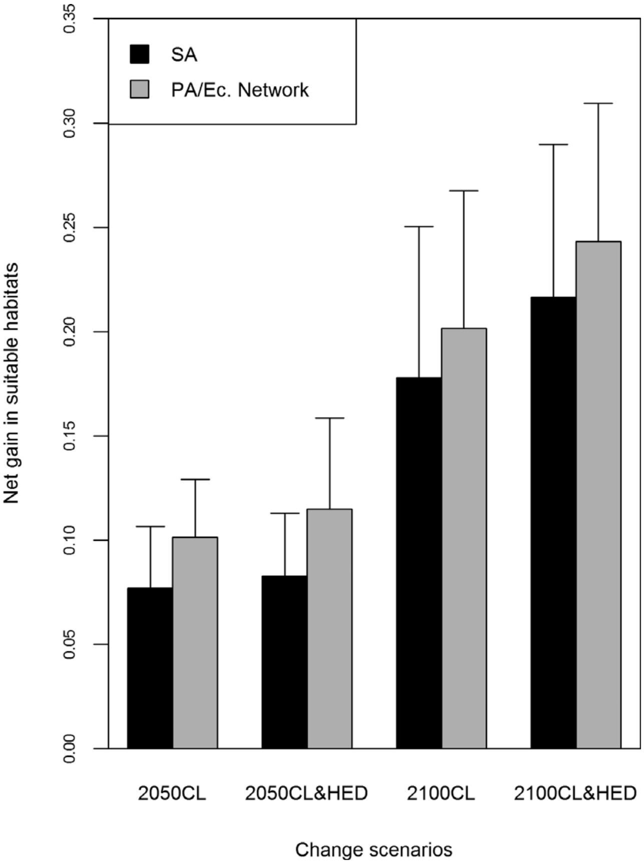

**Figure 5** Comparison of average net gain in suitable habitats across species (proportion of area occupied under future change scenario – proportion of area occupied under current conditions) within the study area (SA) and protected areas (PA, including ecological [Ec] network). CL = climate change scenario, CL&HED = scenario of climate change plus high economic development.

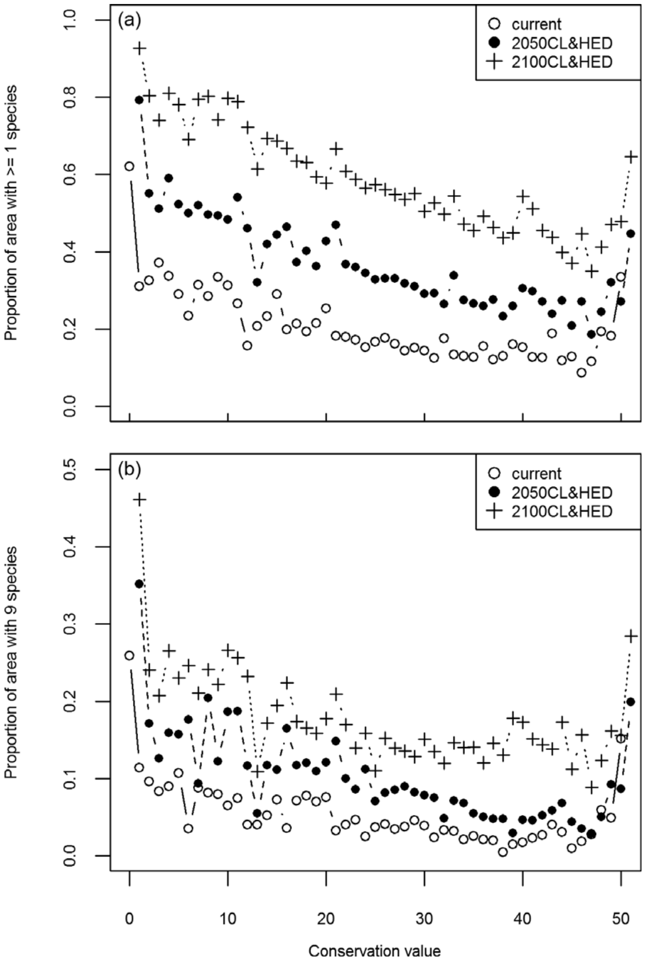

**Figure 6** Invasibility of regions with different conservation values by (*a*) at least one invasive plant species and (*b*) all nine species/genera modelled with Maxent under current environmental conditions and future projections. Invasibility is shown as proportion of total units of a specific conservation value (0–50) within the Ukrainian Carpathians in which at least one or all nine invasives can potentially occur (CL&HED = climate change plus high economic development).

in the south, south-west and east (Fig. 4; Zingstra *et al.* 2009). This suggests that invasive plants are highly likely to become a permanent feature of ecosystems within the currently proposed network if the observed increasing spread continues (Prots & Drescher 2010). Because the invasive species might alter the structure and functioning of natural and semi-natural ecosystems (Botta-Dukàt & Balogh 2008), the potential susceptibility of protected areas and the ecological network to invasion is alarming.

However, the Maxent models used in this study to estimate habitat suitability depict potential establishment sites and not likelihood of invasion, as they do not consider community interactions (such as competitive exclusion) once propagules reach the suitable habitats, or dispersal mechanisms that may facilitate or slow the spread into suitable habitats (Austin 2002; Evangelista *et al.* 2008; Dullinger *et al.* 2009). In addition, projections assumed static niche preferences of the species, although genetic adaptations and thus potential spread into wider habitats can by no means be ruled out (Lavergne & Molofsky 2007; Dlugosch & Parker 2008; Clements & Ditommaso 2011).

## From potential to probable spread

The issue of leaving out covariates related to dispersal, interactions with native species, and adaptation, all of which in part explain the current distribution of the study species, becomes evident by running a Moran's I correlogram (Fortin *et al.* 2006) on model residuals (1 – predictions on presence locations), which, on average, shows significant spatial autocorrelation ($p < 0.001$) at distance categories of 1000–10 000 m (1000 m intervals; spatial weight based on inversed distance). Spatial autocorrelation in the model residuals may be explained by missing predictors on adaptation, community interactions or dispersal (Legendre 1993; Dormann *et al.* 2007) and must be investigated in future studies. In general, detailed genetic and demographic studies on the invasive species to approximate future migrations (see for example

Genton *et al.* 2005; Jongejans *et al.* 2008) and integrative approaches to estimate the likelihood of establishment given habitat suitability and dispersal/community dynamics (see for example Wadsworth *et al.* 2000; Nenzén *et al.* 2012; Smith *et al.* 2012) are needed.

Meanwhile, despite a lack of quantitative data on dispersal within the UA Carpathians, the invasive species at the focus of this study have been chosen precisely because they are successful colonizers and long-distance dispersers that use waterways and/or humans for dispersal of propagules and vegetative parts (Williamson *et al.* 2005; Botta-Dukàt & Balogh 2008). In addition, most areas within the study region are relatively easily accessible and connected via an extensive hydrological network and road system that facilitates potential plant invasions. Thus, species-specific traits and area-specific spatial composition indicate that the study species are likely to reach most, if not all, suitable habitats for establishment, including PAs and the ecological network where, despite protection of riparian habitats, natural disturbances (such as floods) may lead to establishment of invasives, given the availability of progagules (Pyšek & Prach 1994). Model predictions for current conditions do not extend far beyond areas in which one or several species already occur (compare Fig. 1 and Fig. 2).This supports the hypothesis that the species are highly successful in dispersing across the invaded range.

Similarly, although systematic studies on the genetic composition of populations are needed, many of the species have been chosen for this study due to their high potential for rapid evolutionary adaptations (see Bailey *et al.* 2007; Chun *et al.* 2011; Erfmeier *et al.* 2011). Populations of *Heracleum sosnowskyi* have increasingly been observed spreading into grasslands and secondary forests away from linear habitats (B. Prots, personal observation). Thus, a precautionary management approach would consider potential spread of the study species and hence the impact on ecosystems beyond current suitable habitats. In addition, future spread of the invasives beyond the areas estimated as suitable by Maxent is likely because the data on predictors used for model calibration stem from a restricted part of the species' ranges. This leads to an underestimation of the climatic niche (Guisan & Zimmermann 2000; Franklin 2009) and increases the probability that PAs will be affected more seriously under climate change.

Given the high risk of invasion of suitable habitats, analyses of potential introduction of the invasive species into PAs must be incorporated into strategies to protect biodiversity and must be included in the support of the ecological network (Townsend & Levey 2005; Zingstra *et al.* 2009).

### Future change projections

Although potential range expansions of invasive plant species under climate and land-use change have been shown in several studies (see Ficetola *et al.* 2010; Murray *et al.* 2012), projections of potential species distributions must be interpreted with care in this study. First, climate projections used here apply to only one scenario and do not evaluate the range of potential trajectories in regional climate change and thus in potential species distributions. In addition, by adding one value across all climatic pixels for projections, regional differences in climate change, for example between the north-east and south-west, are generalized.

Second, this study does not incorporate detailed scenarios of land-use change and human population development. That is, changes in disturbances/propagule pressure are modelled as intensification (by 10% and 30%) of current spatial patterns for these processes (such as proximity to existing human development). In reality however, changes in disturbances influencing the potential distribution of invasives are expected to be spatially highly dynamic (Verburg *et al.* 1999; Rounsevell *et al.* 2006). Within the study area, increasing illegal forestry practices (Sitko and Troll 2008; Kuemmerle *et al.* 2009), urban and infrastructure development at lower altitudes, and farmland abandonment in the interior of the mountain range (Turnock 2002; Baumann *et al.* 2011) are also important processes. While illegal forestry and urban and infrastructure development increase the likelihood of the introduction, establishment and dispersal of invasives (Colautti *et al.* 2006), farmland abandonment may permit the regeneration of natural communities that act as buffers to invasion (Shea & Chesson 2002). Pauchard *et al.* (2009) observed that plant invasions in mountain regions become problematic in open sites. Thus, a road leading from a focal area of current plant invasion to a deforested patch may provide a corridor for invasives to the open area. In PAs, projected increasing investments into tourism (Webster *et al.* 2001) may create novel suitable habitats for invasives beyond current linear trajectories (see for example Dickens *et al.* 2005).

## CONCLUSION

Regional climatic and land-use projection models at a finer resolution are urgently needed for the UA Carpathians in order to develop more detailed and realistic species distribution projections. Nevertheless, our simple projections clearly illustrate that, given the apparent dispersal success of the 11 study species, invasion of areas of high conservation value is likely if current trends continue, and eradication of invasive species is highly unlikely. Current conservation planning in the UA Carpathians must be amended to include the long-term presence and management of invasive species in PAs and the ecological network.

## ACKNOWLEDGEMENTS

We thank Dr Ivan Kruhlov (Lviv), Dr Tobias Kuemmerle (Berlin), Dr Patrick Hostert (Berlin), Dr Yuriy Andreychuk (Lviv), and Dr Taras Yamelynets (Lviv) for allowing us to use their grid and vector maps on the Ukrainian Carpathians and for providing advice during our studies.

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