Determining the potential distribution of highly invasive plants in the Carpathian Mountains of Ukraine: a species distribution modeling approach under different climate-land-use scenarios and possible implications for natural-resource management

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Independent Graduate Project Report – December 2011
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ABSTRACT

Background: The Ukrainian Carpathian Mountains are one of the most species-rich ecoregions in Europe. High levels of biodiversity can be explained by the heterogeneous geomorphology of the mountain range, its geographic location bridging the Western and Eastern Carpathians, a moderate climate and ample precipitation, and traditional, extensive land use. The introduction and spread of non-native invasive plant species however threatens biodiversity and negatively impacts the structure and functioning of natural and semi-natural ecosystems.

Highly Invasive Plants in the Ukrainian Carpathians: Eleven highly aggressive invasive plant species are the subjects of this study: *Acer negundo* L., *Reynoutria japonica* Houtt., *Reynoutria x bohemica* Chrtek.& Chrtková, *Echinocystis lobata* (Michx.) Torr. & Grey, *Impatiens glandulifera* Royle, *Heracleum sosnowskyi* Manden, *Robinia pseudoacacia* L., *Helianthus tuberosus* L., *Solidago canadensis* L., *Solidago gigantea* Aiton, and *Ambrosia artemisiifolia* L. These species share several interconnected characteristics common to successful invaders: (a) inherent competiveness, (b) occupation of an empty niche, and (c) strengthening of competitive ability due to release from enemies and (d) due to mutualism in the invaded range. Meanwhile, the invasibility of the study area is determined by a favorable climate, an extensive network of linear habitats (rivers and roads) and high levels of disturbances along these habitats as well as in and around human settlements. Simultaneously, invasive plant species are expected to profit from the interactions of future land-use intensification and increases in atmospheric CO_2 concentrations.

Species Distribution Modeling (SDM): This study aims to model/predict suitable habitats for the introduction and establishment of invaders and to determine the contribution of different climatic and anthropogenic factors to the particular patterns of predictions for current environmental conditions and potential future spread under different scenarios. SDM determines habitat suitability by relating the response variable, georeferenced occurrences of species in the Ukrainian Carpathian Mts., to underlying environmental predictor variables through various logistic functions and then extrapolating the fitted models to the entire study area. The choice of predictor variables and ecological interpretation of the outputs are based on the species niche concept and the theory of equilibrium of ecological states. Different algorithms are used on each species because results tend to reflect not only the species' ecology but also differences in modeling approaches between algorithms.

Methods: The study area on which the output of the models is defined is the entire Ukrainian Carpathian Mts.. The response variables are in presence-only format. Six predictor variables are chosen based on expert knowledge of the ecology of the species and on preliminary statistics on the goodness-of-fit of the models. They are: minimum temperature of coldest month (*mintcold*), maximum temperature of warmest month (*maxtwarm*), sum of active temperatures > 10°C (*sat*), proximity to water (*s_dist_water*), proximity to settlements and roads (*s_dist_sett_r*), and slope (*slope*). Two software applications, Maxent and BIOMOD, are used to fit the models and extrapolate to the entire study area. The accuracy of the model predictions is measured with the threshold-independent ROC curve. Predictions are projected onto four future scenarios: (i) climate change/low economic development by 2050; (ii) climate change/high economic development by 2050; (iii) climate change/low economic development by 2100; and (iv) climate change/high economic development by 2100. The significance of predictions and projections is tested with the *Wilcoxon ranked sum test* and *paired Wilcoxon signed-rank test*.

Results: All AUC values are statistically significant, and the spatial distribution of predictions is similar in Maxent and BIOMOD. Under current climatic and land-use patterns, all algorithms predict suitable habitats for establishment to be aggregated in the southwest, east, and northeast along large rivers and roads at elevations up to approximately 600 m above sea level. Taking correlation between climatic variables into account, the spread of species is primarily limited by warm temperatures or proximity to humans, and the aggregation of favorable values of both groups at low elevations in the southwest, east, and southeast explains the spatial patterns of habitat suitability predictions. For all future change scenarios, suitable habitat ranges are predicted to increase significantly. The net gain of novel suitable habitat is significantly higher under scenarios ii and iv than under i and iii, suggesting that the higher the proposed rate of human development, the more suitable habitat is projected to be gained by all species. The differences between algorithms are significant for some species when projecting, but a general trend is discernible: species that become established in a variety of soils and habitats tend to gain more suitable habitat under future scenarios than more specialist species establishing exclusively along rivers. All species are expected to migrate to higher elevations along linear habitats and to expand laterally from habitats predicted as suitable for current conditions.

General Implications for Natural-Resource Management: The eleven invasive plant species have already established viable populations in the regions predicted to contain suitable habitats. Invasion of protected areas is likely if current trends continue and monitoring of areas of high conservation values can be efficiently accomplished using the results of this study as guides to prioritize monitoring efforts. Furthermore, inquiries of why a species is predicted to occur at a certain location and which high-risk locations (in terms of invasibility) are in need of particularly sensitive natural-resource management that reduces anthropogenic pressures can be answered by analyzing the relative importance of predictor variables to habitat suitability. Lastly, the maps produced in this study can be utilized to educate the general public and demand forestry practices and forms of tourism development that minimize the chances of the invaders to spread farther into the mountains.

1. INTRODUCTION

A nonindigenous (non-native) plant is one that is present in an ecosystem only as direct or indirect consequence of human activity; it is characterized as invasive when it establishes self-replicating populations, colonizes areas other than its introduced range, and adversely impacts the community in which it becomes established (Morse *et al*. 2004; Sakai *et al*. 2001; Richardson *et al*. 2000). The introduction and spread of non-native invasive plant species (NIPS here forth) is of great concern to natural resource managers because these species greatly contribute to **biodiversity**[1] loss of the native flora and fauna, alter ecosystem processes, and reduce the availability of ecosystem resources (Evangelista *et al*. 2008; Levine *et al*. 2003; Keane and Crawley 2002). This is why the spread of NIPS has been identified as one of the major causes of the current global species' extinction rates which surpass prehuman rates by a factor of 100-1000 (Chapin *et al*. 1998; Begon *et al*. 2006). Meanwhile, there are few landscapes that are not affected by invasion processes, and the rate of invasion, which Elton (1958) first brought to attention, has escalated in the last decades due to the intensification and globalization of trade, transportation, and migration of human populations (Protopopova *et al*. 2006; Chornesky and Randall 2003). The Carpathian Mountains are one of the regions in which biodiversity is threatened by the advance of NIPS.

The Carpathian Mountains cover an area of more than 200,000 km² in Central and Eastern Europe and are divided between seven countries: Czech Republic, Slovakia, Poland, the Ukraine, Romania, Hungary, and Serbia (Fig. 1). The importance of the Carpathians lies in the high level of biodiversity found in the ecoregion compared to other European mountain ranges. This is the reason why the World Wildlife Fund (WWF) classified the Carpathians "as one of 200 ecoregions globally outstanding for their biodiversity" (WWF Carpathian Programme 2007). Preservation of biodiversity can partly be explained by centuries of traditional land management accompanied by relatively low deforestation and development rates (WWF Carpathian Programme 2007).

The Eastern Carpathians located in the Ukraine (UA Carpathians here forth) mirror the ecological and economic importance of the whole Carpathian ecoregion. The UA Carpathians are home to virgin beech forests that are among the oldest in Europe, and, according to the WWF Carpathian Programme (2007), "with 2,012 species of vascular plants, the Eastern Carpathians are […], after Crimea, Ukraine's richest area in terms of flora." The mountains are also one of the last European bastions for the brown bear (*Ursus arctos*) and wolf (*Canis lupus*) (Keeton and Crow 2009). Furthermore, the wealth of natural resources has for centuries provided the basis for economic development in the form of forestry, agriculture, animal husbandry, and, as of recently, tourism.

However, in recent decades, increasing pressures have been exercised on the UA Carpathians as the region is integrated into a globalized market economy. One major issue threatening biodiversity in the region is the establishment and spread of NIPS that are classified as highly aggressive based on their ecologies and impacts on ecosystems (Prots 2009). These species exploit human-caused disturbance and permanent changes to natural and semi-natural systems particularly efficiently (National Research Council 2002). Disturbance has been significant in the

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[1] Terms in bold are defined/explained in Appendix A, unless otherwise specified.

past and future land-use and climatic changes promise more of the same. In order to maintain high levels of floristic diversity for generations to come, an investigation of the distribution patterns of the invaders and the factors explaining current and predicting future distribution will help to determine habitat suitability and thus areas prone to invasion. Maps depicting suitable areas for NIPS to become established can then be used by local/regional authorities to evaluate the potential spread of species under different land-use and climatic scenarios and thus contribute greatly to creating effective strategies for NIPS prevention and containment (see also National Resource Council 2002; Protopopova *et al.* 2006). The identification of potential suitable habitat and monitoring of such suitable areas before invasion occurs is stipulated in the Convention on Biological Diversity and the Global Strategy of the Global Invasive Species Programme and is in the interest of natural-resource management because proactive management is cheaper than reactive management (see Sakai *et al.* 2001; Ficetola *et al.* 2007), which is a particularly important factor to consider in a region dealing with continuous scarcity of financial resources.

Invasion of a novel habitat by a nonindigenous plant occurs in distinct phases including arrival, establishment, and integration (Petit *et al.* 2004). In order to provide a better understanding of the distribution of NIPS, the suitability of habitats in the UA Carpathians is modeled for the first two steps of invasion. Using two types of species distribution modeling software packages, eleven highly invasive plant species already present in the UA Carpathians are analyzed in order to determine the areas these species are most likely to migrate to and establish viable populations in. The reason for using two approaches to this distribution modeling project are the findings in several studies demonstrating that habitat suitability maps often differ not only based on the descriptor variables used for modeling but also based on the models themselves. That is, different models produce different results for a species given the same parameters, and the most accurate model is not the same for all species in one study area (Thuiller 2003). These inter-model variations can particularly impact predictions under climate change or land-use projections because seemingly small differences in function calibrations between models can be exacerbated in future projections, and it is therefore important to compare several techniques and choose the most accurate one for a given species (Hijmans and Graham 2006; Phillips 2010).

The specific research questions pertaining to the objectives of the study are:

1. What is the relative significance of **predictor variables** used in this study in explaining the distribution of NIPS?
2. What is the spatial distribution of predicted suitable habitats and how does it relate to the distribution of the predictor variables?
3. How will climate change and different land-use patterns affect the future distribution of the invaders?
4. How do the different modeling techniques influence predictions for current environmental conditions and projections into future scenarios?
5. What are some general implications of the modeling results for natural-resource management?
6. How can the outputs of this study be used to implement strategies preventing the introduction and spread of NIPS?

Initially, the following alternative hypothesis is tested:

H_a = Species X is non-randomly distributed over the environmental space, i.e., distribution is conditioned on the values of the predictors. The decision to reject or not reject H_o is based on the predictive performance of the functions calculated for each model. It is assumed that when presence of a species depends on the values of predictor variables, there will be a significant difference between the predicted suitability at presence and random pseudo-absence/background points (see Methods). Should H_o be rejected, one can extrapolate/project the models to different climatic and land-use conditions. By doing this, is following hypothesis is tested:

H_a = there is a significant change in net distribution across species when climatic/land-use variables change.

During model calibration and evaluation of predictive performance, one is also able to determine how each predictor variable influences the response function and thus interpret the role of particular environmental features on the distribution of NIPS.

2. THE UKRAINIAN CARPATHIANS

2.1 Geomorphology

The Carpathian Mountains form an arc of approximately 1500 km across Central and Eastern Europe (Fig. 1). The UA Carpathians comprise most of the eastern part of the Carpathian Arc and extend over a core area of 24,000 km^2.[2] The orientation of the mountains and valleys is northwest-southeast, which corresponds to northeast and southwest-oriented slopes. This geological structuring has been created when the mountain range formed through repeated processes of sedimentation, orogenesis (mountain building) and denudation (weathering of mountains). The width of the mountains reaches from 50 km in its southeastern to over 100 km in its central part, with the length along the north-to-east axis totaling 280 km. The altitude of the study area ranges from 95 to 2030 m above sea level (a.s.l.). The mountain range is therefore relatively narrow and flat, lacking the bold peaks common to the Alps (Kuemmerle *et al*. 2009; Holubets *et al*. 1988). As Fig. 2B demonstrates, the highest elevations are located in the southern parts of the UA Carpathians, part of the Transcarpathians, while particularly the southwest (bordering Romania) and west (bordering the Transcarpathian Lowland) are characterized by extensive valley systems and relatively mild slopes.

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[2]The definition of the exact geographic extent of the UA Carpathians depends on the classification of the UA Carpathian Ecoregion. Some publications consider parts the Precarpathian Highland and the Transcarpathian Lowland in their calculations of the area of the mountain range (see Kuemmerle *et al*. 2009).
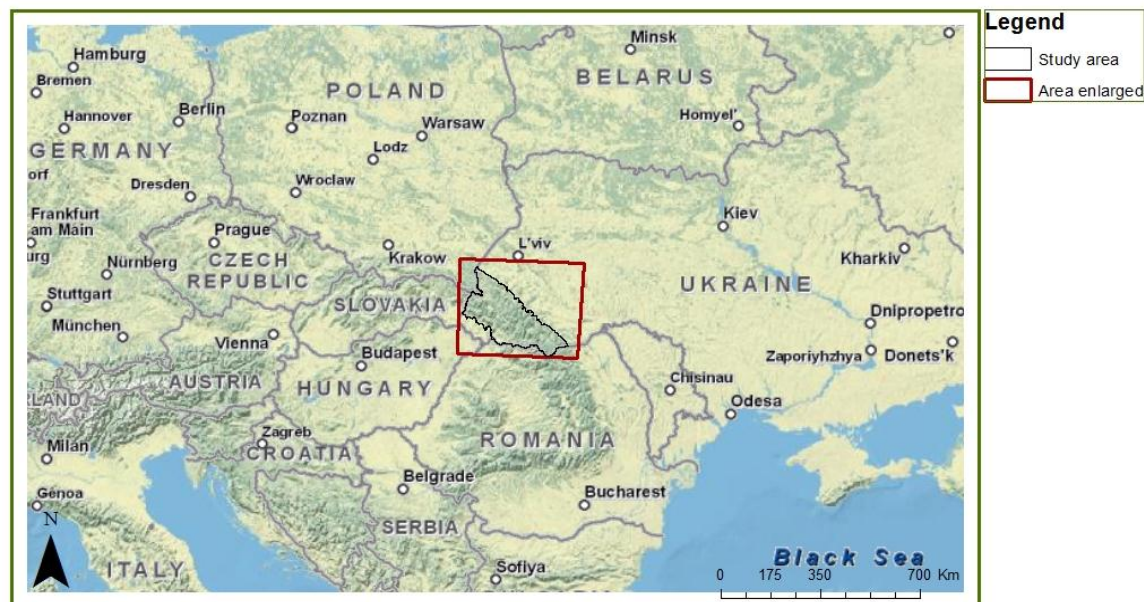
Figure 1: Physical map of the study area (Ukrainian Carpathians) within the Carpathian Mts. in Eastern Europe (ESRI base map); all subsequent figures depicting the UA Carpathians have the extent of "Area enlarged";
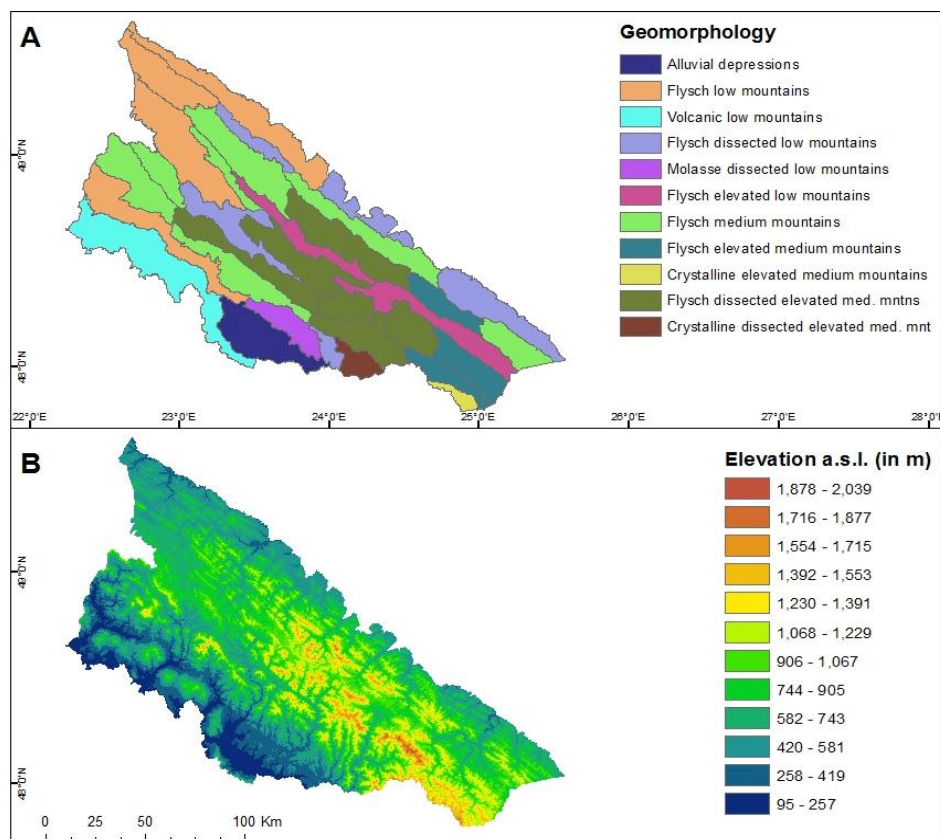
Figure 2: Overview of A – geomorphological types and B – terrain/elevation within the Ukrainian Carpathians (study area)[3]

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[3]The underlying GIS data for the maps shown in Fig. 2-4 was provided by Dr. Ivan Kruhlov from the Geographic Department of the University of Lviv, Ukraine. The maps were created using ESRI's ArcMap 10.

The UA Carpathians have a complex geomorphology reflecting their processes of creation along parallel longitudinal structural-lithological zones. The zones include an outer band of flysch rock - a continuation of the Western Carpathians, a central band of sand-clay sediments, an inner band of crystalline rocks, and a band of ancient volcanic rock that has been partially covered by younger sedimentary rocks (mostly limestone and dolomites) (Holubets *et al*. 1988; Fig. 2A). Given the geomorphology, the main soil types are cambisols and podsols in the mountains and albeluvisols, phaeozems, and fluvisols in the lowlands (Baumann *et al*. 2011).

The UA Carpathians emerged in the young Tertiary Period approximately 65 million years ago when the African tectonic plate, on its collision course with the Eurasian plate, displaced the sedimentary rocks of the ancient Mediterranean basin to create the Atlas, Pyrenean, Alps, Balkan, Caucasus, and Carpathian Mountains. Glaciations of the Ice Ages of the Quaternary Period affected primarily the highest mountains in the south, and species found refuge elsewhere in the mountains (Webster *et al*. 2001).

The geomorphology of the UA Carpathians, in particular the prevalence of broad, little-dissected slopes in the lowlands and large, steeply-sloped valleys along the longitudinal zones at upper elevations, contributes to the most conspicuous landscape features: dense forests interrupted by prominent river valleys. Both forests and slopes impact the distribution of NIPS, which are impeded in their migration away from regions of establishment by dense forest stands and steep slopes.

2.2 Climate and hydrology

The climate of the UA Carpathians is controlled by the height and relief of the mountains and their geographic position. Located in Eastern Europe, the mountain range is under a moderate temperate continental climate regime, which is mainly controlled by Atlantic and transformed continental air flows (Kuemmerle *et al*. 2009). With an annual sum between 500 and more than 1400 mm, precipitation is abundant in the ecoregion. Nine climatic zones are defined (Holubets *et al*. 1988; Kruhlov 2008; Fig. 3B).

Zones 1 and 2: The warm and warm to moderately warm zones on the southwestern slopes receive the most sunlight with a sum of active temperatures above (>) 10° C from 2600 to 3000° C. The mean temperatures in the warmest (July) and coldest (January) months are 19 to 20° C and -3 to -5° C, respectively. This results in an **active growing season** of 185 to 172 days, depending on the elevation, which reaches 200-250 m in this zone.

Zone 3: The moderately warm zone to the northeast and the northern limits of the Transcarpathians has a sum of active temperatures > 10° C from 2400 to 2600° C. The mean temperatures in the warmest and coldest month are 17 to 19° C and -5 to -4.5° C, respectively. This results in an active growing season of 180 to 155 days, depending on the elevation, which reaches 500 m in this zone.

Zones 4 and 5: The moderately warm to moderately cool zones at the southeastern external slopes of the UA Carpathians and reaching further into the interior of the mountain range

(including the Central Carpathian Plateau) have a sum of active temperatures > 10° C from 1800 to 2400° C, zone 4 being slightly warmer. These zones are mainly characterized by south-facing slopes. Mean temperatures in the warmest and coldest month are 15 to 17.2° C and -6 to -4.9° C, respectively. This results in an active growing season of approximately 125 days, depending on the elevation, which reaches 850 m in this zone.

Zone 6: The moderately cool zone, which covers the cleft valleys (mid-range valleys) of the major mountains (Gorgany, Chornogora, Rakhiv), has a sum of active temperatures > 10° C from 1400 to 1800° C. Mean temperatures in the warmest and coldest month are 13° C and -8.5° C, respectively. This results in a short active growing season of around 85 days, depending on the elevation, which encompasses 850-1250 m a.s.l. in this zone.

Zones 7 and 8: The moderately cool to moderately cold zones cover the upper elevations of mostly the interior slopes and have a sum of active temperatures > 10° C from 1000 to 1400° C. Mean temperatures in the warmest and coldest month are 10° C and -10° C, respectively. This results in a short active growing season of around 50-60 days, depending on the elevation, which encompasses 1250-1500 m a.s.l. in this zone.

Zone 9: The cold zone receives the least amount of annual sunlight and covers the subalpine and alpine belts at elevations of around 1500-2000 m a.s.l. The sum of active temperatures > 10° C is below 1000° C here. Mean temperatures in the warmest and coldest month are 10-12° C and -12 to -10° C, respectively. This results in an absence of an active growing season.

The apparent climatic differences between the northeastern and southwestern slopes can be explained by the major air currents passing through the mountains. In winter, cold, dry air masses from the north are intercepted by the mountains, which protect particularly the southern-most slopes. In summer meanwhile, moist, warm air masses from the Mediterranean Sea and Atlantic Ocean bring rainfall that is intercepted mainly at the southern and western slopes. Due to these two barrier effects, the southwestern slopes are warmer and moister than the northeastern slopes, the annual difference in the altitude temperature gradient and radiation balance being 0.31º C/100 m and 10 kcal/y · cm², respectively (Herenchuk 1968). The altitudinal temperature gradients are however generally weaker in the winter months than in the summer months.

Due to the moisture transported to the UA Carpathians in summer, June and July are the wettest months while January and February are the driest. The northeastern slopes in particular, as they intercept dry, cold air in winter, receive 76% of their annual precipitation in the summer months, as opposed to 67% of annual precipitation received on the southwestern slopes in the summer. The July temperature also varies between north and south, 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. Variation in the length of **growing season** is primarily a function of altitude and position of slopes and fluctuates between 290 and 100 days per year.
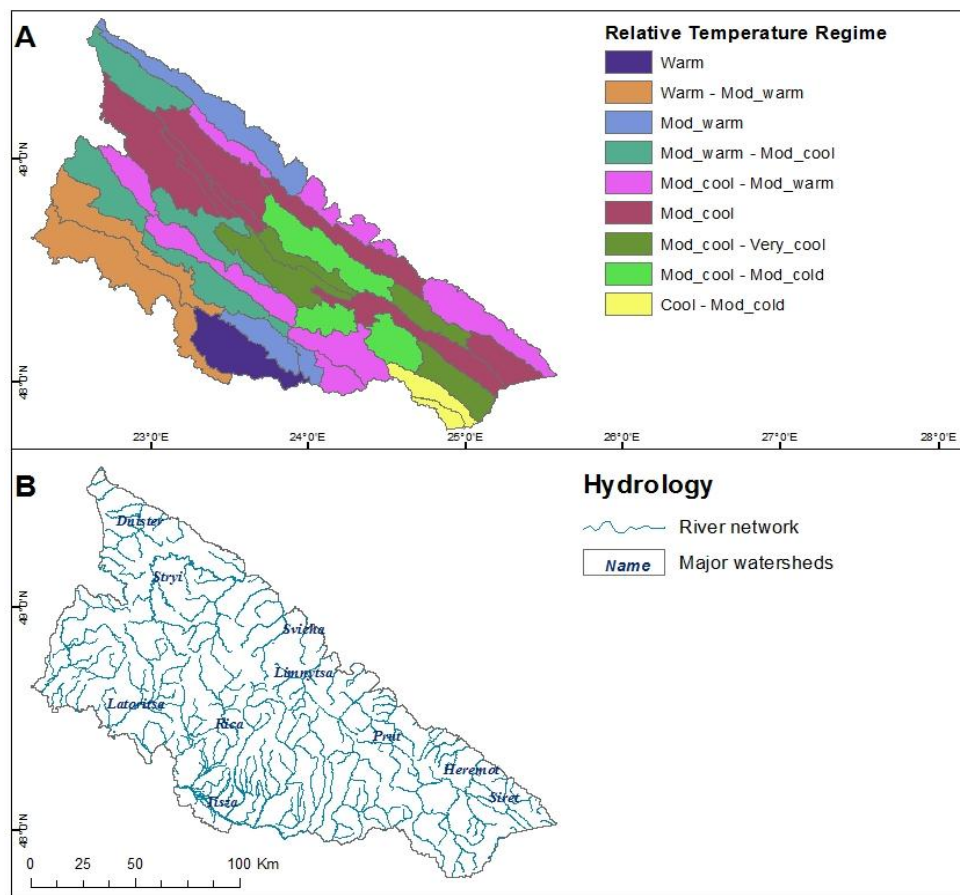
Figure 3: Overview of A - main climatic zones and B – river networks of the Ukrainian Carpathians; in A: "mod" = abbreviation for "moderately"

Ample precipitation throughout the year means that the UA Carpathians are rich in rivers, which are fed mostly by snow and rain; rivers experience frequent flash floods in spring and summer (Holubets *et al.* 1988). The most prominent slopes of the mountains create watersheds oriented in the same direction as the main mountain axes (see Fig. 3B). The main watersheds that receive input from the northeastern slopes are the Dnister (Dniester), Prut, and Siret. Each of these main rivers receives input from 235, 107, and 20 smaller tributaries, respectively (Herenchuk 1968). The main watershed along the southwest oriented macroslopes is Tisza and receives input from 134 tributaries (Baumann *et al.* 2011). Each main watershed in return replenishes the main rivers of the Ukraine: Vistula, which drains into the Baltic Sea to the north, and Danube and Dnister, which drain into the Black Sea to the South (Herenchuk 1968).

Due to the moderate climate and relatively short and mild winters, the main rivers are rarely completely covered by ice in winter. On average, ice cover remains for 15-30 days in the coldest month at upper elevations and is approximately 20-25 cm thick. Standing water bodies (e.g., lakes) are not characteristic features of the UA Carpathians. Most lakes are found in the south and have typically been formed due to rock slides blocking the natural flow of rivers (Hernchuk 1968; Holubets *et al.* 1988). Looking at the vast distribution of rivers across the mountains, it can be concluded that hydrological features are of paramount importance to ecological processes across the ecoregion and are certainly important for understanding and estimating the spread of

invasive alien plants. More generally, the moderate climate provides optimal abiotic conditions for the establishment of NIPS, and river networks provide pathways for their long-distance migration, as numerous studies across Europe have demonstrated (see Pyšek *et al*. 2009; Bartha *et al*. 2008; Brandes and Nitzsche 2006).

2.3 Vegetation

Due to the geomorphologic and climatic heterogeneity of the region and because the Eastern Carpathians provided a refuge for species during the Ice Ages, a high level of floristic diversity can be encountered in the region (Turnock 2002; Haggett 2002). The most recent volume of Flora of Eastern Carpathians (Tasienkevych 2008) records 2745 species of vascular plants in the region. The ten most represented plant families are: *Compositae*, *Rosaceae*, *Gramineae*, *Cruciferae*, *Leguminosae*, *Caryophyllaceae*, *Cyperaceae*, *Scrophulariaceae*, *Ranunculaceae*, and *Umbrellifera*. These families represent 65% of the entire flora. Floristic biodiversity also includes a large number of non-vascular species, among them approximately 500 species of mosses. Around 860 species of lichens are also found in the Eastern Carpathians (Tasienkevych 2008). With 221 species of vascular plants, half of those herbaceous, endemism is also high in the UA Carpathians. Important endemic species include blue columbine (*Aquilegia transsilvanica)*, Hungarian wallflower (*Erysimum hungaricum*), red clover (*Trifolium pratense* subsp. *kotulae*), hanging violet (*Viola declinata*), and many more (see Tasienkevych 2008).

The UA Carpathians are divided into two vegetation zones (mountain and plain) and six vegetation belts common to mountainous areas (Holubets *et al*. 1988). The latter include:

- – At 130 m: The plain belt of broadleaved forests; oak (*Quercus robur*) in association with beech (*Fagus sylvatica*), hornbeam (*Carpinus betula*), and ash (*Fraxinus excelsior*);
- – At 110-250 m: the mountain belt of oak forests (*Quercus petrea*, *Q. robur*);
- – At 250-700 m: the belt of beech forests (*F. sylvatica*); at upper limits in association with fragments of silver fir (*Abies alba*), Norway spruce (*Picea abies*), and sycamore maple (*Acer pseudoplatanus*);
- – At 700-1300 m: the belt of spruce forests with large fragments of beech and silver fir forests; in some areas mixed with grasslands and Swiss Pine (*Pinus cembra*);
- – At 1300-1800: the subalpine belt of shrubs (mountain pine (*Pinus mugo*), green alder (*Alnus viridis*), and juniper (*Juniperus communis* subsp. *alpina*)) and subalpine grassland;
- – At 1800-2060 m: the alpine belt of grasslands (Herenchuk 1968; Kuemmerle *et al*. 2009).

In addition to the dominant woodland species that characterize the vegetation belts, poplars (*Populus alba*, *P. tremula*) and willows (*Salix purpurea, S. fragilis, S. viminalis*) are common woody species in riparian habitats. Other woody tree and shrub species include and birch (*Betula verrucosa*), rhododendron (*Rododendron kotschyi*), common hazel (*Corylus avellana*), common dogwood (*Cornus sanguinea*), and blackthorn (*Prunus spinosa*).

Besides elevation, an important abiotic factor that determines the distribution of plant communities is soil moisture. Because precipitation is ample and the alluvial, mineral-rich soils

hold moisture well, soils have high moisture content throughout the growing season; soil moisture is thus not a limiting factor for most of the region. Soils on gentle slopes, in valleys, and along river terraces hold the most moisture and can be saturated with water while steeper slopes (particularly southern and southwest oriented) retain less water and are dry throughout parts of the growing season (Holubets *et al.* 1988).

Before humans transformed the landscape, the Carpathians were heavily forested (up to the subalpine belt). Today, while it has not taken such extents as was typical in Western Europe (see following section), deforestation has occurred heavily at elevations up to 700 m. At these altitudes, forests form small islands among farms and pastures (Kuemmerle *et al.* 2009). Deforestation also led to lowering of the upper forest limits. Overgrazing in these extended alpine meadows and grasslands resulted in decreased species diversity. However, centuries of traditional, extensive to **sustainable** land management have also created semi-natural ecosystems such as alpine and hay meadows that harbor a wide variety of species and contribute to landscape heterogeneity and thus biodiversity (WWF Carpathian Programme 2007). Meanwhile, species-rich meadows, in addition to forests, can act as effective barriers to the spread of NIPS provided they are not exposed to high levels of anthropogenic disturbances (Pyšek *et al.* 2009). This is because high levels of (meadow) biodiversity increase the chances that some native species will have similar biological/physiological characteristics as a nonindigenous species, which then would not be able to fill an empty niche (Chapin *et al.* 1998; Shea and Chesson 2002; see Chapter 3 for further elaborations).[4]

2.4 Land use and economic development

Two million people are estimated to live in the region, most in urban areas (UNEP 2007; State Statistics Service of Ukraine 2011). The Carpathian foothills and mountain valleys are relatively densely populated (Fig. 4), and of those living in lower latitudes (in valleys), almost 30% inhabit towns located at the intersections of major highways. Fig. 4 also demonstrates that most settlements (approximately 95%) within the UA Carpathians are villages and small towns (see also Maryskevych 2006). Furthermore, the UA Carpathians are ethnically a highly diverse region. Culturally and historically distinct groups include the Lemkos to the west and Boikos and Hutsuls to the east (Elbakidze and Angelstam 2007); and due to centuries of shifting political borders, Hungarians, Slovaks, Romanians, and other nationalities live in the UA Carpathians (WWF Carpathian Programme 2007; Webster *et al.* 2001). Traditionally, the inhabitants of the mountains have cleared forests to create farmland or pastures for animal husbandry (the latter is particularly true for the Hutsuls). Traditional land use in the UA Carpathians therefore consists of mainly sustainable forms of farming and animal husbandry (WWF Carpathian Programme 2007). However, when the Austro-Hungarian Empire controlled the region from 1772-1918, attempts were made to intensify production and exploit the territory for its timber. During the rule of the Empire, vast areas of the Carpathians were deforested. Yet, compared to deforestation levels in Western Europe, relatively large extents of natural forest remained until the late 1930s (Keeton and Crow 2010).

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[4] Please note that the hypothesis on the positive relationship between biodiversity and ecosystem health is under debate in the scientific literature and are yet to be tested in many ecosystems (Chapin *et al.* 1998; Lonsdale 1999).

When Western Ukraine was annexed into the Soviet Union in 1945,[5] the economic structure in the Carpathians changed. While subsistence farming and animal husbandry remained an important source of income to the region as the central governments of the Soviet Union were not able to industrialize agriculture in the relatively narrow, difficult to access river valleys, the forestry sector increasingly intensified consumption and export of raw wood materials throughout the latter half of the 20th century (Sitko and Troll 2008; Süli-Zakar 1998; Webster *et al*. 2001). Deforestation was concentrated to the Carpathians, and in the 1950s, 60% of the timber produced in Soviet Ukraine originated from the Carpathians, albeit the mountainous forests constitute only 22% of Ukraine's total forested areas (Kubijovyč 1984). At the same time, forestry and rural development have largely been regulated by state agencies which generally favored forestry management that sustained long-term regeneration capacity of forests (Keeton and Crow 2010; Nazarov *et al*. 2001). Concretely, forest resources could only be extracted at a rate at or below their natural regeneration rate. This, however, did not ensure biodiversity or a healthy forest structure as will be discussed below. Furthermore, mining was subsidized by the state in the 20th century. Oil and gas are still exploited at low quantities in the Bytkiv, Dashava and Dolyna regions of the UA Carpathians (bordering the Precarpathians), and potassium salts and sulfur are mined in the Kalush and Yavoriv regions, respectively (Turnock 2002).
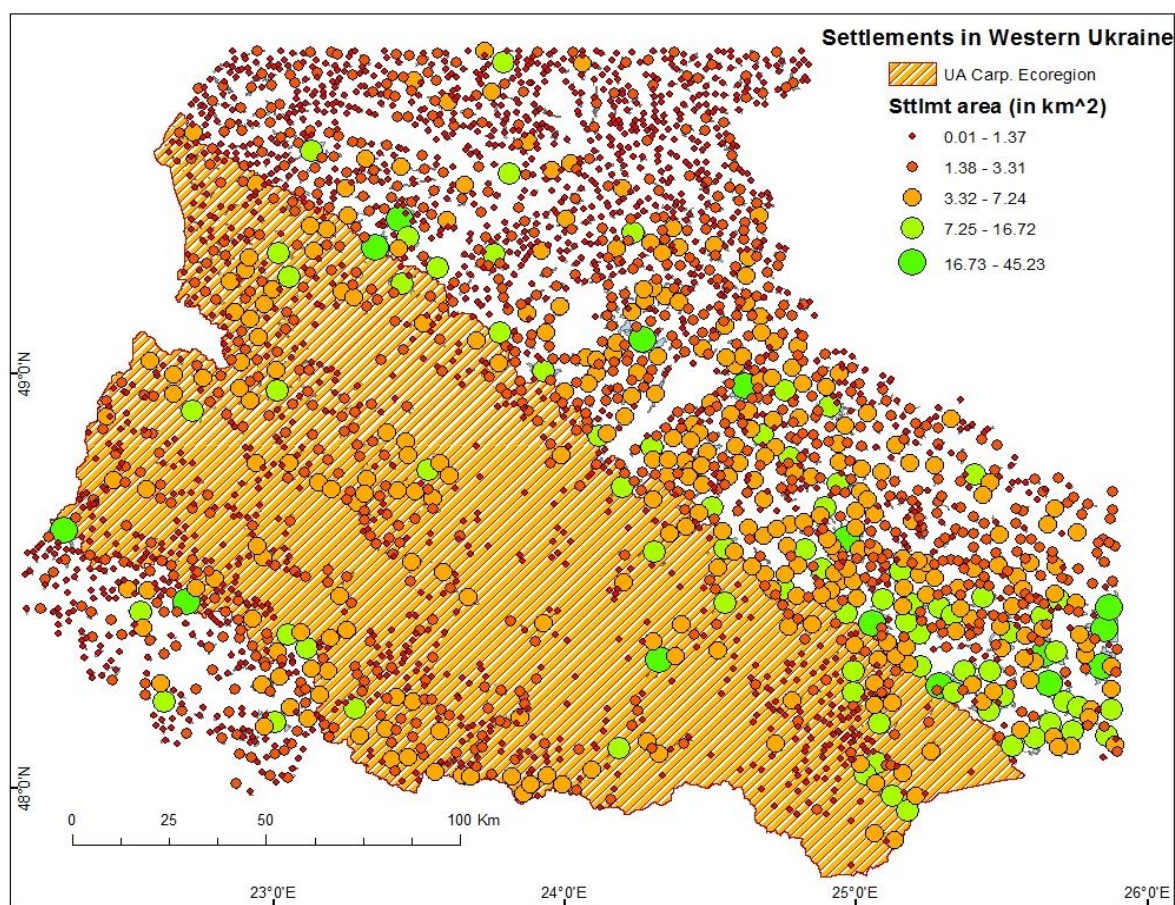
Figure 4: Settlement locations and sizes in km^2 in Western Ukraine; the study region (UA Carp. Ecoregion) is highlighted in the background.

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[5] Western Ukraine was controlled by Poland from 1918 until World War II (Subtelny 2000).

After the collapse of the Soviet Union, a transition from planned to market-based economy ensued, and two general trends in economic development have been discernible: privatization and globalization accompanied by a weakening of government institutions. Forestry has remained the most important economic sector and attempts are made to further intensify production. At the same time, traditional farming and animal husbandry have declined dramatically as major sources of income because the inhabitants of the UA Carpathians ecoregion have been seeking out more profitable sources of income (Sitko and Troll 2008). Among them, tourism is rising in importance as an economic sector. The region, in particular the Volcanic Carpathians, possesses many healthy natural mineral springs and, due to traditionally low rates of industrial development, still holds a promise of "untouched" nature to visitors. Development of the tourist industry comes with a variety of implications for the natural ecosystems as will be explained in the following chapter (see also WWF Carpathian Programme 2007; Fig. 5).
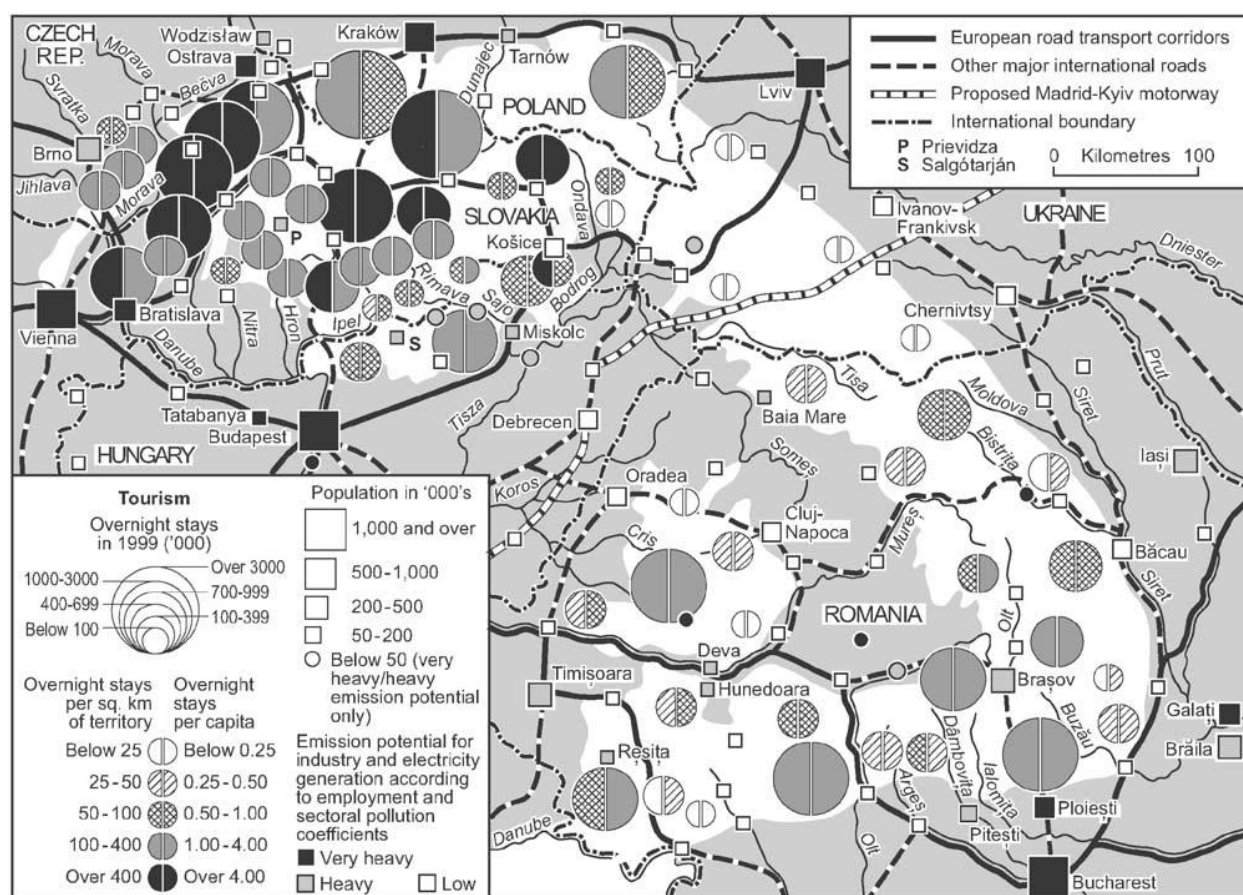
Figure 5: Urban-industrial development, tourism, and major transport routes in the Carpathians (Nefedova 1992; cited in Turnock 2002)

Throughout the 20th century, the UA Carpathians were progressively connected through infrastructure networks. To the Soviet Union, the region was of paramount strategic importance, connecting the Union with several of its satellite states to the west (Turnock 2002). Road and railway construction across the mountains was therefore a priority. This has remained the case in the post-Soviet era. In an effort to stimulate economic development, highways were repaired and new roads constructed (Turnock 2002). Most notably, a large-scale project, the Madrid–Kyiv

motorway that transects the central UA Carpathians, is planned in the context of better accessibility across Europe (Fig. 5; Zigstra *et al*. 2009). Meanwhile, infrastructure development and land-use patterns are a key to understanding the introduction, establishment, and spread of NIPS. As will be elaborated in the following chapters, humans are the main vector for the introduction of species to novel environments and their interactions with native ecosystems ultimately determine success of invasion as much, if not more than, climatic factors do.

2.5 Importance of the UA Carpathians within the Carpathian Ecoregion

The Carpathian Mountains encompass Europe's largest extents of temporal forests and harbor a high level of biodiversity (UNEP 2007; Oszlanyi *et al*. 2004). The mountain range borders the main lowlands of Europe, the North-European Plateau, Pannonia Lowland, and Eastern European Chernozem Lowland, and is home to over one third of Europe's vascular plants species and provides the last refuge to large carnivores such as the brown bear (*Ursus arctos* L.) and wolf (*Canis lupus* L.) (Oszlanyi *et al*. 2004). Within this area, the UA Carpathians are particularly rich in regards to biological as well as cultural diversity because (a) they connect the northern and southern Carpathians and thus provide natural migration corridors, and (b) they constitute a refuge to some of Europe's largest and oldest natural beech forests, which have largely disappeared from Western Europe (Wesolowski 2005). Preventing the establishment of invasive plants in the UA Carpathians will benefit the Carpathians as a whole because **naturalized** populations of these aggressive invaders can disperse seeds or rhizomes well beyond the borders of Ukraine. Preserving biodiversity in the Ukrainian parts of the Carpathian Mountains should therefore always be regarded in the context of the implications for the entire Carpathian Ecoregion.

3. HIGHLY INVASIVE PLANTS IN THE UKRAINIAN CARPATHIANS

3.1 Invasiveness of non-native invasive plant species (NIPS)

3.1.1 Assessment of the invasiveness of NIPS in the UA Carpathians:

In the last decades, ecologists have increasingly investigated the dynamics of plant invasions and the threats alien plants pose to ecosystems around the world. The recent focus on alien species can be explained by the explosion of worldwide trade that has largely augmented the number of intentional (e.g., ornamentals or timber sources) or unintentional (e.g., transport of reproductive plant parts via global trade routes) introductions of nonindigenous plants (Colautti *et al*. 2006; Levine and D'Antonio 2003). Coupled with increasing disturbances of natural ecosystems by human development, NIPS are able to profit from higher rates of dispersion and weakened host environments. It has been estimated that non-**native plants** make up 14% of the total flora in Ukraine, and that their total numbers have risen from approximately 500 in 1950 to over 800 in 2000 (Protopopova *et al*. 2006; Pyšek *et al*. 2009). The UA Carpathians are ecologically still relatively intact but harbor nevertheless highly aggressive NIPS, especially on southwestern slopes (Prots, personal communication).

In the UA Carpathians, a great effort has been put forth in the last decade to rank non-native plants based on their impact on biodiversity (see Prots 2009). Here, an approach developed in the United States has been applied to assess the regional invasive flora: the Alien Plant Ranking System (APRS) developed by the Northern Prairie Wildlife Research Center (APRS Implementation Team 2000). The APRS is designed to rate alien plants based on 23 questions about the ecological characteristics of a species within a specified invaded habitat. The questions are divided into three categories: the current level of impact to a site, the biology of the species, and feasibility and costs of control. Utilizing the APRS, Prots (2009) determined the eleven most aggressive NIPS to be: *Acer negundo* L., *Reynoutria japonica* Houtt., *Reynoutria x bohemica* Chrtek.& Chrtková, *Echinocystis lobata* (Michx.) Torr. & Grey, *Impatiens glandulifera* Royle, *Heracleum sosnowskyi* Manden, *Robinia pseudoacacia* L., *Helianthus tuberosus* L., *Solidago canadensis* L., *Solidago gigantea* Aiton, and *Ambrosia artemisiifolia* L.. These species are the subject of the study. The invasion of the mountain range by these NIPS mirrors general trends of plant invasion in Europe (Pyšek *et al.* 2009). All 11 species at the focus of the study are invaders from either North America or Asia and have been intentionally introduced as ornamentals, timber, or food sources (except for *A. artemisiifolia*, which was introduced accidently). Furthermore, the species belong to plant families that have experienced great range expansions in temperate regions in the last millennia and have "a weedy tendency" (Pyšek *et al.* 2009; Appendix B). Because the eleven species have the most adverse effects on biodiversity, the assessment of their invasion potential in the UA Carpathians is of paramount importance to conservation management.

3.1.2 Ecology of NIPS:

For all eleven NIPS, steep slopes and dense forest stands represent physical and environmental barriers to spread (see Toeroek *et al.* 2003). In addition, based on their current occurrence in the invaded range, the distribution of the plants can be divided into two groups with *Acer negundo*, *Echinocystis lobata, Impatiens glandulifera, Heracleum sosnowskyi,* and *Helianthus tuberosus* found clearly along rivers and the remaining six species preferring medium-wet to dry habitats and thus found more often along roads and in close proximity to human settlements (see Prots 2009). However, this very general differentiation might not be representative of the ecology of the species as it is blurred due to precipitation and soil moisture being abundant in the UA Carpathians, roads and human settlements stretching along river valleys, and the likelihood that the NIPS are still experiencing range expansion.

The highly aggressive NIPS in the UA Carpathians utilize the particularities of the regional climate to their competitive advantage. Unlike non-native plants in Mediterranean habitats, the most successful invaders here are not drought tolerant (Levine *et al.* 2003). Instead, the species are highly adapted to a high level of soil-moisture and utilize the length of the growing season to their advantage by beginning growth very early in the season. The plants also exhibit tolerances to the seasonality of the temperate climate, and most require periods of frost to break seed dormancy. However, despite their adaptability to a wide range of environmental conditions, tolerance limits to seasonality are also the primary climatic factors that limit the distribution of the NIPS (Appendix B; Table 1). At the same time, because many more non-native species are present and are continuously introduced in the UA Carpathians, and because it is generally assumed that only about 1% of introduced species become invasive, one must ask what

differentiates the highly invasive plants from the majority of non-natives that do not proliferate in the introduced range? Although a common "invasive syndrome", a generalization of traits common to all NIPS, does not exist (Petit *et al*. 2004; Pyšek and Richardson 2007), highly invasive plants in the Carpathians share a range of characteristics that guarantee their competitive advantage (see Appendix B):

- Life-history theory states that there is a tradeoff between high fecundity and competitive ability (Begon et al. 2006; Sakai *et al*. 2001). That is, a survival strategy of a plant may be either to produce a great number of seeds but with a low survival probability of any given seed/seedling or to produce fewer but more competitive seeds. NIPS however have been observed to break this pattern because they experience some sort of enemy release effect. The concrete patterns explaining the release of an invasive species from its enemies are complex and therefore debated (see Colautti *et al*. 2004), but in general it is acknowledged that while a plant and its competitors are under equal pressure from herbivores and pathogens in the native community, the same species loses its specialist enemies and is less under pressure from generalist enemies not habituated to the plant in the invaded range. According to Petit *et al*. (2004), "84% fewer fungi and 24% fewer virus species infect plant species in their naturalized range compared to their native ranges" (see also Hierro *et al*. 2006). Thus, species rapidly gain or gradually evolve an increased competitive ability and capitalize on these competitive advantages over a native species by investing relatively more resources in growth and reproduction as opposed to survival/defense mechanisms (Fig. 7; Jacobs *et al*. 2004; Keane and Crawley 2002; Reinhart and Callaway 2004). This leads to stark increases in abundance and distribution (Elton 1958).
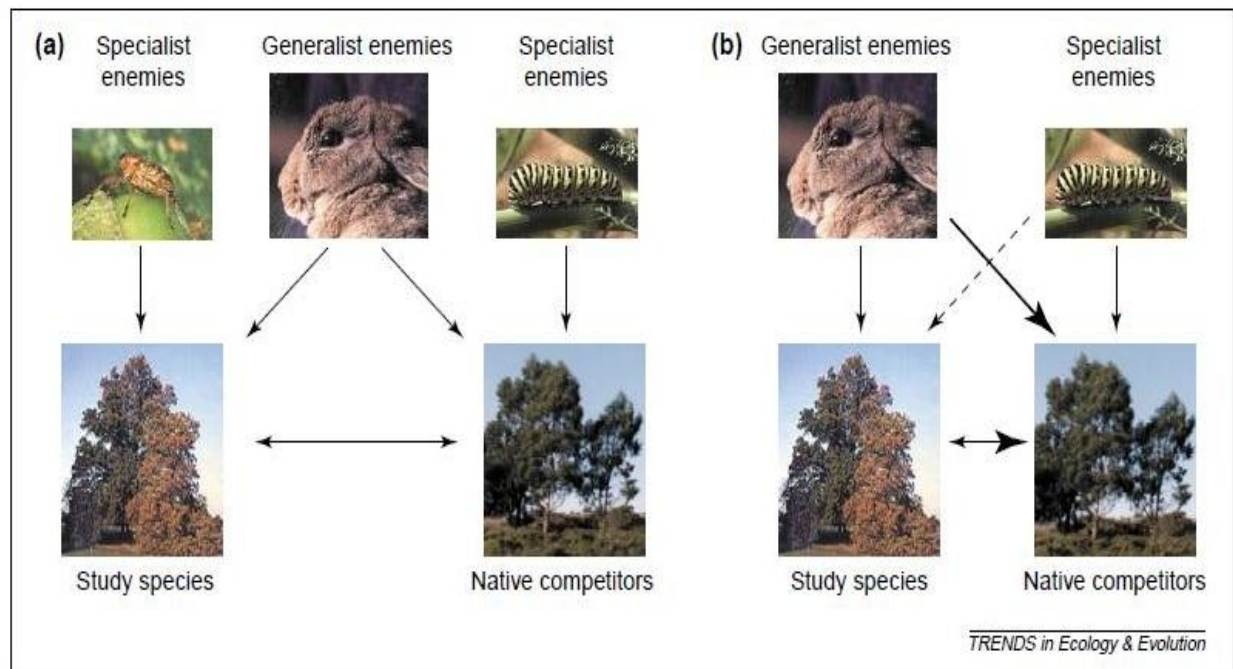
Figure 6: Simplified depiction of the Enemy Release Hypothesis; (a) native and (b) invaded community; abundance of species is controlled by enemies - arrows indicate the direction and strength of control (from Keane and Crawley 2002);

- The Enemy Release Hypothesis (Fig. 6) is also strengthened by the fact that NIPS are able to enter mutualistic relationships in their invaded ranges and thus substitute mutualists from their home ranges (Petit *et al*. 2004). For example, *Robinia pseudoacacia* relies on close mutualism with nitrogen-fixing bacteria in its invaded range, and *I. glandulifera* is a successful invader because it attracts many pollinators present in the invaded range (for more details see Appendix B).

- The NIPS in the UA Carpathians have inherent competitive abilities which allow them to exclude native species from a habitat. These include high fecundity and recruitment, fast growth rates, tolerance to environmental stressors (e.g., seeds enter dormancy when exposed to environmental stress), **vegetative reproduction**, and high adaptability to long-distance dispersal. Most importantly, the NIPS exhibit high levels of **phenotypic plasticity** (which in some cases is strongly related to genetic variability) and can thus adapt to a range of environmental conditions and foremost to relatively high levels of disturbances (Petit *et al*. 2004; Sakai *et al*. 2001). All NIPS capitalize on anthropogenic or, albeit to a lesser degree, natural disturbances; in fact, the species rely on periodic disturbances as most require and some (i.e., *I. glandulifera, Solidago canadensis*, *S. gigantea*) prefer abundant sunlight to grow and reproduce (Appendix B). However, not all species possess all the inherent traits commonly associated with **invasiveness**. *Reynoutira japonica*, for example, does not produce seeds but instead spreads exclusively vegetatively, and *I. glandulifera* is a relatively specialist invader that does not exhibit high phenotypic plasticity (Pyšek and Prach 1994). The main source of difficulty in teasing out common traits in NIPS is the many confounding factors such as the structure of the native community and most notably **propagule pressure** that influence invasion success and the fact that different traits may be important at different stages of invasion (Lonsdale 1999; Sakai *et al*. 2001; Mack and Lonsdale 2001).

- Related to inherent life-history traits that promote invasiveness, the empty niche hypothesis states that non-native species are able to invade novel habitats because they find an empty niche in them (see Chapter 4 on the theory of niches). That is, it is assumed that communities are not **saturated**, and NIPS successfully populate a community because native species with similar physiologies and functions in that community are not present or have been eliminated (or weakened) by frequent anthropogenic disturbances (Callaway and Maron 2006; Pyšek and Richardson 2007). The empty niche hypothesis would provide an explanation for the trend of the species to flower either early in season or for prolonged periods. It would also explain why the NIPS studied here occur along frequently disturbed habitats. For example, *Ambrosia artemisiifolia* can accumulate and neutralize toxins in its tissues and thus thrives on contaminated soils too toxic for most native species. However, the empty niche hypothesis does not apply to all communities and is debated, often by proponents of the enemy release hypothesis who argue that NIPS dominate communities primarily because they can invest more resources into reproduction and survival and not due to inherent genetic traits that allow them to occupy an empty niche (Callaway and Maron 2006). The distinction between the ecological theories explaining invasion is however fluid. Shea and Chesson (2002) for example, identify the release from enemies in the invaded range as one factor defining an empty niche, or "niche opportunity," for NIPS. That is, species can be regarded to occupy an empty niche precisely because they can shift allocation of resources to growth and reproduction.

Species	Trait							
	Plasticity	growth	Seed production	Veget. reprod.	Seed/rhizome dispersal	Reaction to stress	Ecological niche	Limiting factors
Acer negundo	high	Reaches sex. maturity in 5 years, earlier than native flood plain species	high	yes	Wind, water	Seed survival in water for week; dormancy	Extremely wide	Shade, drought, extreme frost
Ambrosia artemisiif.	high	Grows rapidly in spring (annual)	Very high (up to 62,000 per plant)	no	Water, animal, humans	Long dormancy (~30 years)	Wide	Shade, extreme frost and heat (drought)
Echinocystis lobata	medium	Fast growth of leaves	moderate (6 seeds per fruit) but high germination rate	Not known	water	Dormancy	wide	Shade, Extreme temperature (particularly frost)
Helianthus tuberosus	medium	Grows rapidly in spring	Relatively low	yes	Seeds mostly local; rhizomes by water	Dormancy of tubers, rhizomes	Extremely wide	Shade, drought, cool and dry winters
Heracleum sosnowskyi	high	Grows rapidly in spring	Very high (up to 100,000 per plant)	no	Water, humans	Dormancy	wide	Shade, drought,
Impatiens glandulifera	medium	Grows rapidly in spring	High (average 1000 per plant)	yes	Water,	Dormancy, seed germination under water	Relatively narrow	frost, drought
Reynoutria spp.	high	Grows rapidly in spring	Moderate (only in *R. x bohemica*)	yes	Rhizomes by water, humans	rhizomes	Extremely wide	Shade, length of growing season
Robinia pseudoac.	medium	Rapid growth of seedlings (up to 2m per year in first 5 years)	High (0.28 kg per year per plant)	yes	Wind, water	Dormancy; root suckering	moderate	Shade, length of growing season, excessive flooding
Solidago spp.	high	Grows rapidly in spring	High (up to 10,000 per shoot)	yes	Seed by wind and water, rhizomes by water	Dormancy, rhizomes	Extremely wide	Drought, Length of growing season

Table 1: Traits associated with invasion and their distribution among the highly invasive plant species in the Ukrainian Carpathians; "-" means that no information was available; more detailed descriptions can be found in Appendix B.

In conclusion, despite disagreements and uncertainties about the overall ecological framework for assessing plant invasion, one can nevertheless conclude that the NIPS in the UA Carpathians possess (or evolved) similar physiological/reproductive traits, albeit in different combinations, which permit them to colonize novel habitats. Species characteristics are however not the only factors contributing to invasion. Equally, and sometimes more, important are interactions in the invaded community. That is, competitive superiority of the NIPS is enabled by the absence (or presence of fewer) enemies, the presence of resource opportunities such as water, nutrients, and mutualists, and weakening of native communities by disturbances.

3.1.3 Impacts of NIPS on ecosystems and humans:

The impacts of NIPS in the introduced range are evident on several ecological levels of organization. At the genetic level, native species can potentially lose genetic variability and thus viability due to hybridization with nonindigenous relatives. Although species losses due to hybridization have not been reported in the UA Carpathians, at least one genus of NIPS established in the region, *Helianthus* spp., is known to contaminate the gene pool of native relatives elsewhere in Ukraine (Protopopova *et al*. 2006). Another way in which invasive plants weaken the genetic pool of native species is by "insularization" of habitats and alteration of selective pressures on species as will be discussed in the following.

At the individual level, the highly aggressive NIPS present in the UA Carpathians adversely impact the growth, survival, and migration of components of native plant populations. At the population level, this leads to a decrease in abundance and population growth rates and can cause extinction of entire populations (see National Academy of Sciences 2002). More precisely, NIPS suppress other species in a habitat by means of fast **colonization** of available space, successful competition for resources (e.g., light or pollinators), and production of allelopathic soil compounds that inhibit growth of other species (Appendix B; Chornesky and Randall 2003; Hulme *et al*. 2009). In addition, due to fast growth and reproduction, virtually all of the NIPS at the focus of the study can form thick monocultures in invaded areas, thus displacing native species. This is particularly problematic when species that lose their habitat to NIPS include endangered ones as is demonstrated in Fig. 7. Populations of native species can also become isolated on island-like habitats when populations of invaders starkly expand their range. Above all, this holds true for linear habitats along rivers and roads and can lead to local extinction of small, genetically unstable fragmented populations (Protopopova *et al*. 2006).

At the community level, the invasion of novel areas decreases biodiversity of the native flora and fauna. Many studies point to a decrease in the richness of native species in areas where the NIPS dominate the community (Appendix B; Protopopova *et al*. 2006). One exception may be *Impatiens glandulifera* which has shown to shift species richness towards nutrient-demanding species instead of diminishing it per se (Hejda and Pyšek 2006). Such a restructuring of plant communities is no less problematic however.

Figure 7: *Heracleum sosnowskyi* invasion in species-rich meadow in the Ukrainian Carpathians; several orchid species are threatened by *H. sosnowskyi*, including the Red Listed fragrant orchid (*Gymnadenia conopsea*) seen here (Bilz *et al.* 2011).

At the ecosystem level, by manipulating biotic or abiotic components of an ecosystem, NIPS change its functions. Nitrogen-fixing plants such as *Robinia pseudoacacia* substantially change the soil microbial and chemical composition by increasing the amount of soil nitrogen and the rate of nitrogen mineralization, i.e., microbial conversion of nitrogen to ammonium and nitrate – forms that can be taken up by plants and assimilated into tissue. *Acer negundo*, meanwhile, prevents the regeneration of natural willow/aspen communities along riparian corridors, and *Heracleum sosnowskyi* can significantly slow natural succession of herbaceous communities to shrubs and forests (Appendix B). In general, the high rates of NIPS biomass production and subsequent decomposition lead to changes in nutrient loads in soils (Academy of Sciences 2002). Changes in ecosystem functions can also be attributed to genetic changes in the native species as a response to the competitive pressures posed by invaders (Sakai *et al.* 2001). NIPS may exercise selection pressures on the native flora favoring genotypes that potentially change the niches of native species and thus their ecosystem functions. Such niche shifts can have wide-reaching consequences for communities and ecosystems. For example, if willow-aspen communities are driven to the periphery of riparian habitats by *A. negundo*, species that rely on these trees for food and shelter but cannot migrate will suffer population declines. Furthermore, NIPS such as *Reynoutria japonica* and *I. glandulifera* change hydrological features along riparian habitats. These species not only impede the growth of trees along these habitats but also produce shallow root systems; both processes destabilize soil and increase levels of disturbances (by exacerbating flooding), which in turn promotes further spread of the species (Appendix B).

Lastly, invasive species cause economic damages and can negatively impact human health. In Europe, NIPS are estimated to have caused tens of billions of dollars in damages to this date due to the multitude of adverse impacts they have on ecosystems (Hulme *et al*. 2009). Some species, most notably *Ambrosia artemisiifolia* and *H. sosnowskyi*, can cause allergic reactions and severe skin burns, respectively. At the same time, populations of native species and entire ecosystems in the UA Carpathians are threatened mostly by the cumulative impacts of NIPS. Rarely does one find only one species in an ecosystem; instead, in ecosystems currently highly impacted by NIPS, i.e., riparian and roadside communities, one encounters several of the species competing with each other – having almost completely displaced native herbaceous vegetation. Fig. 8 for example demonstrates the invasion of linear habitats by several species. It is clearly visible that the presence of several highly aggressive NIPS strongly dominates plant communities and impoverishes biodiversity.
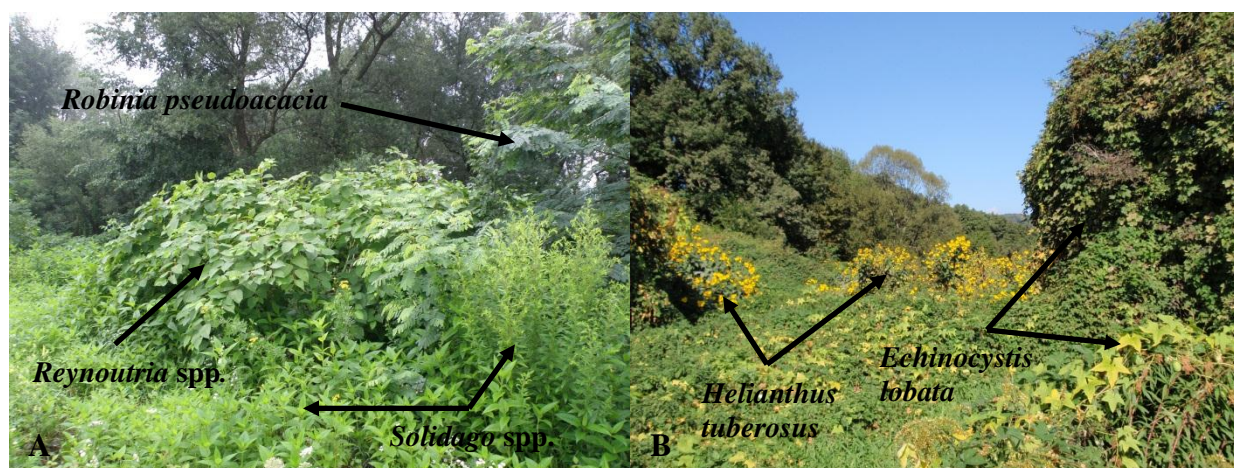
Figure 8: Cumulative impact of plant invasion; A **-** Three of the highly invasive plants in the UA Carpathians along river in the Transcarpathian region; B – two of the NIPS by a railway track and small stream (note how *E. lobata* is completely covering the canopy of native tree species);

Such trends are alarming because they suggest that with range expansion of NIPS, which may occur even more rapidly if individual invasive species evade other invaders rather than competing with them for space, adverse impacts on ecosystems and humans in the UA Carpathians will amplify. At the same time, efforts to control the spread of invasive plants must above all first identify the processes driving introduction and establishment of NIPS in the UA Carpathians.

3.2 Introduction pathways into and within the UA Carpathians

3.2.1 Human development and land use and NIPS:

The spread of invasive plants occurs in four phases:

1. Introduction of a species to a novel habitat;
2. Establishment of a persistent founder population in the novel habitat by growth and reproduction;

3. Local expansion of the population and establishment of further populations through (long-distance) transport of seeds or reproductive plant parts (e.g., **rhizomes**);
4. Large-scale range expansion by increases in the number and density of populations, typically after a lag phase (Weber 1998; Petit *et al*. 2004; Richardson *et al*. 2000).

Humans play a major role in all four phases as they exercise pressures on natural and semi-natural ecosystems in the mountains (Prots *et al*. 2011). The magnitude of anthropogenic pressures can be attributed to several factors of socio-economic development and institutional responses in the UA Carpathians. Despite the richness in natural resources, the UA Carpathians have remained one of the poorest regions in Ukraine and Europe. Unemployment is around 20%, and emigration is high with 15-20% of the population working abroad (WWF Carpathian Programme 2007; Elbakidze and Angelstam 2007). In addition, institutional reforms have been slow and natural-resource management operates under lack of funding, antiquated structures and policies, and corruption (Nazarov *et al*. 2001; see Chapter 7). Some of the consequences are that "the prodigious natural resources… [have come] under increasing pressures including illegal logging and poaching as well as habitat fragmentation, habitat destruction from changing land use and destruction from infrastructure development"; and regional authorities struggle to adjust policies and regulations to the demands for natural resources from a global economy and the demands of the local population for more economic opportunities (WWF Carpathian Programme 2007; see also Kuemmerle *et al*. 2009). High levels of human-caused disturbances thus occur on several fronts and increase the **invasibility** of many habitats. This is because the interactions between humans and ecosystems not only enable the introduction and facilitate the spread of NIPS to novel communities but also increase the propagule pressure for NIPS and thus the chances of a species to establish viable populations and become invasive (Protopopova *et al*. 2006; Keeton and Crow 2010; Thuiller *et al*. 2006; Colautti *et al*. 2006).

First, rivers and riparian habitats suffer from increasing trends of pollution. Sources of pollution include not only industrial and agricultural but above all inadequate waste management (Prots *et al*. 2011). Riparian areas receive influxes of nitrites and other chemical compounds that alter soil composition due to improperly treated sewage and municipal waste being disposed in or along rivers (Zingstra *et al*. 2009; Nazarov *et al*. 2001). Meanwhile, plants that are fast-growing and nutrient-demanding, characteristics that apply to the NIPS present in the UA Carpathians, are able to capitalize on the increased nitrification of soils at the expense of slow-growing native species (Chapter 6; Chapin *et al*. 1998). In fact, a comprehensive study by Chytry *et al*. (2008) comparing invasion rates of different habitats across Europe discovered that **neophytes** are often found in riparian habitats and have a "stronger affinity to wet habitats and disturbed woody vegetation." Meanwhile, Protopopova *et al*. (2006) note that "expansions of alien plants are powerful factors of destruction of the integrity of linear populations along the rivers of the Carpathian Mountains." Thus, **unsustainable land management** along riparian habitats in the UA Carpathians is a very strong contributing factor to the establishment of invasive species.

Second, one major ecological issue in the UA Carpathians is unsustainable forestry. As Song and Prots put it (1998), "the human impact increases the diversity of secondary and artificial habitats and decreases the territory of natural and semi-natural forests." In the forestry sector, the Soviet-era management, while favoring policies that maintained overall forest cover quantity, diminished the quality of forests by replacing heterogeneous, complex communities with

homogenous plantations (Kuemmerle *et al*. 2009), a process that had already been initiated under Austro-Hungarian rule and intensified further on. Turnock (2002) points out that "large clear-cuts were generally restocked with spruce to the extent of 95 percent (with some larch and Douglas fir), at the expense of beech and oak, while the average age of the woodlands decreased sharply." Since the second half of the 18th century, beech and oak forests have decreased from 55 to 33% and from 13 to 10%, respectively (Turnock 2002).

Today, as global demand for raw forestry products is booming, the UA Carpathians may lose vast areas of old-growth forests. In an important study on the trends of forest cover change in the Ukrainian Carpathians 1988-2007, Kuemmerle *et al*. (2009) revealed "forest cover increase in peripheral areas, forest loss in the interior Carpathians, and increased logging in remote areas." The authors come to the conclusion that "unsustainable forest use from socialist times likely persisted in the post-socialist period, resulting in a continued loss of older forests and forest fragmentation" (see also Nazarov *et al*. 2001; Zingstra *et al*. 2009). High rates of deforestation are known to increase the frequency and severity of spring and summer floods and decrease the importance of the mountains as a source of moisture (Keeton and Crow 2009). As mentioned above, several of the invasive plants studied here capitalize on the increased levels of disturbance following deforestation around riparian areas. Furthermore, unregulated development of the forestry sector is highly problematic in controlling the spread of invasive plants because creating disturbance-based corridors such as transport roads for wood materials within ecologically resilient forest stands creates (increased disturbance and light availability) or connects (cutting through otherwise unsuitable sites of dense forests) habitats for invasive plant species (von der Lippe and Kowarik 2006). Such corridors are an even bigger issue in single-species forest plantations that can be found in the study area. These plantations lack the structural complexity and hence resilience of heterogeneous natural communities and might be more susceptible to invasion by vascular plants (Toeroek et al. 2003; Sakai *et al*. 2001).

Meanwhile, reforestation has occurred via natural secondary **succession** throughout the Carpathians where farmland and alpine pastures have been abandoned due to urbanization and emigration, and the national government implemented a nation-wide tree planting program (Kuemmerle *et al*. 2008; Zingstra *et al*. 2009; Sitko and Troll 2008). However, the Land Code of Ukraine (2001) allowed for acquisition of private land across the region including abandoned, previously state-owned farmland, which has resulted in high developmental pressures, encroachment upon and fragmentation of natural areas, and thus avenues for invasion by alien plants (Deodatus and Protsenko 2010). Much of the private land is acquired for urban expansion and in particular tourism. Several new ski resorts, among the biggest in Europe, are proposed in the southwestern parts of the mountains (Zingstra *et al*. 2009). Tourism meanwhile has been shown to act as a major stressor to ecosystems around the Carpathian range because this sector has not been well developed to follow principles of **sustainability** (Turnock 2002). Some areas in the Western Carpathians have been characterized by mass tourism, which is accompanied by construction of extensive road networks and resorts that fragment natural habitat and drastically increase anthropogenic pressures to previously "pristine" areas (Turncok 2002). Meanwhile, it has been demonstrated that the rate of plant invasions in nature reserves is positively correlated with the number of visitors to the reserves (Lonsdale 1999). The UA Carpathians are very much susceptible to such negative effects of tourism due to a lack of strong regulations of the infrastructure and tourism sectors (Zingstra *et al*. 2009; Deodatus and Protsenko 2010).

In addition, plans to boost the economy in the region include development of highways and secondary roads, one example being the Madrid-Kyiv motorway mentioned in 2.4. Major highways that go along and cut across the main geological axes of the mountains may impede the function of the UA Carpathians as a bridge connecting the entire mountain range and North and South Europe because roads can pose effective barriers to movement of species and genes (Deodatus and Protsenko 2010; Turnock 2002). For non-native plants and NIPS, on the other hand, expanding transportation networks provide opportunities for introduction and spread. Vehicle transport acts as the major dispersal agent of seeds and increases the propagule pressure for non-native plant species (Zingstra *et al*. 2009; Pyšek and Prach 1994).

Even if former farmland and meadows remain unused, invasion of these habitats by aggressive vascular plants has the potential to retard or prevent natural succession to secondary forests (Ibanez *et al*. 2009). Stands of *Heracleum sosnowskyi*, for example, can cover entire meadows and prevent most native (late-successional) species to become established (see Appendix B).

Lastly, many of the species, for example *Robinia pseudoacacia* and *Acer negundo*, have been used as ornamentals since the 19th century but have only recently been recognized as invasive (Basnou 2006). The species were long regarded as harmless because they most likely exhibited the typical lag phase common to invasion dynamics of most alien species. A lag phase depicts the time of low population sizes between the initial naturalization (escape from controlled cultivation) and exponential population growth and subsequent stark expansion of invaded area (Petit *et al*. 2004; Thuiller *et al*. 2007). Such lag phase can be attributed to (a) low initial population sizes (a sort of Alee effect) and/or (b) low genetic variability of the founder population so that adaptations to the initial ecological inappropriateness of the novel range correspond to the evolution (after a lag phase) of key genetic shifts in the population favoring genotypes with a higher competitive ability over ones producing strong defensive mechanisms (Peterson 2003; Jacobs *et al*. 2004; Sakai *et al*. 2001). But in either case, evidence amounts that repeated introduction events of a species to a novel environment, which occurs mostly through human vectors, is correlated to the eventual success of a species as these events increase the likelihood of a founder population to increase in size and stabilize its genetic structure (Sakai *et al*. 2001).

In conclusion, land use strongly impacts the chances of invasive plant species to establish populations in a nonindigenous habitat. The introduction of NIPS into novel areas in the UA Carpathians is largely enabled by "linear habitats" such as human transport routes or riparian areas. Habitat fragmentation meanwhile creates local foci in which invaders can potentially establish viable populations. Such scattering of several small populations of invasive weeds across a landscape has been observed to enhance the invasion potential of a species as it can invade more neighborhood patches than a larger but more isolated and clustered population can (Mack and Lonsdale 2001; Petit *et al*. 2004). Habitat suitability modeling that includes measures of anthropogenic pressures can thus reveal the importance of such variables on the occurrence of invasive plants and aid in designing development strategies that minimize the chances of invaders to become established and spread (see Chapter 7). Furthermore, future projections can be made that approximate the potential spread of species when invaders are dispersed over long distances with the aid of humans while natural systems come under increasing pressure.

3.2.2 Climate change and spread of NIPS:

Sustainable land management in the UA Carpathians ultimately means proper allocation of protected and actively managed areas. At the same time, determining the extent of these areas depends on predictions of ecosystem responses to climate change – this is true for possible migrations or extinctions of native as well as alien plants under new climate regimes. Apart from landscape features, climatic and resource features are strong limiting factors in determining the distribution of a species. Climatic features determine "the seasonal conditions for establishment, recruitment, growth and survival" while resource features determine the accumulation of minerals fundamental for growth and survival (Thuiller *et al*. 2007; Stern *et al*. 2003; see Chapter 7). Accordingly, increased levels of CO_2 affect plants in two distinct ways.

First, higher atmospheric CO_2 concentrations can directly or indirectly affect resource accumulation in plant tissues. The carbon in CO_2 is used to make sugars during photosynthesis. Thus, increased levels of CO_2 can directly increase the sugar load in plants which is an organism's most important energy source for growth. The energy retrieved from the sugars can also increase the assimilation of major nutrients. For example, it has been determined that elevated atmospheric CO_2 concentrations are positively correlated with nitrogen allocation to reproductive parts in *Ambrosia artemisiifolia* (Brandes and Nitzsche 2006). Furthermore, plants react to a saturation with carbon (following increased accumulation of CO_2)[6] by closing their **stomata** (because CO_2 enters plants via stomata in leaves and stems), which in turn slows transpiration and the loss of water through stomata (Stern *et al*. 2003). If less water is lost by the plant, less must be taken in through the roots. This has two major consequences: (a) plants that require a lot of water for photosynthesis, e.g., fast-growing, early-successional **C_3 plants**, improve their water efficiency in addition to responding positively to elevated CO_2 by quicker growth; and (b) the soil moisture content in an ecosystem may be altered which can cause niche shifts or create new niches favorable to water-demanding plants (Dukes 2000; Stern et al. 2003).

Second, increases in atmospheric CO_2 are correlated with increases in average atmospheric temperatures. Assuming CO_2 concentration levels of 532 ppm and 717 ppm by 2050 and 2100, respectively, the estimated average annual increases in ambient temperatures are about 1-2 °C and 3-4 °C for 2021-2050, and 2071-2100, respectively, while precipitation is expected to maintain current patterns until 2070 and slightly increase in fall and winter and decrease in spring and summer in the Eastern Carpathians thereafter (Bartholy *et al*. 2011). A warming climate thus means, in addition to changes in soil water content, a prolonged growing season, and retreating of limiting climatic factors (i.e., short growing season and frost) into higher altitudes. These changes in climatic regimes will alter existing and open novel habitats, create new niches along temperature gradients, and trigger a latitudinal and altitudinal upward migration of plants (Thuiller *et al*. 2005). In response, species with wide ecological niches and highly adaptable to disturbances will profit from ecosystem changes, and these competitively superior species will also be able to colonize new habitats more successfully.

In conclusion, although many hypotheses on the responses of plants and ecosystems to climate change must still be tested in different ecosystems due to the inherent complexity of interactions,

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[6] There is a saturation level at which plants are not able to assimilate the additional CO_2. This level depends on other limiting factors on growth and reproduction (for more information see Chapin *et al*. 1998; Dukes 2000).

elevated concentrations of CO_2 seem to favor particular groups of plants (Dukes 2000). Research indicates that among these, NIPS in temperate climates, which are generally fast-growing (and sometimes nitrogen-fixing), water-demanding, and opportunistic C_3 plants, have a high potential to profit from climate change and dramatically expand their ranges (Broennemann *et al*. 2007; Dukes and Mooney 1999; Nagel *et al*. 2004; Drake *et al*. 1997). For instance, a greenhouse experiment in which six highly invasive C_3 plants in the U.S. were exposed to three levels of CO_2, showed an average increase of biomass by 46% at elevated concentrations, more than the average increases in biomass known across several hundred plant taxa exposed to elevated CO_2 concentrations (Ziska 2003). The results of this study and other ones (see Dukes 2000; Poorter 1993) suggest that climatic changes in the UA Carpathians will likely enhance the competitive properties of many NIPS; and because these species have wide ecological niches, they are more adapted to migrate northward and into higher altitudes (Guisan and Theurillat 2000).

In contrast, particularly the specialist endemic species in the UA Carpathians that evolved very specific niche requirements might not only be unable to migrate but might also be weakened in their potential response to invaders when climatic regimes change in their current ranges (Thuiller *et al*. 2007). For example, a study by Guisan and Theurillat (2000) demonstrates that specialist plants adapted to gentle slopes will be starkly inhibited in their potential altitudinal upward migration by the greater percentage of steep slopes and different slope angles (due to the conic shape of mountains). Other studies on the impact of climate change on the flora in Europe have demonstrated a high species turnover (more than 40%) in a warmer future (Thuiller *et al*. 2005; Thuiller *et al*. 2007). Such dynamics create levels of disturbances in ecosystems that invaders can capitalize on. While designing land management strategies, it is thus of uttermost importance to consider the threat and minimize the possible future introduction of NIPS to areas of high conservation priorities. Here, analyses of habitat suitability for the establishment and spread of invasive plants under climate change can be of great value as they can, for example, be compared to areas of high conservation priority in order to create appropriate measures of protection.

Looking back at the impacts of land use on the spread of invasive vascular plants, it becomes evident that it is the synergism between these land-use and climatic changes that can greatly influence the rate of invasion. Thuiller *et al*. (2007) developed a great diagram (Fig. 9 below) that depicts the impacts climate and land-use changes have on invasions:
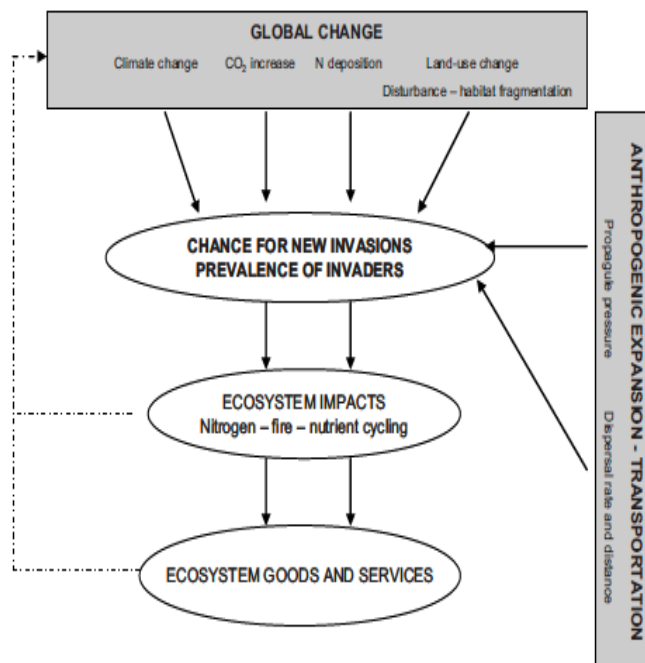
Figure 9: "Impacts of global change on invasion and associated processes" (Thuiller *et al*. 2007)

The diagram depicts the complex feedbacks between invasion and climate and land-use change. Human-caused disturbance and climate change together amplify invasion processes, and these invasions then have impacts that "feed back" to local to global change regimes (Yates *et al*. 2010). For example, native species might be impeded to migrate in response to climate change due to fragmentation of their habitats by human infrastructure such as roads; these barriers meanwhile might operate as corridors for invaders, which further disturb natural habitats and alter ecosystem functions (Chapin *et al*. 1998). Some studies also suggest that elevated atmospheric CO_2 levels slow succession (Dukes 2000). Thus, invaders that function as early-successional species in their invaded range and establish populations immediately after a community has been disturbed might persist in a habitat longer under climate change. Once established therefore, aggressive NIPS, profiting from changes and disturbances to natural ecosystems, might fuel their own propagation in the invaded range, making the call for proactive management particularly compelling in the wake of major transformations to ecosystems across the UA Carpathians.

4. SPECIES DISTRIBUTION MODELING

4.1 Ecological concepts

4.1.1 The ecological niche:

The relationship between species and their abiotic and biotic environments is a central theme in ecology (Begon *et al*. 2006, Gotelli 2008). Assessing the fitness of an (invasive) species therefore requires a theoretical concept of the underlying biological, environmental, and physical gradients determining its distribution. Many models that mathematically approximate the

response of a species to a given set of environmental predictors operate under certain assumptions about the distribution of the response (or likelihood of presence) along the gradient of values for predictor variables in the study area. And even if no such prior knowledge is required, it is nevertheless critical to know what predictors limit the distribution of a species and at what scales they do so (Austin 2002).

The widely accepted *species niche concept* provides such a theoretical framework of causal factors determining the distribution of a species. This concept characterizes the niche of a species as "the hypervolume defined by the environmental dimensions within which that species can survive and reproduce" (Hutchinson 1987, cited in Franklin 2009). The idea of an environmental volume is what differentiates niche from habitat, as the latter is formally only defined as the area where an organism lives (Begon *et al.* 2006). Following Hutchinson's definition, a niche can be further distinguished as *fundamental*, a species' potential survival and reproductive success amidst favorable global environmental conditions such as climate, and *realized*, the actual occurrence of a species in space that depends not only on favorable environmental conditions but also on local biotic interactions (competition, predation, facilitation of dispersal) and anthropogenic influences (see Franklin 2010; Begon *et al.* 2006; Phillips *et al.* 2006; Ficetola *et al.* 2007; Shea and Chesson 2002). The distinction between the fundamental and realized niche is important because it allows an ecologist to determine whether a predictive model is based on theoretical abiotic restraints to the distribution of a species (fundamental niche modeling) or actual field sampling of species distribution (realized niche modeling) (Guisan and Zimmermann 2000; Jeschke and Strayer 2008; Peterson 2006).

The environmental data that predict species distribution in this study represent the species' realized niches. That is so because the statistical response functions of the models rely on spatial **species occurrences**, i.e., locations where a species is actually found, or its realized niche (see Phillips *et al.* 2006). More specifically, climatic variables and their derivatives represent the abiotic, environmental gradients that define suitable conditions for establishment overall, i.e., the fundamental niche, while the topographic variables are indirect indicators for actual restrains to dispersal and biotic interactions due to human presence, i.e., the realized niche (Baker *et al.* 2000; Guisan and Thuiller 2005). Meanwhile, it must be emphasized that the influences of different predictors on the distribution of a species are scale dependent. Climatic variables exert their influence on much coarser scales than topographic ones. Including variables at finer scales therefore generally improves the performance of models, and the accuracy of models is often limited by the available resolution of the data (Ficetola *et al.* 2007).

4.1.2 Equilibrium vs. non-equilibrium:

Another central theme in ecology is the distinction between equilibrium and non-equilibrium of ecological states. The equilibrium paradigm with regards to species distribution assumes that when sampling species occurrence or **prevalence**, there is an equilibrium "between the geographical distribution of a taxon and its requirements on abiotic as well as on biotic site conditions," i.e., the species has a stable niche which is occupied as much as dispersal limitations allow (Dullinger *et al.* 2009; Austin 2002; Peterson 2006). The non-equilibrium paradigm on the other hand assumes dynamic and stochastic environments and thus a constant transient state of species distribution in which equilibrium rarely exists (Dullinger *et al.* 2009).

Statistical distribution models that relate the presence of species to suitable habitat and (pseudo) absence to unsuitable habitat, including the approaches used in this study, assume an equilibrium state between the occurrence of species and environmental factors, "since they do not distinguish between the transient and equilibrium response of species to a stochastically and dynamically changing environment" (Guisan and Zimmermann 2000). The implicit assumption that a study species has occupied its full realized niche is particularly problematic for the NIPS in the UA Carpathians as they are still experiencing exponential population growth and have not yet occupied all potentially suitable habitats. Furthermore, the distribution of the species is highly dependent on anthropogenic disturbances and is thus always as dynamic as these disturbance patterns (Dullinger *et al*. 2009). The study deals with the inaccurate assumption of equilibrium mainly by including anthropogenic disturbance as a predictor variable which (a) approximates a measure of stochasticity and propagule pressure (see Dullinger *et al*. 2009); and (b) calculates suitable habitat more tightly connected to areas corresponding to these disturbance regimes and not to the entire potential range (based solely on environmental variables). Particularly the latter point makes clear that the aim is to model areas where the species are most likely to become established and can potentially migrate from. This approach makes sense when one considers the current establishment strategies of the NIPS studied. All species are confined to linear habitats along relatively high disturbance and long-distance dispersal routes, i.e., riparian zones and roads. These patterns suggest that the species act as specialists in terms of dispersal, and it has been demonstrated that the distribution of specialist invasive vascular plants can be modeled with high accuracy if equilibrium is not achieved (see Evangelista *et al*. 2008).

In addition, the geographic choice of predictor variables reflects the discussion on equilibrium and non-equilibrium. Two approaches are possible: (a) fitting the model in the natural range of the species and then projecting to the invaded range; or (b) fitting the model in the invaded range and projecting to potential source sites in the regions of invasion that have not yet been invaded. In general, it is assumed that the former approach produces more accurate results based on the paradigm that plants conserve their climatic niche when introduced into novel landscapes and that invasive plant species are unlikely to be in equilibrium with their invaded environment (Peterson 2006; Guisan and Thuiller 2005). However, several studies have demonstrated that using environmental variables and species occurrence from the invaded range is more appropriate (a) for species that possess high phenotypic plasticity and thus can shift their niches when introduced into novel habitat; (b) for species that were introduced as food sources or ornamentals and thus experienced artificial selection, making their genetically distinct populations difficult to compare with populations in the native range; and (c) due to the fact that the realized niche in an invaded environment can differ greatly compared to the natural range as species are subject to different types of biotic interactions, e.g., lack of competitors or herbivores (see Dullinger *et al*. 2009; Broennimann *et al*. 2007; Broennimann and Guisan 2008; Ibanez *et al*. 2009; Jeschke and Strayer 2008; Genton *et al*. 2005). The NIPS modeled here (with one exception: *Ambrosia artemisiifolia*) were intentionally introduced as either ornamental or food sources, and comparisons between native and invaded ranges demonstrate that the alien plants occupy distinct habitats in their invaded range (Appendix B; see in particular Bartha *et al*. 2008; Medrzycki 2007). Therefore, modeling solely in the invaded range is assumed to be more accurate.

4.2 Modeling approaches

Species distribution models (SDMs) are static models that relate field observations of the occurrence of a species to predictor variables assumed to control the patterns of occurrence. The relationship is described by formulating statistically or mechanistically (machine-learning) derived response surfaces. SDMs essentially operate in four steps (Fig. 10; see also Franklin 2009; Guisan and Thuiller 2005; Guisan and Zimmermann 2000):

First, one must choose the appropriate data and modeling parameters, or predictor variables. Based on the objectives of the study, species responses to direct (e.g., temperature), resource (e.g., water), or indirect (e.g., slope, disturbance) gradients can be modeled. There is however a tradeoff between precision and generality of the results. That is, direct and resource gradients allows for generality and transferability of the models at large scales because these gradients are global and usually measured at scales of at least 1 km^2. Indirect gradients on the other hand can typically be measured on finer scales and allow for greater precision but poor transferability because they differ between regions, and because "species tend to compensate [for] regional differences in climatic conditions by selecting comparable microsites by changing their topographic positions" (Guisan and Thuiller 2005; Guisan and Zimmermann 2000). Regardless of which types of gradients one chooses to work with, there should be a strong relationship between the occurrence of a species and the predictor variables; and one must avoid correlation between the predictor variables (Franklin 2009). Often times, a researcher is confronted with a large number of possible predictor variables and must determine the best possible subset of the data. Such decision can be based on statistical tests (e.g., principal component analysis, correlation coefficients), on expert knowledge, or both (Franklin 2009).

Second, after a set of suitable predictor variables has been determined, the modeling algorithms extract values for environmental variables at locations of species occurrences. Here, spatially explicit presence points (**response variable**) can be linked to layers of environmental data (predictor variables) at the georeferenced location, and the values of environmental predictors and species distribution within these values are extracted (Phillips *et al*. 2009).

Third, the relationship between predictor and response variables is described through (fitted to) different response functions – the models that define how likely a pixel is to contain the response variable given a set of predictor variables. The algorithms used in this study all use some variations of logistic regression analysis to define the functions, and the outputs are continuous values from 0 to 1. Meanwhile, the algorithms here are either statistical or machine-learning. The former require the user to define the shape of the response (linear, bell-shaped, etc.) prior to modeling while the latter define the shape of the response during the modeling process. Different statistical methods (e.g., **Binomial Test** or **Akaike Information Criterion – Appendix F**) can then be utilized to assess the goodness-of-fit of the models, or how well a value predicted by a model fits an actual empirical or theoretically expected value (Thuiller *et al*. 2009a).

Fourth, the models are then used to predict the potential occurrence of a species temporally or spatially. Predictions are possible because the response functions developed on the data entered into the algorithms can be extrapolated to an entire study area. That is, for every pixel in the study area, which describes a certain combination of values for predictor variables, the

algorithms can predict the probability of species occurrence based on the model calibrated on the occurrence data. The strength of the predictions depends on the accuracy and resolution of values for predictors and sample size of the response variables. That is, if a study area is small but the resolution of layers containing data on predictor variables is large, fine-scale distinctions between suitable and unsuitable habitats may not be possible. Similarly, if the sample size of species occurrences within a study area is small, some value ranges for predictor variables may be under-sampled, thus weakening the accuracy of predictions (Guisan and Zimmermann 2000; see section 5.1.2 for further details).

Lastly, the predictive power of the fitted models is evaluated. To do so, the species occurrence data is usually divided into training and test data. Steps 2-4 use the training data while the predictive power is assessed with the test data. This is done by comparing, at the locations of the test data, predicted values and the actual observed test values using, in the case of this study, threshold-independent evaluation techniques as detailed in section 5.3 (see Thuiller *et al*. 2009a, Frankin 2009). Because the aim of the study is to create maps that accurately predict the potential establishment of NIPS, statistical tests will focus on determining the significance of the predictive performance of the models.
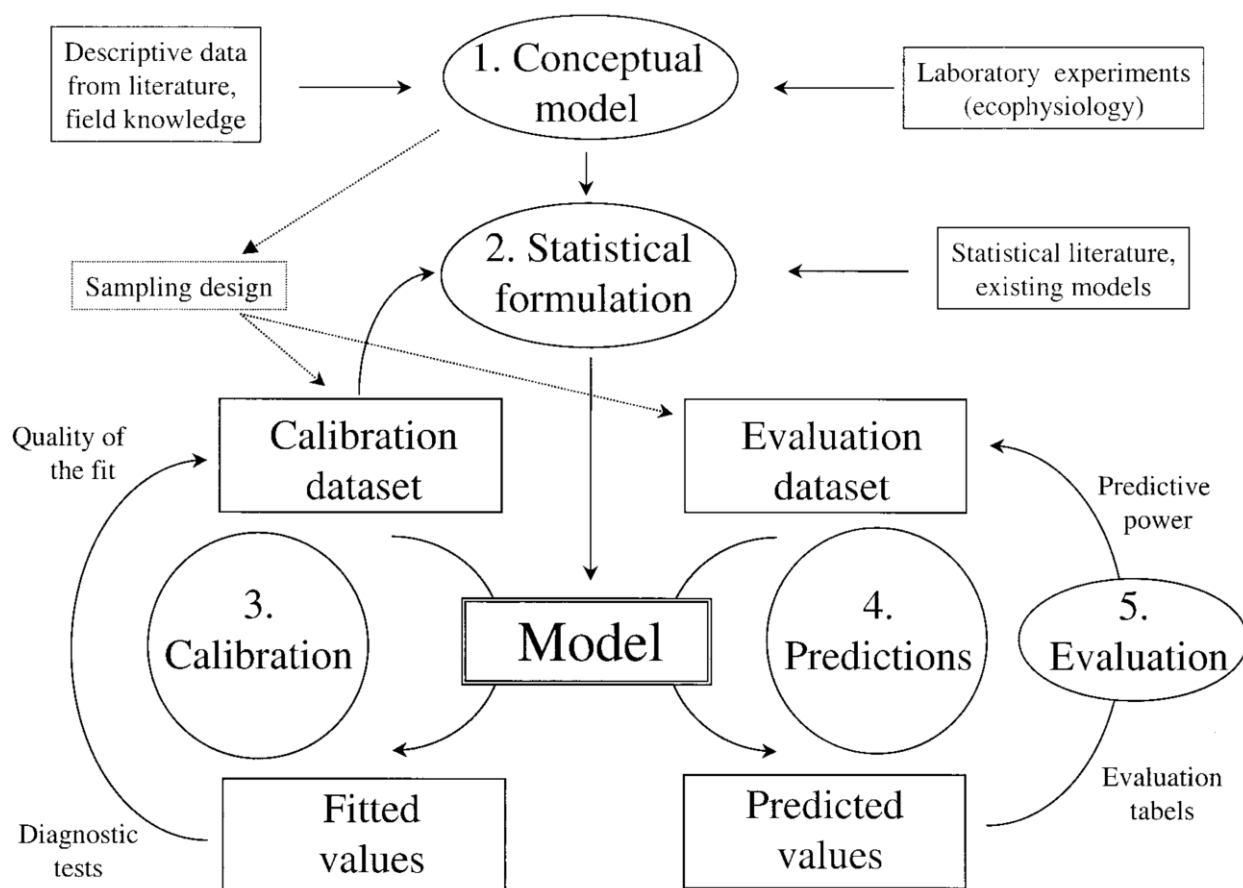
Figure 10: Species Distribution Model (SDM) building process (Guisan and Zimmermann 2000)

It is clear that SDMs operate under simplistic ecological assumptions about the nature of distributions. Complex ecological processes are boiled down to a few layers of data, and interactions between these layers are often not known and difficult to model (Franklin *et al*. 2009). In addition, optimal accuracy can often not be achieved due to the lack of data on causal ecological factors and the necessity to use proxies (Hernandez *et al*. 2006). In this study, for example, economic activity and human footprint are potentially stronger causal factors determining the establishment of NIPS than their proxy, distance to settlements and roads. However, data on these variables are either not available at all or available only on a much coarser scale than required for this study. Nevertheless, SDMs have been shown to be an extremely valuable tool for natural-resource managers because of their apparent predictive power despite limitations (Jeschke and Strayer 2008). SDMs are particularly significant for climate and land-use change studies. Although the performance of projection of fitted models to future scenarios is rarely tested,[7] SDMs are the most important tool in estimating future changes in geographic ranges of species. Thus, assessment of the spread of aggressive NIPS within the UA Carpathians relies on SDMs to gain insight into the potential range expansion of the established alien species, working under the assumption of universal migration potential of the NIPS within the invaded range (Jeschke and Strayer 2008).

5. METHODS

5.1 Data requirements

5.1.1 Study area:

Although the distribution of the invasive organisms is not confined to the political borders that separate the Ukrainian area of the Carpathians from the rest of the mountain range, the choice of the study area (i.e., the UA Carpathian Mountains as described in Chapter 2) has practical as well as ecological applicability. From the practical point of view, the scope of this study, the lack of data on the predictor and response variables for the entire Carpathians, and the objective to provide relevant information for regional and local authorities justify the focus on the UA Carpathians. From the ecological point of view, the UA Carpathians present topographic gradients of values of the predictor variables that limit the distribution range of the invasive plants (Guisan and Thuiller 2005). That is, outside the UA Carpathians, excessive summer heat and soil moisture deficit limit the distribution of most of the NIPS, while within the mountains, the shortening of the growing season and cold temperatures at higher elevations do the same. Ensuring that the study region encompasses relevant environmental gradients for a species, particularly limiting factors, decreases the risk of faulty model fitting (see section 4.2). Furthermore, as has been detailed in previous chapters, the UA Carpathians have been chosen for this study due to an urgent need for an assessment on plant invasions in this region. The (potential) impacts of expanding populations of NIPS on the high levels of biodiversity in the region and implications for natural-resource management have not been analyzed thus far.

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[7]It is possible to test an algorithm's ability to project to changed conditions by fitting the models to past conditions (e.g., climate and past species occurrences) and testing the projections to current conditions with current species occurrences.

5.1.2 Species presence data:

The potential distributions of the eleven NIPS identified as highly aggressive (see Chapter 3; Table 2) are modeled. Each of the species is modeled individually, with the exception of *Solidago* spp. and *Reynoutria* spp. These two taxa have very similar physiologies and realized niches in their invaded range, and the probability is high that mistakes were made in older datasets (herbarium records and literature data) in identifying the genera as separate species (Prots, personal communication). Therefore, each genus/taxon is modeled as one complex, i.e., the complex of *Reynoutria* spp. (*R. japonica* and *R. x bohemica*) and the complex of *Solidago* spp. (*S. canadensis* and *S. gigantea*).

For each species/taxonomic complex, georeferenced locations are available from herbarium specimens, field-observation records, and literature data (see Table 2 for list of plants modeled and number of presence points). The records are based on long-term studies, some reaching back as far as 40 years, and have been collected from herbaria of 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). Meanwhile, the majority of all records (85-95% depending on species) consist of field-observation data that have been collected by B. Prots from years 1990-20011 and by B. Vykhor (2009-2011). These records are georeferenced to a precision of at least 10 m. When observation points were taken, all locations were at least 50 m apart in order to avoid spatial autocorrelation, e.g., sampling two records for one individual consisting of several attached clones. There is a potential source of error in the herbaria data due to uncertainty in the accuracy of the presence locations and resulting uncertainty in georeferencing accuracy (for a review on potential errors in museum data see Newbold 2010). Thus, the potentially most erroneous locations indicated by herbaria records were revisited to ensure the actual presence of the species.

Species	Total number of presence records
Acer negundo	339
Ambrosia artemisiifolia	240
Echinocystis lobata	367
Helianthus tuberosus	343
Heracleum sosnowskyi	563
Impatiens glandulifera	265
Reynoutria spp. (*R. japonica* and *R. x bohemica*)	581
Robinia pseudoacacia	365
Solidago spp. (*S. canadensis* L. and *S. gigantea*)	330

Table 2: Highly invasive plant species studied and total number of presence records used for distribution modeling in the Ukrainian Carpathians

In addition, collection of recent records (2009-2011) was accomplished along major environmental gradients ecologically relevant to the distribution of the NIPS (i.e., climate and location in relation to water and anthropogenic structures) in order to prevent sampling bias. The detection of sampling bias is important because one must assure that records along linear

corridors (roads and rivers) are truly representative of the species' distribution and not an artifact of oversampling in easily accessible areas (see Phillips *et al*. 2009). Spatial bias can have serious consequences for modeling because it may result in environmental bias. That is, if species are conveniently sampled along roads and rivers although they are also present in farther distances from these locations, one may erroneously under-sample the environmental gradients the species occupy (e.g., soil moisture) and thus produce flawed prediction maps (see Newbold 2010; Phillips *et al*. 2009). Lastly, only locations where permanent populations have become established (occupying a sampling unit of 50 m^2 in consecutive years) have been included in the modeling in order to minimize model inaccuracies due to **casual**, opportunistic observations.

All data are in a presence-only format. Presence-absence data sets are not available for the species studied here and, even if available, could be potentially misleading for the reasons explained above, i.e., the species are not in equilibrium with their environment. Nevertheless, the SDM approaches used in this study (see below) require a basis for distinguishing between suitable and unsuitable habitat. Maxent does so by sampling 10,000 random background points from the entire study area, and BIOMOD extracts 10,000 random pseudo-absence points from the study area outside a radius of 3 km around each presence point.

5.1.3 Predictor variables:

A set of different environmental predictor variables is selected based on the review of similar ecological studies that chose the optimal variables to reflect "the three main types of influences on the species" (Giusan and Zimmermann 2000): limiting factors controlling the eco-physiology of a species (e.g., extreme temperature events), natural or human-induced disturbances (e.g., floods, traffic), and resources that can be assimilated by organisms (e.g., water, light energy). Initially, 20 bioclimatic and 5 topographic/land-cover variables were available for modeling. Of the 20 bioclimatic variables, 19 were retrieved as ESRI grids from the WorldClim global database (Hijmans *et al*. 2005). The climatic layers "were generated through [thin spline] interpolation of average monthly climate data from weather stations on a 30 arc-second (or 1 km²) resolution grid" (Hijmans *et al*. 2005). Bioclimatic variables used in this study were derived from the monthly values for a particular region. The 20th bioclimatic variable, sum of active temperatures > 10°C, as well as vector maps on hydrology and roads, a digital elevation model (DEM), and land-cover and ecoregion (based on relative climatic regimes – see Fig. 3A) data were provided by I. Kruhlov from the Geography Department of the University of Lviv, with the permission of T. Kuemmerle and P. Hostert (Hostert *et al*. 2008; Kruhlov 2008; Kuemmerle *et al*. 2009). Layers relevant to the ecology of the NIPS, proximity to water and to settlements and roads, were derived from these maps using the *simple (Euclidean) distance* function in ArcMap 10. Because the establishment of the species and their distribution is also limited by relative changes in elevation, i.e., steep slopes are barriers to expansion, slope is included as a variable. The main reason to use slope as a separate variable instead of including it as a cost factor in the proximity calculations and thus deriving effective-proximity maps is that creating a cost layer out of the continuous slope data would have required subjective partitioning of slope values into categories.

Initial models were run with all or many of the variables and consistently demonstrated in both Maxent (**jackknife** and **binomial** tests – see Appendix F) and BIOMOD (**stepwise regression –**

Appendix F) that choosing fewer relevant bioclimatic variables instead of the 20 available ones and particularly including slope and distance to water and human structures as variables significantly improved the performance of the models. In general, environmental variables with a Pearson's correlation coefficient r > 0.9 and that contributed little to model fitting were not included into the models. The final environmental variables are thus: minimum temperature of coldest month (*mintcold*), maximum temperature of warmest month (*maxtwarm*), sum of active temperatures > 10°C (*sat*), proximity to water (*s_dist_water*), proximity to settlements and roads (*s_dist_sett_r*), and slope (*slope*) (see Table 3 below).

Variable	Abbreviation	Measured in	Original geometric accuracy/ resolution	Description
Minimum temperature of coldest month	*mintcold*	°C x10	1 km (resampled to 30 m)	Invasive species tolerate a wide range of environmental conditions but are sensitive to extremes; periods of extreme frost diminish survival of these generalists (see Ibanez *et al.* 2009).
Maximum temperature of warmest month	*maxtwarm*	°C x10	1 km (resampled to 30 m)	The NIPS do not tolerate excessive xerothermic (dry and hot) conditions (see Ibanez *et al.* 2009).
Sum of active temperatures > 10°C	*sat*	°C	1:100,000 ecoregion map (rasterized to 30 m)	Sat approximates the length of the growing season, and species are sensitive to short seasons at upper altitudes (see Pearson *et al.* 2002).
Proximity to water	*s_dist_water*	m	1:200,000 hydro map (rasterized to 30 m)	All species become established predominantly along river corridors; water plays a vital role for the soil moisture and water balance of the species and provides the most important vehicle of long-distance dispersal and accessibility of suitable habitat (see Evangelista *et al.* 2008; Herborg *et al.* 2007; Peterson 2006).

Proximity to settlements and roads	*s_dist_sett_r*	m	1:200,000 roads/settl. map (rasterized to 30 m)	Human settlements and roads provide a measure of disturbance that can be beneficial to the spread of the invasive species, provide corridors to suitable habitat, and approximate propagule pressure (see Dullinger *et al*. 2009; Ibanez *et al*. 2009; Thuiller *et al*. 2006).
Slope	*slope*	degrees	30 m	The geographical distribution of all species is limited by steep slopes (to different degrees dependent on species); most species are confined to flat river valleys; slope also determines the distribution of anthropogenic structures (see Evangelista *et al*. 2008).

Table 3: Description of predictor variables used for distribution modeling of NIPS (non-native invasive plant species) in the Ukrainian Carpathians

The DEM held the finest resolution (30 x 30 m). Therefore, to fit the resolution of slope, the climatic variable were resampled to a resolution of 30 m^2 using the *cubic resampling* function in ArcMap 10. Similarly, the sum of active temperatures was interpreted (by contour interpolation) from the ecoregion map at a resolution of 30 m². Lastly, hydrology, infrastructure, and settlement maps were rasterized to the same resolution (see Table 3). This yields a 9460 x 7380 grid, with 23,357,345 pixels containing values for all variables. All layers are projected onto the UTM grid, zone 34 with WGS84 datum.

Because the bioclimatic variables and slope were produced by various means of interpolation/generalization, their values are by definition spatially autocorrelated, i.e., each value is to some degree dependent on the values of its neighbors. This however is not a major problem for model calibration as long as the species records do not exhibit environmental autocorrelation. In fact, it may improve the performance of the models because inaccuracies in georefencing of the data, i.e., a presence record that has inaccurate coordinates assigned to it and is thus positioned into a cell that does not correspond to the variable value at the actual position of the record, may be cancelled out by the similarities of the neighborhood cells (Newbond 2010). At the same time, it must be noted that, while the chosen bioclimatic variables are important ecological factors, ordinary least-square regression (with **Pearson's r statistic**) showed strong correlation ($0.9 > r > 0.8$) between the climatic variables (i.e., maximum and minimum temperatures and sum of active temperatures). Therefore, while the algorithms chosen for modeling can handle correlation of a small number of predictor variables when fitting the models, interpretation of variable importance must be done cautiously, as will be explained below.

Lastly, the choice of a combination of climatic and topographic/land-use[8] variables is based not only on ecological relevance but also on a compromise between generality and precision. Although the climatic variables represent direct resource gradients, they are less precise (1 km resolution) than topographic and land-use characteristics. In addition, because the bioclimatic data were interpolated from records of climatologic research stations, their accuracy depends on the number of research station from which data could be obtained. Only few stations can be found in the UA Carpathians, which introduces uncertainty in the interpolation of the variables. Meanwhile, the vector data originally have a coarser resolution than 30 m because a scale of 1:200,000 corresponds to a resolution of approximately 100 m (Goodchild 1997). Thus, the DEM is essential to alleviate some of the issues associated with coarse data, most importantly the inaccuracy of model predictions at fine resolutions. Meanwhile, as one objective of the study is to model predictions of species distribution under future climatic changes, climatic variables must be incorporated. In conclusion, by choosing variables that operate at different scales, a compromise between model accuracy based on precise data (reliance on topographic/land-use variables) and the ability to generalize to future scenarios (reliance on climatic variables) is made (see Guisan and Zimmermann 2000).

5.2 The modeling algorithms

5.2.1 Maximum Entropy – Maxent:

Maxent modeling is a general-purpose machine learning method for making inferences from incomplete information (Phillips *et al*. 2006). Maxent assumes that "a probability distribution [of suitable habitat] with maximum entropy (the most spread-out, closest to uniform), subject to known constraints [the response function defined on the predictor variables], is the best approximation of an unknown distribution because it agrees with everything that is known but avoids assuming anything that is not known" (Franklin 2009; Phillips *et al*. 2006). The software application for SDM is freely available at: http://www.cs.princeton.edu/~schapire/maxent/. It has specifically been developed for presence-only data because it does not make assumptions about absences. Maxent estimates two probability distributions, a probability distribution of predictor variables over presence locations and probability distribution of predictor variables across the study area, and defines response functions based on these distributions. The values for the response variable (suitability of an area for the establishment of NIPS) in the entire study area are then estimated by finding the most uniform distribution of suitable areas given the constraint "that the expected value of each environmental predictor variable under this estimated distribution matches its empirical average (average values for the set occurrence data)" (Hernandez *et al*. 2006; see also Phillips *et al*. 2006; Elith *et al*. 2011; Dudik *et al*. 2007). Maxent has been shown to outperform other presence-only modeling methods.[9]

For the study area, the background data (all the pixels in the study area) are treated as potentially available habitat and compared to habitat use, which is determined from the presence locations,

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[8] When referring to land use in the context of modeling from now on, roads and settlements are meant.
[9] For further information on the advantages of Maxent see Phillips *et al*. 2006; Franklin 2009; Elith *et al*. 2011.

based on density distribution of the six predictor variables within a sample of the entire study area and at presence locations. Fig. 11 demonstrates the derivation of density distributions.
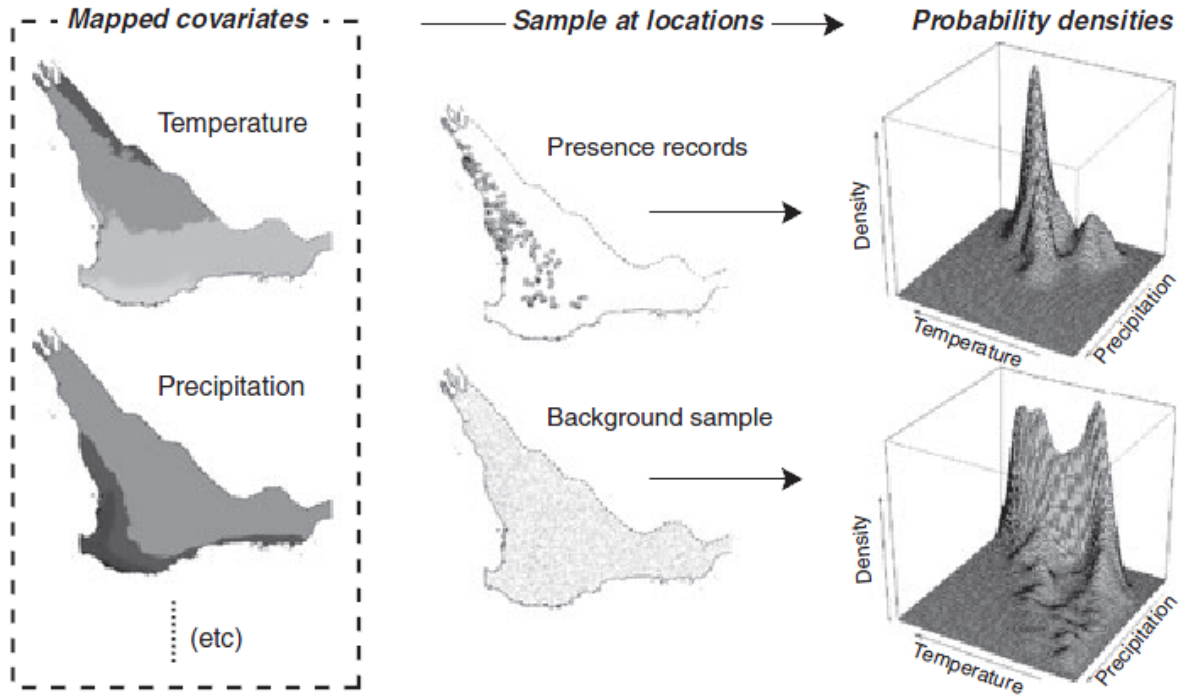
Figure 11: Illustration of density distributions derived from two covariates (i.e., predictor variables) at presence locations and background samples (Elith et al. 2011)

The Maxent algorithm attempts to minimize the distance (relative entropy) between $f_1(z)$ and $f(z)$, the probability densities of predictor values at presence locations and background sample, respectively, and calculates the ratio of $f_1(z)/f(z)$ using the following formula:

$$f_1(z) = f(z)e^{\eta(z)};$$

where $\eta(z) = \alpha + \beta h(z);$

and α is a normalizing constant that ensures that $f_1(z)$ sums to 1, β is the vector of weighting coefficients that determine the contribution of each feature, and $h(z)$ is the vector of features (functions of predictor variables). Because the model is exponential, $\log(f_1(z)/f(z))$ is performed to create a continuous logistic output. Mathematically, the algorithm is very similar to generalized regression used in BIOMOD (see section 5.2.2; Appendix C). The main idea is that, when estimating $f_1(z)$, many types of distributions are possible depending on how the predictors are arranged and weighted. Maxent solves this problem by assuming that the best fitted density distribution is one that minimizes the distance, or relative entropy, to $f(z)$. The rules, or functions, of how the probability distributions are determined and matched in multivariate space are described by the features, or linear transformations (here $h(z)$) of potentially complex relationships between the density of predictors and presence/background locations. The features are fitted into one complex model. The interactions between the features can be linear (adding

predictors), products (multiplying combinations of predictors where interactions exist), quadratic (square of variable to detect variation/tolerance to unsuitable conditions), threshold/hinge (returning values of 0 or 1 based on threshold values for each predictor variable), and categorical (for categorical variables) (Elith *et al*. 2011, Phillips, *et al*. 2006, Phillips *et al*. 2009).

Each of the nine species/taxa is individually modeled with Maxent. All feature types are enabled. For each species, 80% of the records are 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 is minimized by the 5k cross-validation. This method divides the occurrence data into five equal-sized folds, and models are created leaving out each fold in turn. The left-out fold is used for evaluation. A final run will be made for each species using all the presence records for model fitting in order to derive the most robust classification for visual interpretation (see Hernandez *et al*. 2006). In order to minimize the dependence of model results on a particular sample of background points, all modeling is done twice, each time choosing a different random seed of background points.

5.2.2 Biodiversity Modeling - BIOMOD:

BIOMOD models habitat suitability using nine common techniques in species distribution modeling: Generalized Linear Models (GLM), Generalized Additive Models (GAM), Multivariate Adaptive Regression Splines (MARS), Classification and Regression Tree Analysis (CTA), mixture discriminant analysis (FDA), Artificial Neural Networks (ANN), Generalized Boosted Models (GBM), Random Forests (RF), and a Rectilinear Envelope (SRE) (see Appendix C for full description of techniques; Thuiller 2003; Thuiller *et al*. 2009). All techniques can be characterized as either statistical or machine-learning, although the debate on the exact definition of the methods is ongoing (Franklin 2009). The former includes GLM, GAM, FDA, and ANN, and modeling is based on a predefined form of distribution of the response variable, which then determines how a regression function is fit to describe the relationship between predictor and response variables. The latter includes CTA, MARS, GBM, RF, and SRE, and modeling requires algorithms to "learn" the response function directly from the species data that is analyzed without assuming a certain distribution (Glossary; Franklin *et al*. 2009; Hastie *et al*. 2009). The greatest advantage of BIOMOD is the ability to model the distribution of species using several methods and thus compare the results of the various techniques. Fig. 12 below demonstrates the BIOMOD working process.
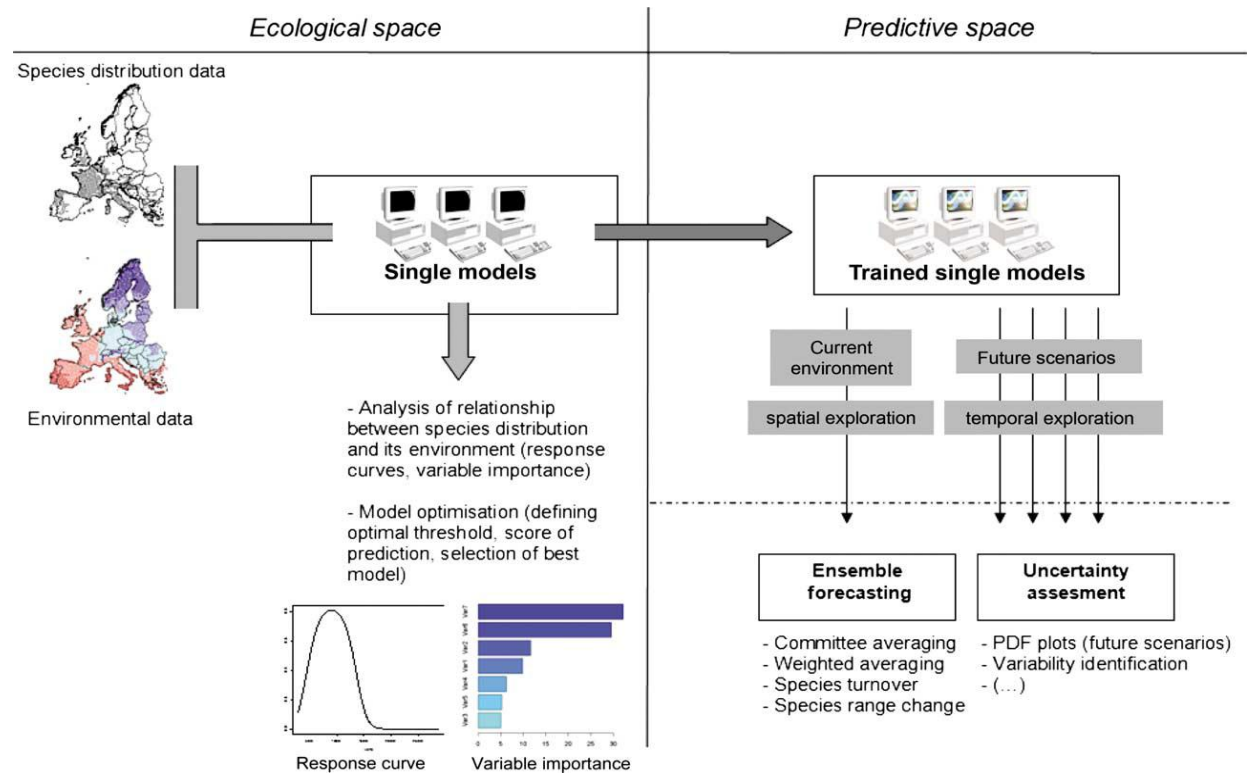
Figure 12: A schematic overview of the modeling processes occurring in BIOMOD (Thuiller *et al.* 2009)

Albeit using different strategies, both statistical and machine-learning approaches utilize regression analysis to fit the models, and it is important to highlight its basic principles here. In linear regression, the response variable, Y, is predicted through a linear function of a vector of multiple predictor variables, $\mathbf{X} = (X_1, ..., X_n)$. The general equation is:

$Y = \alpha + \beta_1 X_1 + \ldots + \beta_n X_n + \varepsilon$, where β are the coefficients, ε is the error term and α the intercept.

However, because the relationship between predictors and response are not necessarily linear, and because the response variables in this study are not normally but binomially (presence/absence) distributed, the regression equation must be expanded to include more complex terms (as is done in Maxent with features) and transformed to account for the binomial distribution. Incorporating non-linear interactions between the variables and a logistic transformation, for example, the equation becomes:

$$g(E(Y)) = LP = \alpha + \beta_1 X_1 + \beta_1 X_1^2 + \ldots + \beta_1 X_1^n + \ldots + \beta_n X_n + \beta_n X_n^2 + \ldots + \beta_n X_n^n$$

and $g(\ldots) = \left(\dfrac{p}{1 - p} \right)$.

Here, $\beta_1 X_1^n$ the nth polynomial term for the predictor X_1, which produces nonlinear response curves, and LP is the linear predictor and is the result of ordinary regression above. The expected value of Y is however not equal to LP but instead related to it through a link function $g(\ldots)$. The logistic regression ln(...) is such a link function. In essence, for each value of the predictor variables, the probability of species presence (p) is calculated, and then the natural logarithm (ln)

of the ratio p = E(Y) to 1 − p is taken (Franklin 2009). All the models in BIOMOD use some variation of linear or logistic regression for model fitting.

For this study, five of the techniques known to perform well in similar studies were chosen and are: GLM, GAM, MARS, GBM, and RF (Franklin 2009; Phillips *et al*. 2009). The predictive performances of the models generated by the five algorithms are compared using the receiver operating characteristic (ROC) curve as explained in the next section. Based on the results, the most accurate model, i.e., the one with the highest scores for the area under the curve (AUC) that at the same time does not overfit the model, for each species is chosen for projections (Thuiller 2003; Appendix D).

Unlike Maxent, which does not explicitly regard the background as pseudo absences but rather as potential habitat, the algorithms in BIOMOD are discriminative and rely on binary presence/absence data, and pseudo absences must thus be drawn from the background. This is accomplished with the *NbRepPA* function, which is calibrated to extract 10,000 random background points at a minimum distance of 3 km from each presence location (see Thuiller *et al*. 2009a). The procedure is repeated two times to minimize the dependence of the set of pseudo absences on one particular extraction.

Similar to Maxent, BIOMOD is able to split the distribution data into several groups, leave one group out of model fitting each turn, and cross-validate fitted models with the left-out group. In order to compare the results between models within the BIOMOD framework and between BIOMOD and Maxent, a 5k cross-validation is performed (see Thuiller *et al*. 2009b). Just like in Maxent, a final run is made for each species/taxonomic complex using all the presence records for model fitting in order to derive the most robust classification for visual interpretation.

To summarize, 648 models are run, 72 per species/taxonomic complex:

2(5 repetitions Maxent + 1 final model Maxent) + 2x5(5 repetitions BIOMOD + 1 final model BIOMOD)] x 9(species/genera) = 648

5.3 Model evaluation

The accuracy of model predictions in Maxent and BIOMOD is evaluated by adaptations of the confusion matrix:

Figure 13: Confusion matrix: a – true positive;
b – false positive (commission error);
c – false negative (omission error);
d – true negative (Fielding and Bell 1997);

Measure	Calculation
Prevalence	$(a + c)/N$
Overall diagnostic power	$(b + d)/N$
Correct classification rate	$(a + d)/N$
Sensitivity	$a/(a + c)$
Specificity	$d/(b + d)$
False positive rate	$b/(b + d)$
False negative rate	$c/(a + c)$
Positive predictive power (PPP)	$a/(a + b)$
Negative predictive power (NPP)	$d/(c + d)$

Figure 14: Measures of accuracy derived from the confusion matrix; N = total number of observations (Fielding and Bell 1997);

The approach is to estimate *commission* (a pixel is described as suitable where it is actually unsuitable background/pseudo absence) and *omission* (a pixel is described as unsuitable background/pseudo absence where it is actually suitable) or the absence of both (see Fielding and Bell 1997). In order to measure omission and commission, the logistic suitability indices displaying continuous data must be transformed into binary data (suitable/unsuitable, presence/absence, or +/-) based on a threshold value. A model can then be tested for omission rate and 1 - commission (the fraction of the pixels correctly predicted as suitable). The choice of a threshold in the suitability values is however problematic because several distinct modeling tools are used in this study and each might assign different optimal thresholds, which then affect the comparison of predictive performance between BIOMOD and Maxent (Phillips *et al*. 2006; Thuiller 2003). To ensure optimal comparison between the different algorithms, a threshold-independent method, the receiver operating characteristic (ROC) curve, is used to measure predictive power.

Using test data, the ROC plots model *sensitivity* on the *y* axis against 1 - *specificity* on the *x* axis for all possible thresholds. S*ensitivity* is the fraction of presence locations correctly predicted to overlay suitable habitat, and *specificity* is the fraction of background/pseudo-absence locations correctly predicted to overlay unsuitable habitat. The area under the ROC curve (AUC) can then be interpreted as "the probability that a random positive instance and a random background/negative instance are correctly ordered by the classifier" (Phillips *et al*. 2006; see also Evangelista *et al*. 2008). For example, an AUC value of 0.8 indicates that 80% of the time when a presence and background/pseudo-absence site are drawn at random, the first will have a higher predicted suitability value than the second. The AUC is independent of the relative number of omissions and commissions and can therefore be used to compare model results between Maxent and BIOMOD.

The statistical significance of the AUC can be determined by comparing the results to random predictions, which would have an AUC of 0.5. Guisan *et al*. (2007) propose a classification scheme to assess the significance of AUC values above 0.5: 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 and Strayer 2008). However, because the AUC does not consider the significance of predicted probability values (Lobo *et al*. 2007), a *Wilcoxon ranked sum test* is applied for each model and each species to test whether the suitable predictions have a higher score than a set of background predictions randomly sampled from the study area (for further explanation see McDonald 2009; Phillips *et al*. 2006).[10] The nominal variables are test locations (presence) and 10,000 background/pseudo-absence points, and the measurements variable is habitat suitability as determined by the algorithms.[11] Lastly, in order to see how Maxent and BIOMOD AUC results differ between the algorithms, a *paired Wilcoxon signed-rank test* is performed to test whether there are significant differences of model accuracy between the best-performing model in BIOMOD and Maxent (Broennimann and Guisan 2008). The statistical testing is performed using the *stats* package in the R statistical software (R Development Core Team).

5.4 Variable importance

Maxent and each model in BIOMOD assess the contribution of each predictor variable to the model. Both software packages use specific internal procedures to determine the contribution/importance of each of the six predictor variables to the final model. Maxent utilizes the jackknife test to measure model performance. This test fits presence data to each predictor variable independently leaving out the other five; and then excludes each variable in turn, creating a model with the remaining variables (Phillips 2010). The individual models in BIOMOD meanwhile use different internal measurements, based on either stepwise regression or classification error rates. A list of measurements in all algorithms and their results can be found in Appendix F. Meanwhile, both Maxent and BIOMOD provide a permutation test: after the final model has been calibrated using model-specific measures of variable contribution (expressed as coefficients in regression), each predictor is randomly permutated in turn, and the decreases in model performace (AUC on training data) are recorded (Phillips 2010; Thuiller *et al*. 2009a). The results of the permutation test across models are used to compare the importance attributed to predictors in Maxent and the algorithms in BIOMOD.

5.5 Climatic and land-use projections

Both Maxent and BIOMOD estimate habitat suitability under different conditions by applying a model trained on one set of environmental layers to another set of environmental layers – a

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[10] Maxent applies the binomial test on test significance of prediction; the statistic tests the null hypothesis that the omission rate is not significantly better than expected under a random prediction for a given area (Phillips 2010). BIOMOD does not utilize this statistic.

[11] Note that unlike Maxent, BIOMOD does not display information on the presence points that are reserved for testing during each cross-validation run. Thus, the Wilcoxon ranked sum test for BIOMOD results is performed on the predictions for all the presence points (not just test points) generated by each cross validation and then again on five subsets of the data for each cross validation (splitting the presence data in five portions).

process called "projection" (Phillips 2010; Thuiller *et al.* 2009). Because regional interpretations of the climate and land-use change scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) are largely missing for the Ukraine, this study applies four simple projections based on average assumed temperature shifts by 2050 and 2010 and high and low anthropogenic pressure. Climatic projections assume the A1B scenario developed by IPCC Special Report on Emission Scenarios (SRES): an estimated increase in CO_2 concentration levels of 532 ppm and 717 ppm by 2050 and by 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.* 2011). Their calculations extend into the UA Carpathians and are used to adjust the predictor variables according to the proposed increases in temperature, which are an average of +1.8°C and +3.8°C in winter and +1.5°C and +3.5°C in summer by 2050 and 2100, respectively. Based on these increases, new values for the bioclimatic variables are created through simple addition of the mean increases for each pixel value and represent the new set of environmental variables used for projections.

Meanwhile, future distributions of invasive species cannot be predicted accurately without incorporating changes in anthropogenic pressures on ecosystems (Thuiller *et al.* 2006). Based on a review of literature elaborating on scenarios of future land-use change (Bouma *et al.* 1998), two simple scenarios are developed: (a) habitat fragmentation by means of human development will not increase above the current status and intensification of land-use will not occur at significant levels due to low economic development and/or strong environmental protection; and (b) habitat fragmentation will gradually increase and more land around settlements and roads will be disturbed due to high economic development and/or weak environmental protection. The former scenario assumes that the distance to any given potential anthropogenic pressure point (i.e., roads and settlements) will have no net increase or decrease. Thus, changes in the climatic regimes for 2050 and 2100 are modeled without incorporating changes to the land-use variables. The latter scenario meanwhile assumes a net decrease in the distance to any given potential human introduction point because there will be more such points and the impact of existing points may be greater (for a similar approach see Rouget and Richardson 2003). That is, for any pixel in the study area, the distance to roads and settlements that has been determined for current conditions will decrease by 10 and 30% by 2050 and 2100, respectively. In conclusion, four future scenarios are modeled: (i) climate change/low economic development by 2050; (ii) climate change/high economic development by 2050; (iii) climate change/low economic development by 2100; and (iv) climate change/high economic development by 2100. To test whether there is a significant range expansion across algorithms, *a paired Wilcoxon signed-rank test* is performed.

It must be kept in mind meanwhile that projections of species distribution into the future are problematic due to the inherent uncertainties in developing regional scenarios of climate and particularly land-use change. Thus, the scenarios are purely illustrative in the sense that specific regional climate-change scenarios for the UA Carpathians have not been developed and only one scenario per timeframe is used; and the land-use projections consist of two overly simplistic scenarios and lack many important variables such as projections of environmental protection, population growth, or economic development (see Verburg *et al.* 1999; Rounsevell *et al.* 2006). The projections are primarily intended to portray general trends and estimate the potential of the NIPS to profit from climate and land-use changes.

5.6 Visual comparison of results

Besides comparisons of AUC values, a key point of the study is to visually compare and combine the Maxent and BIOMOD maps in order to create habitat suitability maps that profit from both algorithms. To do so, predictions for current distributions and future projections calibrated on all presence points are transformed into binary suitable (= 1) unsuitable (= 0) values using an optimized threshold based on the ROC curve which maximizes the percentage of correctly predicted presences and background/pseudo absence points. The resulting maps are combined using the *combine* function in ArcMap 10.

6. RESULTS

6.1 Accuracy of model predictions

Across scenarios (averaged over species), AUC values on test data for both Maxent and the best models in BIOMOD are statistically significant ($p < 2.2E-16$), as determined by the *Wilcoxon ranked sum test*. Furthermore, *the paired Wilcoxon signed-rank test* shows that the best performing BIOMOD models continuously display significantly higher AUC scores than the equivalents in Maxent (Table 4).

	Maxent	BIOMOD
Acer negundo[*]	0.965	0.987
Ambrosia artemisiifolia[*]	0.968	0.989
Echinocystis lobata[*]	0.96	0.985
Helianthus tuberosus[*]	0.956	0.983
Heracleum sosnowskyi[*]	0.929	0.97
Impatiens glandulifera[*]	0.956	0.981
Reynoutria spp. (*R. japonica* and *R. x bohemica*)[*]	0.941	0.983
Robinia pseudoacacia[*]	0.941	0.978
Solidago spp. (*S. canadensis* and *S. gigantea*)[*]	0.958	0.99

Table 4: Average area-under-the-curve (AUC) scores on accuracy of models predicting distribution of invasive plants in the Ukrainian Carpathians; AUC values averaged over 5k cross-validation for 1st background/pseudo-absence run; * = all predictions significant at $p < 2.2E-16$ (*Wilcoxon rank sum test*); BIOMOD has significantly higher scores for all runs ($p = 0.001$)

Meanwhile, it must be noted that both Maxent and BIOMOD predict with great accuracy as the AUC values for all species are higher than 0.9 (see Guisan and Zimmermann 2000). Differences in AUC values between the algorithms can be in part explained by the tendency of presence/absence algorithms (i.e., all models in BIOMOD) to model potentially suitable habitats to very closely approximate empirical data (i.e., the values of predictor variables at actual presence locations). That is, Maxent conceptually regards all unoccupied space in the study area (the background) as potentially suitable and restricts the suitability based on similarities between the average values of a background pixel to averages at presence locations. Meanwhile, the algorithms in BIOMOD choose random locations at a prescribed distance from presence locations as absence of species and thus assume a certain set of locations (and the pixel values

overlaying these locations) to be strictly unsuitable – an assumption that constricts the distribution of potentially suitable areas for introduction. Maxent thus produces logistic outputs with a greater range (few highly suitable areas) and gives more leeway to commission and omission errors; while BIOMOD does the exact opposite (see Fig. 15). Models that are fitted closely to empirical data may actually cause more errors if the species modeled have wide niches, but the NIPS modeled here become established along narrow linear habitats and act rather as specialists in terms of introduction pathways to novel areas and establishment of viable populations (at least at the scale of this study), giving BIOMOD algorithms a slight advantage.

In conclusion, considering the tendency of presence/absence models to fit closely to empirical data, the differences in predictive performance between algorithms are minimal. The interspecific differences within Maxent and BIOMOD are also small and cannot be clearly attributed to the ecologies of the species (e.g., wider vs. narrower current niches) and must therefore depend on model fitting.

6.2 Suitability predictions for current conditions

Suitable habitats for the eleven NIPS to become established are predicted strongest along large rivers and roads at elevations up to approximately 600 m above sea level, corresponding to the warm to moderately warm climatic zones. Fig. 15 below shows the suitability map derived for *Acer negundo* (see Appendix E for maps of all species).
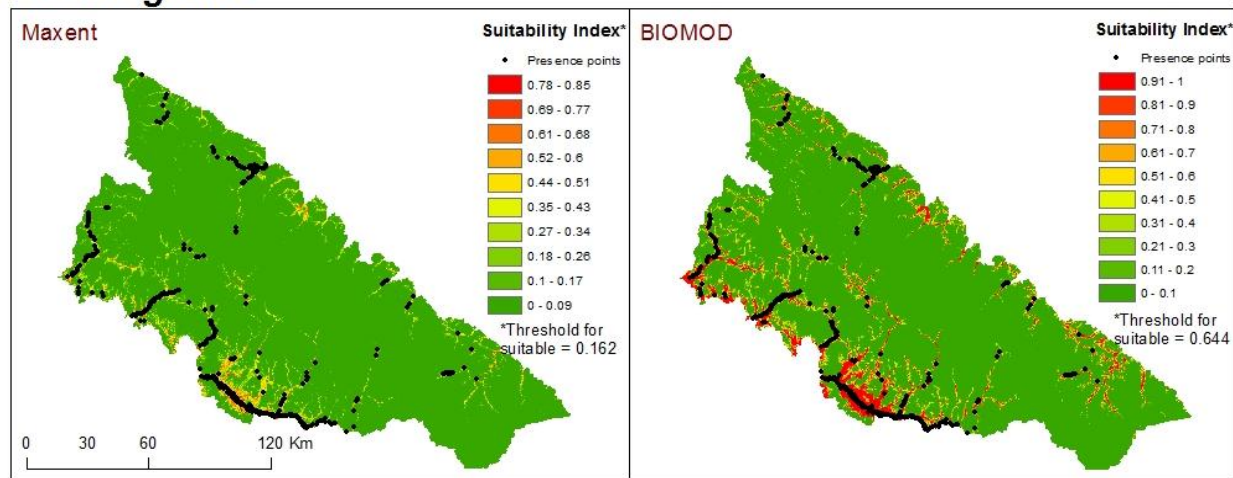
Figure 15: Relative suitability for establishment of *Acer negundo* in the Ukrainian Carpathians determined by Maxent and BIOMOD best model (GMB); higher numbers indicate higher suitability; for binary predictions (suitable/unsuitable), the indicated optimized threshold should be used;

The spatial distribution of areas suitable for establishment of *A. negundo* shows a clear preference for major watersheds and highways, and larger clusters in the southwest of the UA Carpathians and to a lesser degree in the east and southeast are predicted to be highly suitable (> 0.61 for Maxent and > 0.9 for BIOMOD). These correspond to centers of high anthropogenic pressure in moist and warm lowlands. The species is already present in many of the areas predicted as suitable (i.e., above the optimized threshold), and the predictions made by either

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algorithm do not extrapolate far beyond areas which are already infested by *A. negundo*. This indicates that this invader has already become established in large parts of the areas suitable for survival and reproduction and that farther spread is imminent. But are the (potential) distribution patterns observed for *A. negundo* similar for all study species? Comparisons between species are best accomplished by overlaying the binary predictions for each species as determined by an optimized threshold (see section 5.6). This is because the relative suitability indices vary by species and algorithm in terms of the optimized threshold. For example, in Fig. 15 a value of 0.2 is regarded as suitable by Maxent but unsuitable by BIOMOD. For a given species and algorithm, all optimized thresholds are given below in Table 5.

Species	Threshold Maxent	Threshold BIOMOD
Acer negundo	0.162	0.644
Ambrosia artemisiifolia	0.063	0.55
Echinocystis lobata	0.124	0.597
Helianthus tuberosus	0.111	0.62
Heracleum sosnowskyi	0.189	0.63
Impatiens glandulifera	0.121	0.62
Reynoutria spp. (*R. japonica* and *R. x bohemica*)	0.174	0.577
Robinia pseudoacacia	0.156	0.585
Solidago spp. (*S. canadensis* and *S. gigantea*)	0.162	0.628

Table 5: Optimized thresholds for binary predictions of invasive plant distributions within the Ukrainian Carpathians; suitable = above the threshold; thresholds based on the final models (calibrated on all presence points) in Maxent and BIOMOD best model algorithms

As Fig. 16 demonstrates, Maxent generally predicts a larger area to be suitable than BIOMOD for reasons discussed in section 6.1, in particular for *Heracleum sosnowskyi* and *Robinia pseudoacacia*. The two exceptions are *A. negundo* and *Solidago* spp. Here, BIOMOD algorithms predict a slightly greater proportion of the study area to be suitable.
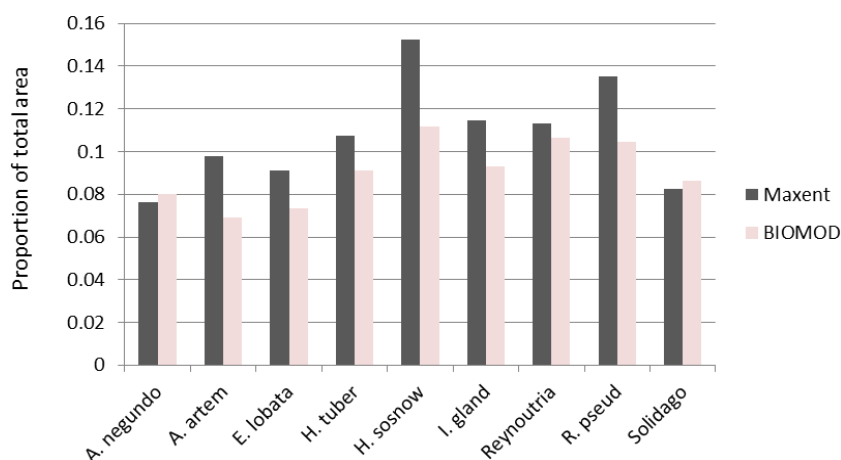
Figure 16: Proportion of total area within the Ukrainian Carpathians predicted as suitable for establishment of invasive species with Maxent and BIOMOD best models

Using binary predictions, a visualization of the sites within the study area where conditions are suitable for a number of different species clearly demonstrates that the predicted distribution patterns noted for *A. negundo* indeed largely corresponds to that of all NIPS (Fig. 17). Of the pixels predicted as suitable for the establishment of at least one species, i.e., 20 and 17% of the total pixels for Maxent and BIOMOD, respectively, 26% overlap for all nine species in Maxent and 20% in BIOMOD. At the same time, for Maxent, only 7 and 6% of these pixels overlap as suitable for 8 and 7 NIPS, respectively. For BIOMOD, the overlap of suitable areas for 8 NIPS is 10% of pixels predicted suitable for at least one species; for 7 NIPS it is 7 %. These numbers suggest a spatial aggregation of suitable habitats for establishment across species.
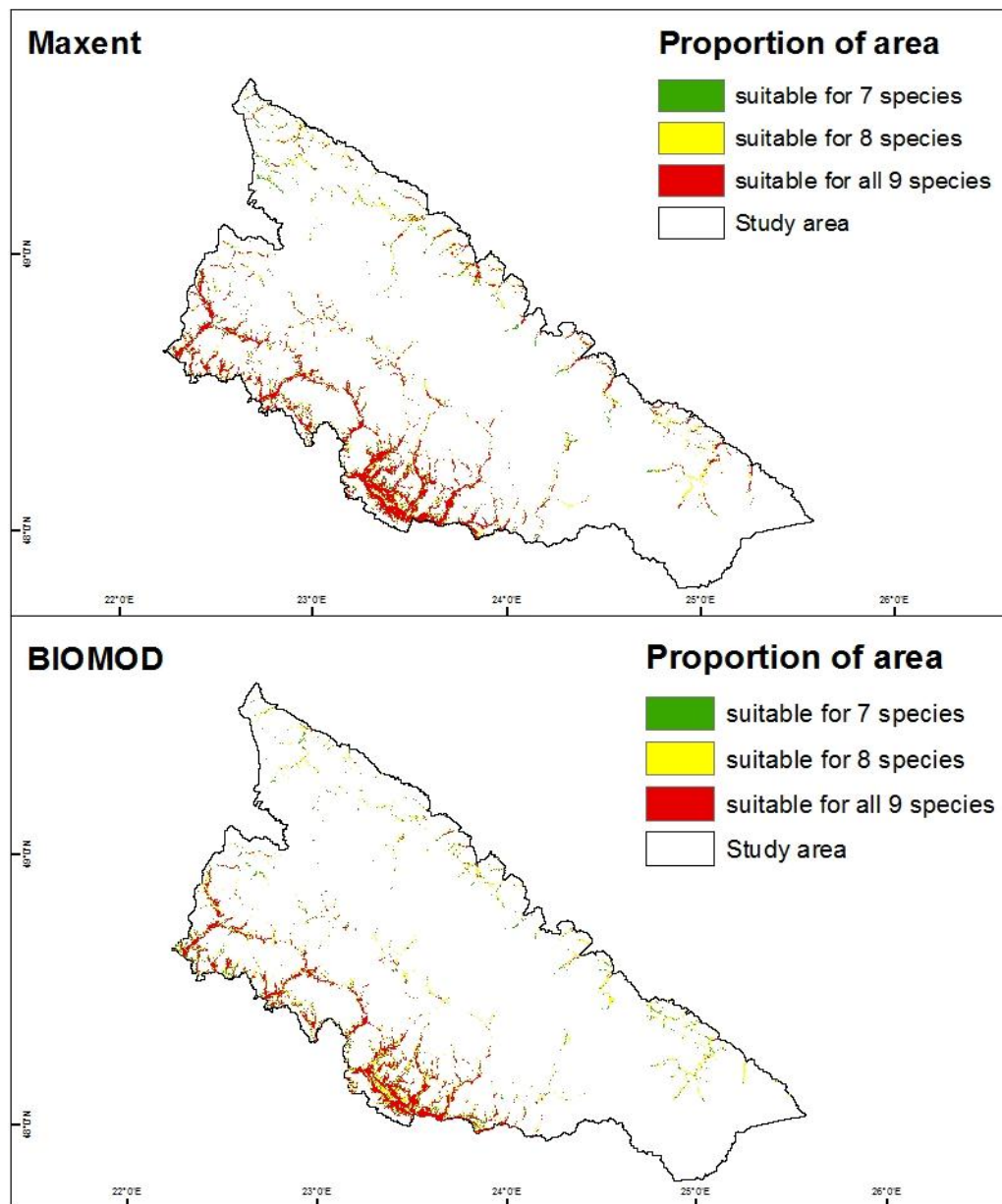
Figure 17: Overlap of Maxent and BIOMOD binary predictions of invasive plant distributions in the Ukrainian Carpathians

As has been observed for *A. negundo*, the potential for establishment of a large number of aggressive NIPS is particularly high in the southwest and west and at low elevations in the east and southeast. In these regions, across species, virtually all riparian habitats and linear habitats along roads and in close proximity to settlements are predicted to be suitable. Suitability decreases when one moves farther into the region to higher elevations. In areas farther away from the centers of aggregation of suitable habitats, suitable habitats for establishment are predicted only for a few species, such as *Heracleum sosnowskyi* or *Robinia pseudoacacia*. Again, as is the case for *A. negundo*, the other NIPS have already established thriving populations across these areas of aggregation (Appendix E). Simultaneously, Fig. 18 shows that this particular distributional pattern coincides with the density of settlements and roads. In fact, there is a significant correlation between the aggregation of areas suitable for establishment and density of human development/infrastructure ($p = 0.001$) for both Maxent and BIOMOD.
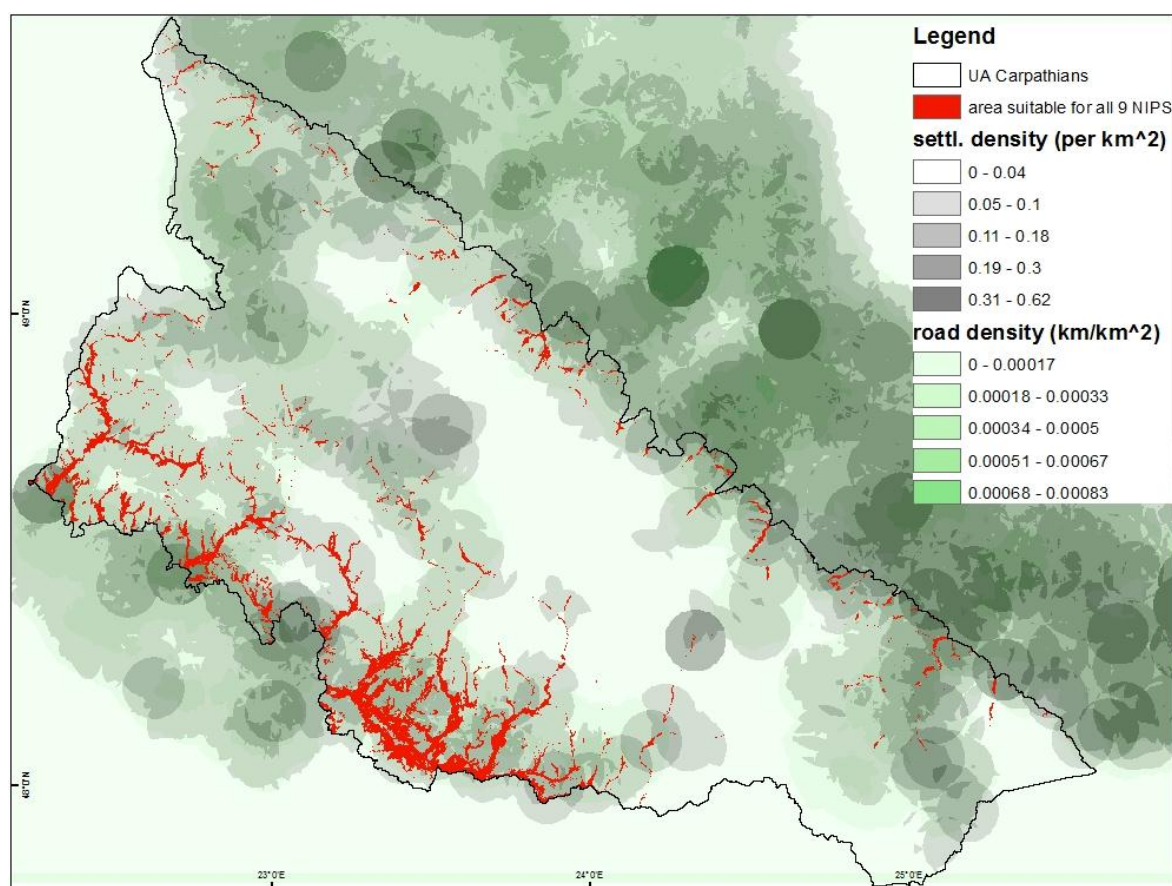
Figure 18: Spatial correlation between density of roads (polylines) and settlements (points) in the Ukrainian Carpathians and the areas predicted by Maxent to be highly suitable for all modeled invasive plant species; point and line densities calculated as kernel densities in ArcMap 10; correlation significant ($p = 0.001$);

Correlation, of course, does not mean causation, and in order to understand the particular spatial patterns of predictions for any of the nine species/taxa in terms of model fitting, one must take a closer look at the predictor variables and the weight each was given during model calibration.

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6.3 Importance of predictor variables

Permuation importance of the predictors for Maxent and BIOMOD is shown in Fig. 19 and Fig. 20, respectively. A full list of relative variable importance for Maxent and BIOMOD best models based on different tests can be retrieved from Appendix F.
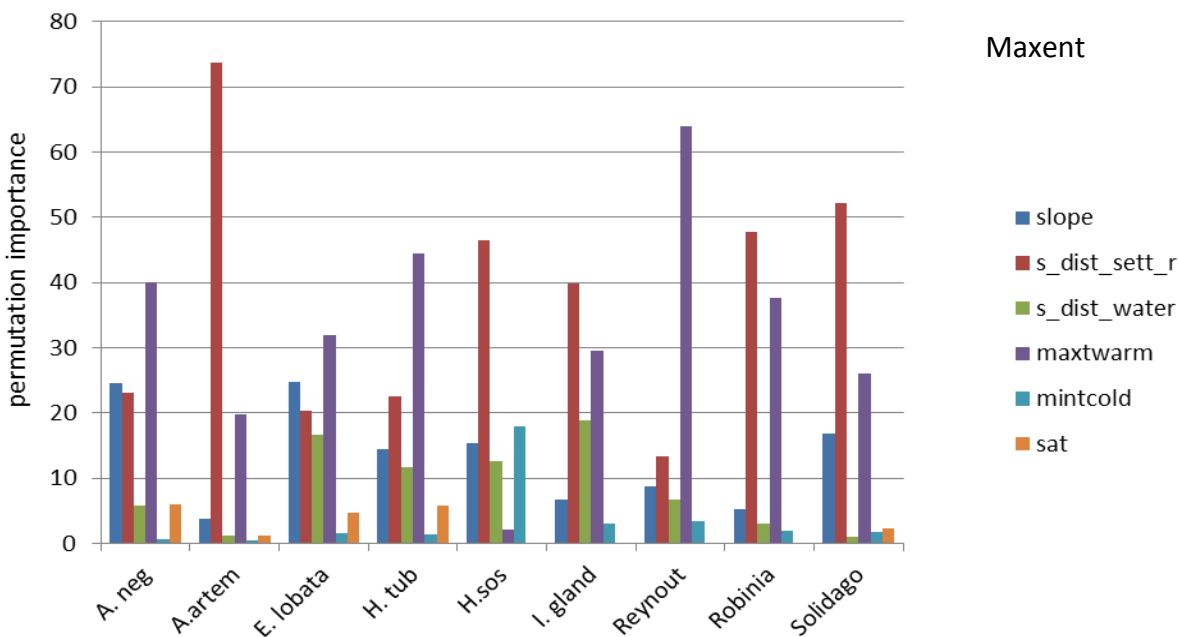
Figure 19: Maxent - contribution of predictor variables per invasive species for distribution models within the Ukrainian Carpathians; expressed as permutation importance in %; higher values indicate that a variable is relatively more important to model accuracy; note that species names are abbreviated;
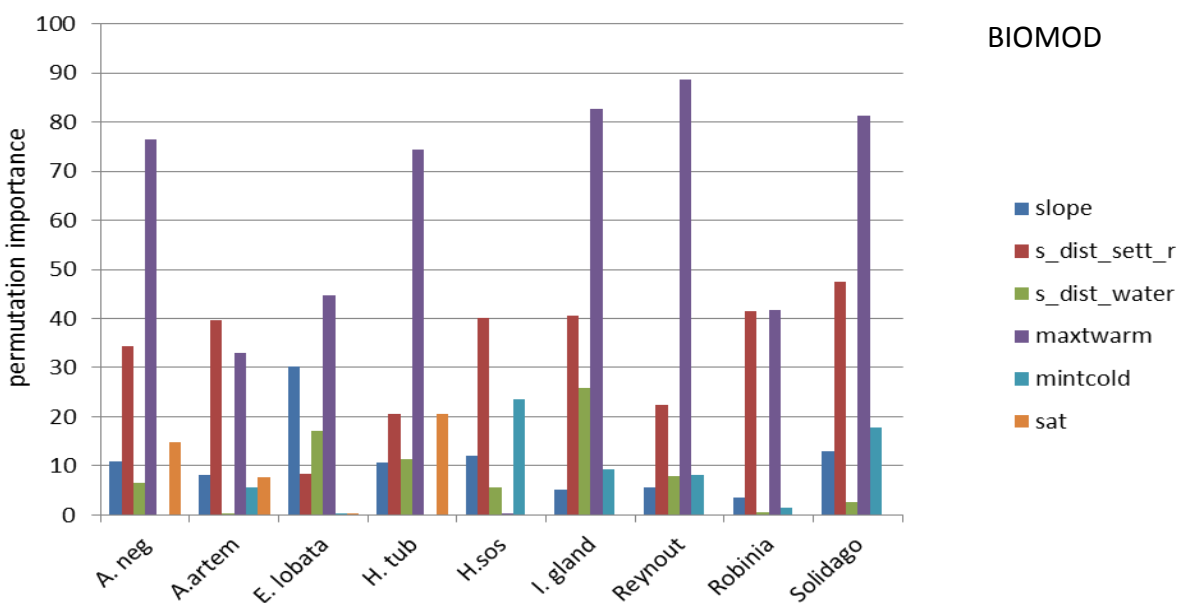
Figure 20: BIOMOD - contribution of predictor variables per invasive species for distribution models within the Ukrainian Carpathians; expressed as permutation importance in %; higher values indicate that a variable is relatively more important to model accuracy; note that species names are abbreviated;

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Interpretation of the contribution of each variable must be done with caution because the calculation of contribution is dependent on the path a model takes. For example, if a model is first calibrated with *maxtwarm*, then the (spatially) correlated variables *mintcold* and *sat*, if picked thereafter, might contribute little information to model building because the distribution of their values, and consequently the distribuiton of the NIPS along the value gradients, is correalted to the values of *maxtwarm*. To demonstrate the issues connected to correlation, one can look at the jackknife results in Maxent in Fig. 21, where a model was built with only one of the six predictor variables and the gain (the accuracy of the model) was anaylzed:
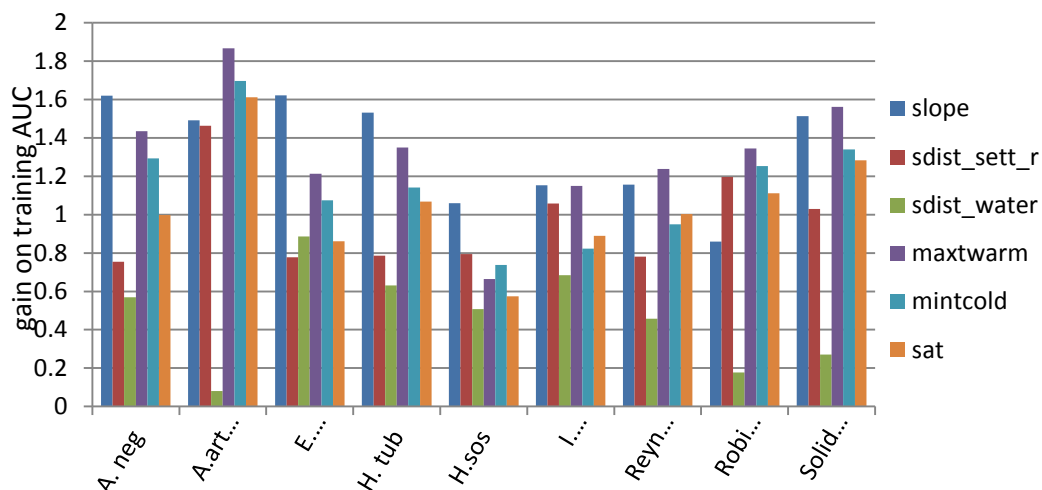
Figure 21: Maxent - contribution of predictor variables to model gain per invasive species for distribution models within the Ukrainian Carpathians; results are based on a jackknife test that builds an algorithm with only one predictor and measures the goodness-of-fit of the model; note that species names are abbreviated;

One gets quite different results than shown in Fig. 19, most notably that every predictor is relevant for each species. However, analyzing variable contribution based on such isolation techniques is problematic because ecologically relevant interactions between variables and their relative importance when compared to the others are not taken into account. Thus, keeping correlation in mind, one can at the very least clearly differentiate between the roles of climatic variables on the one hand and topographic/land-use variables on the other as there isn't a significant correlation between the two groups.

Maximum temperature of the warmest month, *maxtwarm*, is indicated as the most important contributing variable when looking at permutation importance in four NIPS and eight NIPS in Maxent and BIOMOD, respectively. The importance of climatic predictors makes sense from an ecological perspective because settlements, roads, rivers, and flat slopes can be found throughout the UA Carpathians, but the climatic gradient is a consistent limiting factor for species highly sensitive to the length of the growing season and temperature extremes. For example, even if there are favorable topographic gradients in the interior of the mountains, i.e., several villages connected by roads in close proximity to rivers, establishment of a species will not be likely if the growing season is too short for growth and reproduction. The significance of climatic variables also partly explains the observed aggregation patterns of species occurrences and suitable habitats in the warmer and moister southwest as opposed to the colder and drier northeast despite high population densities in both regions. Furthermore, the consistently high

importance of *maxtwarm* as compared to other climatic variables (Fig. 21) is ecologically sensible as well despite the effects of correlation. All NIPS are more or less adapted to frost, and the lowest temperatures in winter are not sufficient to permanently damage seeds or plant parts in this temperate climate regime. Drought and a short growing season, however, are more critical factors for the short-day hydrophilic NIPS. In this sense, it is astonishing that sum of active temperatures, *sat*, does not play a bigger role in model calibration. Maxent does not attribute much importance to *sat* for any of the species modeled, and BIOMOD only does so for *Acer negundo* and *Helianthus tuberosus*. Correlation between the climatic predictors is the main reason for the downplay of the significance of *sat*; another reason is the fact that the layer depicting *sat* values was interpolated from a very general map and most likely underestimates the actual variability of the values.

For some species, climatic variables are second to topographic/land-use ones in their relative contribution to model building, particularly in Maxent. Ecologically, this indicates a potentially wide niche of these NIPS with regards to climate. *Heracleum sosnowskyi,* for example, originates from cool climates and is adapted to short growing seasons. The temperature gradient is thus not a strong limiting factor for this species. *Ambrosia artemisiifolia* and *Robinia pseudoacacia* meanwhile belong to the most wide-spread NIPS in Europe and are found in a multitude of climatic regions but are highly dependent on anthropogenic vectors for dispersal (Appendix B). In fact, all species studied here rely on human vectors for dispersal of seeds and reproductive parts and for creation of new habitats through disturbances. Therefore, it is not surprising that distance to settlements and roads, *s_dist_sett_r*, significantly contributes to the models and is the most important non-climate variable for most species in both Maxent and BIOMOD, closely followed by *slope*. This demonstrates the high significance of disturbance and propagule pressure for the distribution of suitable habitats for establishment and greatly explains the aggregation of suitable areas to linear habitats in geographic centers characterized by a high density of human structures. Again, because the *slope* layer (derived from a DEM) has the finest original resolution (30 m) of all layers, its importance as a predictor in limiting the potential range of species improves the spatial accuracy of all models.

Surprisingly, distance to water is less important to model building than its observed ecological significance would suggest (i.e., the major route of long-distance dispersal of seeds), and contributes relatively little to model accuracy when modeled by itself (Fig. 21). This can be explained in part by the fact that rivers are so abundant in the UA Carpathians that they are less of a limiting factor than anthropogenic development. The presence of rivers by itself does not mean that NIPS become established. It is the anthropogenic disturbances along rivers that cause their establishment. The models make this important fact clear. Furthermore, the locations of large river valleys, roads, and settlements tend to be clustered, creating a correlation between *s_dist_sett_r* and *s_dist_water* (simple distance to water) in many locations where the density of NIPS is already high. This correlation, in turn, may lower the importance of hydrology in model building. At the same time, it is also true that *s_dist_water* is a relevant predictor overall and improves model performance; and especially for the NIPS that currently are found exclusively along rivers, jackknifing and stepwise regression give a relatively higher weight to *s_dist_water* in model building (Appendix F for details). Particularly the latter point is consistent with the observed role of rivers in the ecology of the NIPS.

In conclusion, once correlation and scale problems are accounted for, all predictor variables are significant for the models in all algorithms, and the synergisms between suitable climatic regimes, high density of anthropogenic structures, and large watersheds create centers within the study region at high risk of invasion by a multitude of species. Meanwhile, the relative significance of climatic factors and land-use variables vary across species more so than across algorithms and can be explained largely by the particular ecologies of species, suggesting the high accuracy of both Maxent and the BIOMOD best models.

6.4 Potential species distribution under future projections

To recall, the four scenarios on which the potential future distribution of the NIPS is based are: (i) climate change and low economic development by 2050; (ii) climate change and high economic development by 2050; (iii) climate change and low economic development by 2100; and (iv) climate change and high economic development by 2100. For all scenarios and all algorithms, binary maps of future projections were created and the proportion of pixels determined as suitable was compared to the binary maps for suitability under current conditions. The results show that the net range change as compared to results for current conditions (new area gained – areas lost) is positive and significant ($p < 0.001$) for all scenarios (Table 6).

				Net Gain*		Net Gain*		Net Gain*		Net Gain*
		Current	2050 (i)		2050 (ii)		2100 (iii)		2100 (iv)	
A. negundo	Maxent	0.076	0.166	**0.089**	0.171	**0.095**	0.240	**0.163**	0.277	**0.200**
	BIOMOD	0.080	0.218	**0.138**	0.224	**0.144**	0.449	**0.369**	0.491	**0.411**
A. artem	Maxent	0.098	0.167	**0.069**	0.175	**0.077**	0.236	**0.138**	0.280	**0.182**
	BIOMOD	0.069	0.133	**0.064**	0.139	**0.070**	0.180	**0.111**	0.214	**0.145**
E. lobata	Maxent	0.091	0.153	**0.062**	0.157	**0.066**	0.218	**0.127**	0.246	**0.155**
	BIOMOD	0.073	0.106	**0.032**	0.108	**0.034**	0.148	**0.074**	0.159	**0.086**
H. tuber	Maxent	0.107	0.185	**0.077**	0.191	**0.083**	0.304	**0.196**	0.350	**0.243**
	BIOMOD	0.091	0.238	**0.147**	0.243	**0.152**	0.572	**0.480**	0.600	**0.509**
H. sosnow	Maxent	0.152	0.247	**0.095**	0.256	**0.103**	0.315	**0.163**	0.358	**0.206**
	BIOMOD	0.112	0.164	**0.052**	0.167	**0.055**	0.190	**0.078**	0.199	**0.087**
I. gland	Maxent	0.115	0.153	**0.038**	0.158	**0.044**	0.218	**0.103**	0.249	**0.135**
	BIOMOD	0.093	0.117	**0.024**	0.120	**0.027**	0.161	**0.068**	0.178	**0.084**
Reynoutria	Maxent	0.113	0.170	**0.057**	0.175	**0.062**	0.290	**0.177**	0.330	**0.217**
	BIOMOD	0.106	0.118	**0.012**	0.121	**0.015**	0.118	**0.012**	0.243	**0.136**
R. pseud	Maxent	0.135	0.276	**0.141**	0.282	**0.147**	0.491	**0.356**	0.525	**0.390**
	BIOMOD	0.104	0.200	**0.096**	0.207	**0.103**	0.320	**0.216**	0.358	**0.254**
Solidago	Maxent	0.083	0.145	**0.063**	0.151	**0.068**	0.258	**0.175**	0.304	**0.221**
	BIOMOD	0.087	0.133	**0.046**	0.136	**0.049**	0.314	**0.227**	0.338	**0.252**

Table 6: Relative changes in suitable habitats for invasive species within the Ukrainian Carpathians after projections to assumed future environmental conditions; proportion of the entire study area that is suitable is given for current conditions and future scenarios (i-iv); net gain is calculated as proportion for a given future scenario minus proportion for current conditions; * = net gain significant at $p < 0.001$; note that species names are abbreviated;

Fig. 22 visualizes the median range changes across algorithms (averaged over study species). For all NIPS, suitable habitat ranges are predicted to increase, for some (the outliers) to a great extent. Furthermore, the net gain of novel suitable habitat is significantly higher ($p = 0.002$) under scenarios ii and iv than under i and iii, respectively. Decreasing the distance to points of anthropogenic pressures by 10 and 30% significantly increases the proportion of the total study area to be projected as suitable for species establishment. It is quite interesting to see that depending on the algorithm, two species are expected to gain disproportionately on novel suitable habitat – *Robinia pseudoacacia* and *Helianthus tuberosus* for Maxent and BIOMOD, respectively. *R. pseudoacacia* is a pioneer species capable of tolerating drought and a variety of soil types and highly dependent on anthropogenic disturbances to become established. *H. tuberosus* establishes populations mostly along riparian habitat in the UA Carpathians, but across Europe it is often found in a variety of habitats (e.g., at edges of agricultural fields) as it relies on human vectors for dispersal of reproductive parts as much as on water. Similarly, among the species that gain relatively fewer novel suitable habitats for establishment are ones that are predicted to behave like specialists in their introduced range, i.e., all models predict suitable habitat for establishment under current conditions to align along narrow strips of rivers and be concentrated to low elevations and warmest climates. Two examples are *Impatiens glandulifera* and *Echinocystis lobata* (see Appendix E). These species are also currently observed to become established exclusively along riparian habitats.
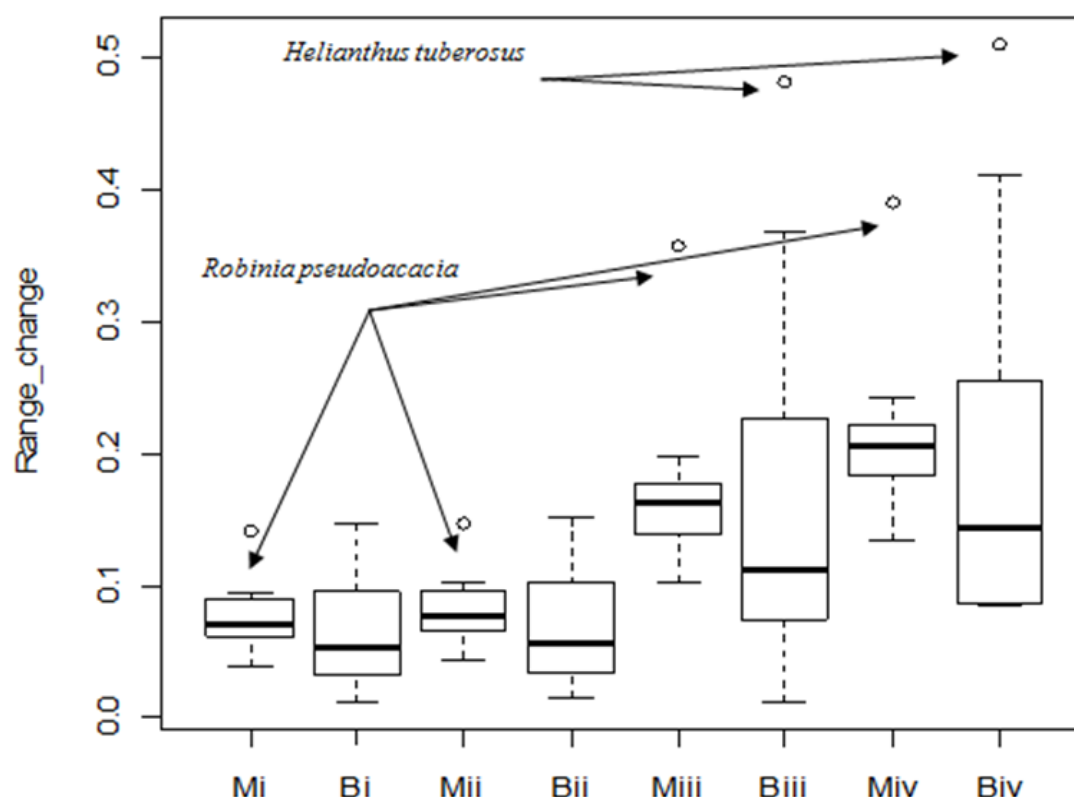
Figure 22: Boxplot of range change of suitable habitats for invasive plant species in the Ukrainian Carpathians across future change projections; M = Maxent, B = BIOMOD, i-iv = future scenarios; ° = outliers; changes significant at $p < 0.001$;

Indeed, when one compares range change across species averaged over models and scenarios, there is a trend in the projections to define a relatively greater proportion of suitable-area gain based on whether a species behaves like a generalist or specialist (see Fig. 23).
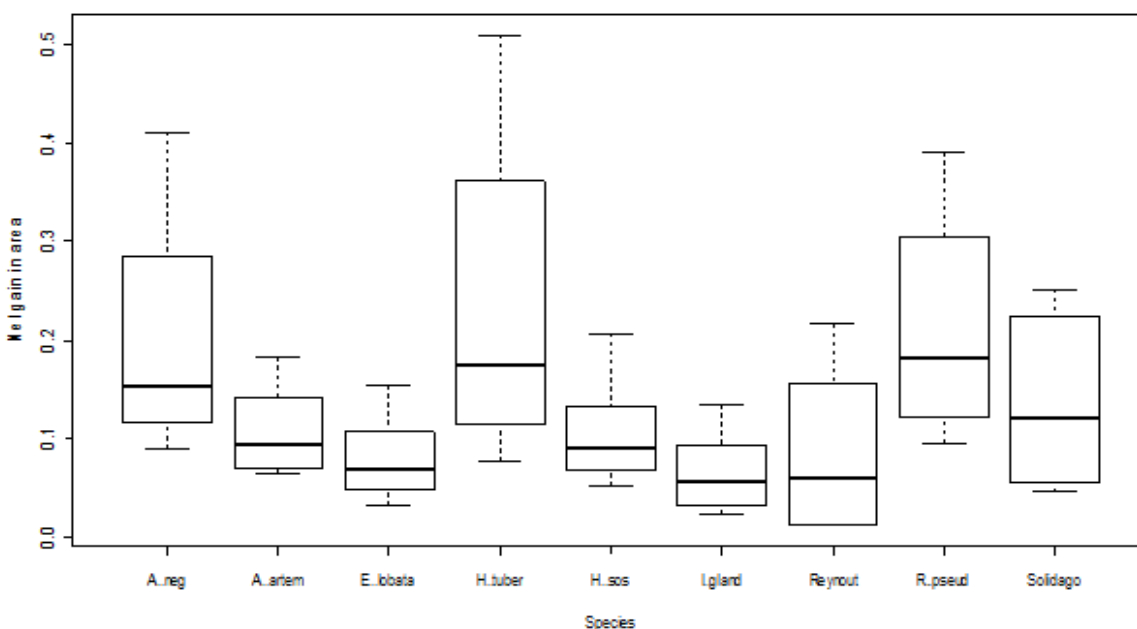
Figure 23: Boxplot of range change of suitable habitats for invasive plant species in the Ukrainian Carpathians across study species; averaged over algorithms and scenarios; note that species names are abbreviated;

This trend is however not always true; and it is difficult to categorize range expansion based primarily on species ecologies. For example, *Acer negundo* is clearly only found in riparian habitats in the UA Carpathians and is a floodplain species in all its introduced ranges but is projected to gain a great deal of suitable areas particularly under BIOMOD models compared to other species that are expected to behave more like generalists, e.g., *Ambrosia artemisiifolia*. And of course, there is the question of why Maxent and BIOMOD have different outliers. Furthermore, it is noticeable that there is great variation between the algorithms in BIOMOD, in particular for scenarios iii and iv. These patterns strongly suggest that, unlike the model predictions for current conditions, the projections to future scenarios are highly sensitive to small variations between the algorithms. The dependency of projections on particular algorithms explains the, at times great, discrepancies of projections for a particular species between Maxent and BIOMOD and the greater variations within the BIOMOD framework as compared to Maxent for any given scenario (Fig. 22). Maxent deploys the same type of model for all species while the best models in BIOMOD vary by species, and projections differ according to the model chosen (Appendix D). For example, Fig. 24 shows that beginning with a similar spatial distribution of predictions for *A. negundo* and *E. lobata*, projections for 2100 based on GLM for *A. negundo* are far less conservative than the ones based on GBM for *E. lobata*. The implications of the dependence of projections on algorithms are discussed in the next section.
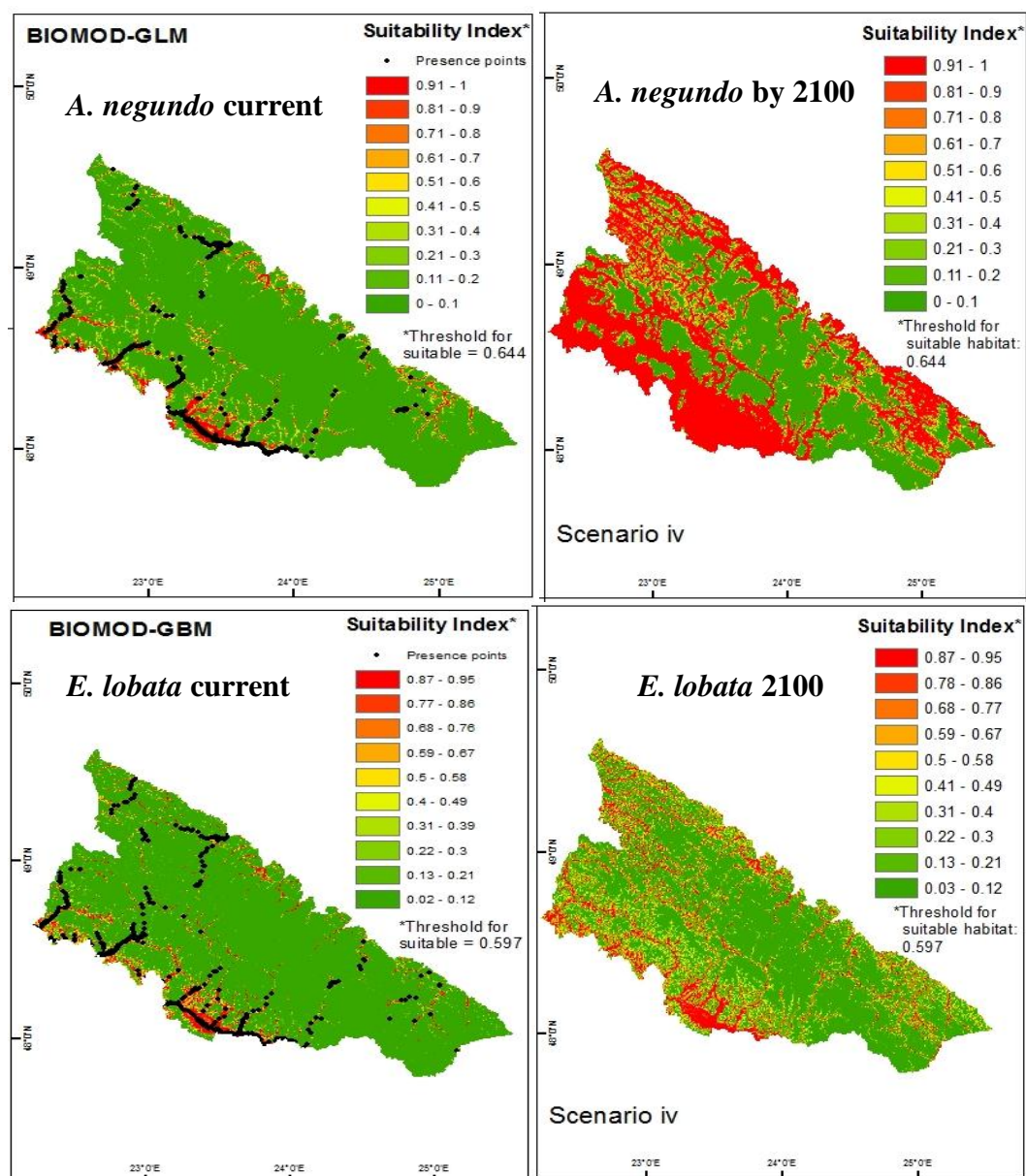
Figure 24: Spatial pattern of model predictions of suitable habitats in the Ukrainian Carpathians for *Acer negundo* and *Echinocystis lobata* based on current conditions and projections (to scenario iv) in BIOMOD

Despite the difficulties to categorize projections based on the ecology of the NIPS, clear patterns in spatial distribution of the areas suitable for establishment of species under future change scenarios are nevertheless discernible. Figs. 25-28 demonstrate the potential spread of two species as projected by Maxent: (a) *R. pseudoacacia* expected to gain a great amount of novel potential habitat and (b) *I. glandulifera* expected to gain little (for maps of all species please refer to Appendix G). Both species are expected to migrate to higher elevations along linear habitats. Figs. 25-28 also clearly demonstrate a lateral spread of suitable areas, away from the linear habitats predicted as suitable for current conditions, and this spread is particularly true at lower elevation. These latter patterns are correlated to the high densities of human settlements and roads and the predicted increase in densities of anthropogenic structures by 2050 and 2100. Again, the relative future distribution of individual species (i.e., the rate of expansion into higher

altitudes and beyond major linear habitats) depends on the ecology of the species and on the algorithms.
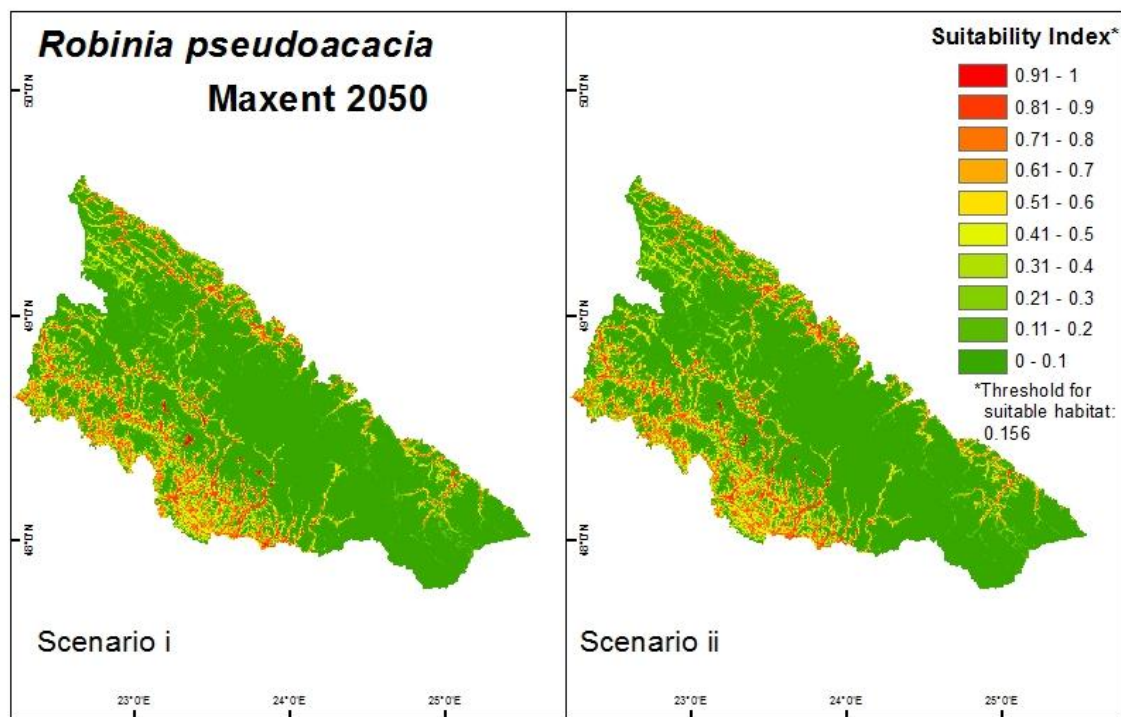
Figure 25: Maxent projections for scenarios i and ii (2050) of potential distribution of *Robinia pseudoacacia* in the Ukrainian Carpathians
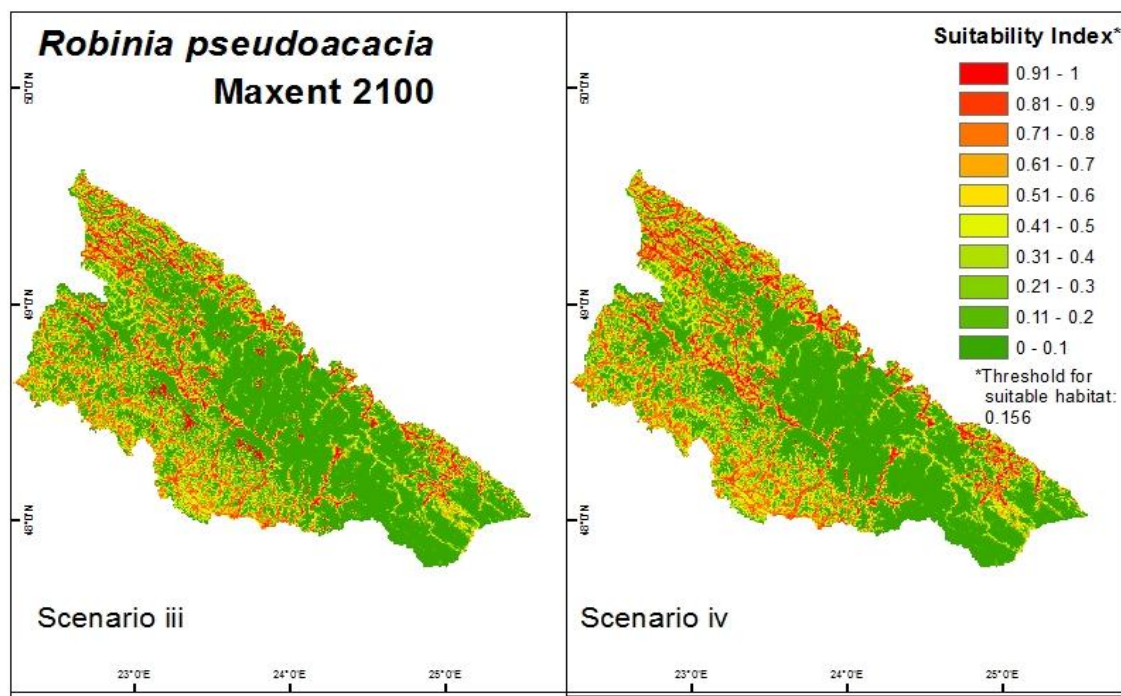
Figure 26: Maxent projections for scenarios iii and iv (2100) of potential distribution of *Robinia pseudoacacia* in the Ukrainian Carpathians
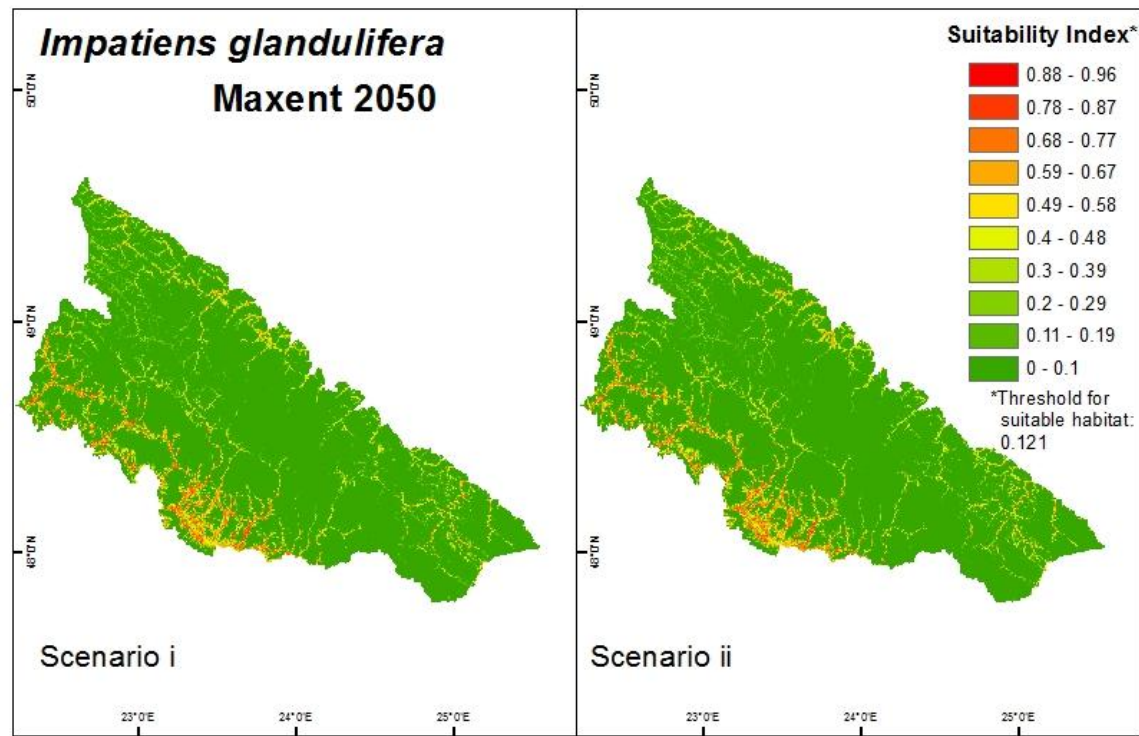
Figure 27: Maxent projections for scenarios i and ii (2050) of potential distribution of *Impatiens glandulifera* in the Ukrainian Carpathians
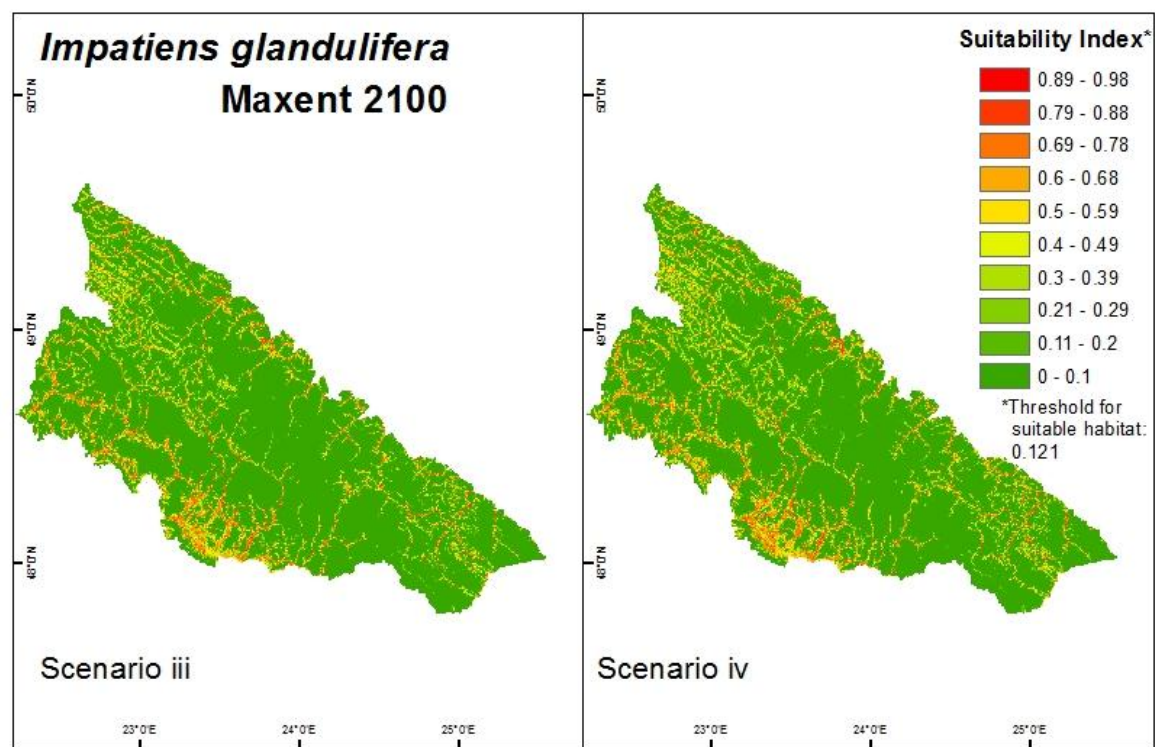
Figure 28: Maxent projections for scenarios iii and iv (2100) of potential distribution of *Impatiens glandulifera* in the Ukrainian Carpathians

It is also of note that neither species loses a significant amount of currently suitable area in future projections. In general, BIOMOD algorithms tend to project less loss of suitable areas for establishment while Maxent generally projects some small areas in the southwest to be lost (see Appendix G). These differences depend on the interpretation of species' responses to climatic variables by each algorithm, and are discussed in the following section. Furthermore, an expansion of roads and settlements (scenarios ii and iv) decreases the number of pixels predicted as unsuitable under change scenarios for all algorithms. This present more evidence for the high importance of anthropogenic disturbance and propagule pressure for the establishment of NIPS in particular areas.

The trends presented for *R. pseudoacacia* and *I. glandulifera* hold true for all NIPS across models. Fig. 29 depicts areas where at least seven species are projected to find suitable habitats for establishment by Maxent and BIOMOD models. It is evident that the interior of the UA Carpathians becomes increasingly suitable under a warming climate. By 2050, when solely climatic changes are expected (i.e., scenario i), 27 and 29% of the total study area are assumed to be suitable for at least one species in Maxent and BIOMOD, respectively; an increase by 7% for Maxent and 12% for BIOMOD compared to predictions for current conditions. Of these areas, 45% in Maxent and 33% in BIOMOD are suitable for at least seven species. Expected increases in temperature by an average of 1.8°C in winter and 1.5°C in summer and the related extension of the growing season by 2050 cause a migration of suitable habitat into climatic zones that are currently unsuitable for the establishment of permanent populations of NIPS (i.e., moderately warm to moderately cool zones). For all NIPS, this migration occurs primarily along rivers and roads and emphasizes the importance of these linear habitats for the spread of the eleven species. By 2100, average temperature increases of 3.8°C in winter and 3.5°C in summer create further suitable habitat reaching far into the interior of the mountain range and particularly increasing invasion risk in the northeast and south, where relatively cool climates limit the potential distribution of NIPS today. By 2100, modeling climate change alone, 37 and 60% of the total study area are assumed to be suitable for at least one species in Maxent and BIOMOD, respectively. Of these areas, 52% in Maxent and 23% in BIOMOD are suitable for at least 7 species.

Furthermore, current invasion foci (areas already or potentially highly infested by the NIPS) play a major role in the future distribution of the NIPS because the size and location of novel suitable areas are positively correlated to the locations of current invasion foci. That is, even if two areas in the interior of the mountains possess similar climatic and hydrological features, the clustering of suitable areas for current conditions in the southwest and west translates, under future projections, to a higher density of suitable areas in the higher-elevation zones closest to these current foci. These patterns suggest that climate alone cannot explain the projected range change across models and point to the importance of propagule pressure and disturbances. It is also the presence and assumed intensification of human pressures on ecosystems (10 and 30% by 2050 and 2100, respectively) that explain the lateral expansion of suitable areas away from major rivers and roads, as this expansion occurs primarily in areas with high densities of settlements and roads today (see Fig. 28). By 2050, under scenarios incorporating climate change and economic development (ii and iv), 34 and 30% of the total study area are assumed to be suitable for at least one species in Maxent and BIOMOD, respectively; an increase by 7% for Maxent and 1% for BIOMOD compared to climatic projections. By 2100, 55 (+ 18% compared to iii)

and 63% (+ 4% compared to iii) of the total study area are assumed to be suitable for at least one species in Maxent and BIOMOD, respectively. When one looks at the likelihood of establishment of several species (Fig. 29), the trend of outward migration of suitable areas under scenarios ii and iv is visible. For Maxent, 25% of the total study area is suitable for at least 7 species by 2100 when projecting to scenario iv as opposed to 19% when doing so to scenario iii. For BIOMOD, the statistics are 16% (iv) and 13% (iii).
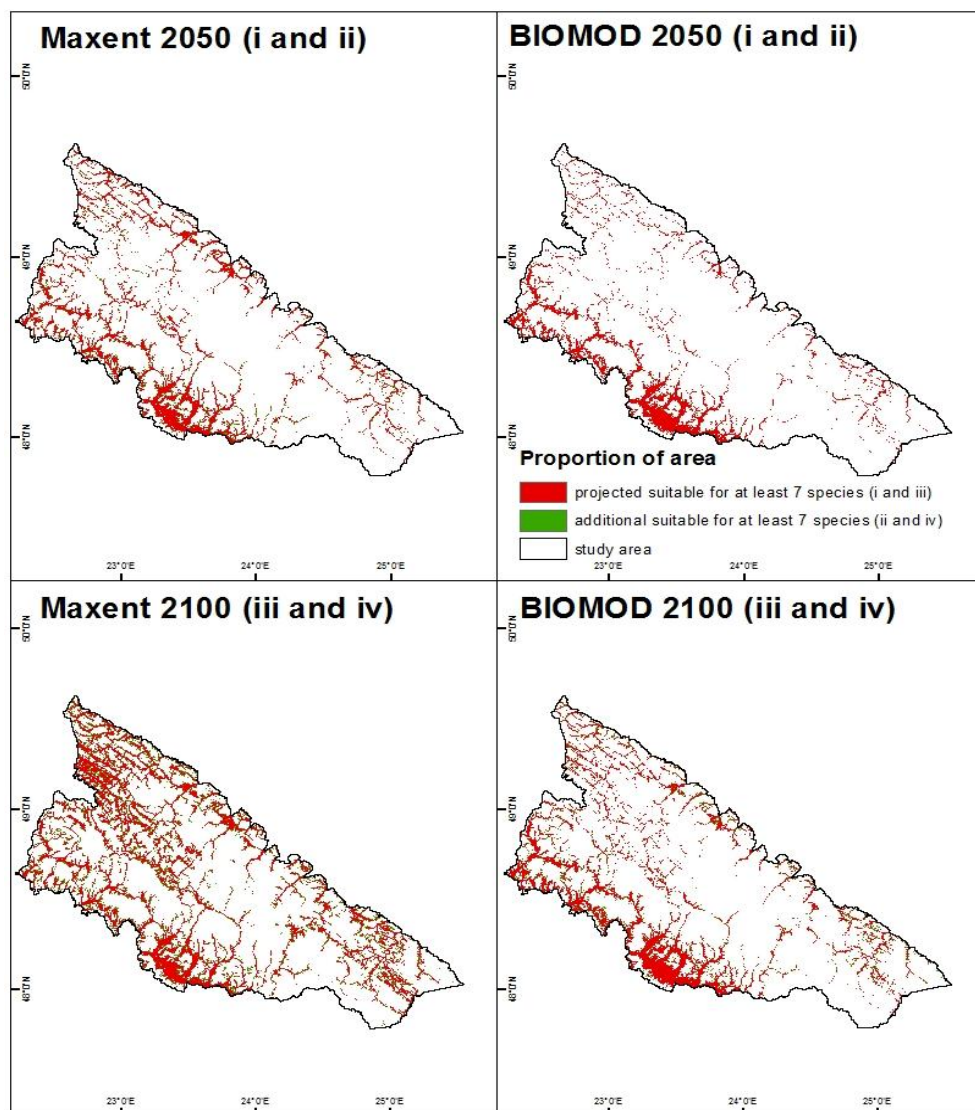
Figure 29: Overlap of binary predictions (at least 7 invasive study species) of suitable habitats for invasion within the Ukrainian Carpathians as projected by Maxent and BIOMOD under future climate and land-use change scenarios

In conclusion, while there are marked differences between projections that cannot be solely attributed to the ecology of the study species but are also dependent on the algorithms used to model the habitat suitability, a few general trends for the future of the NIPS in the UA Carpathians are revealed across algorithms. First, all NIPS gain novel suitable areas for establishment along linear habitats in the interior of the mountain range and lose only few areas predicted to be suitable under current conditions. Second, at lower altitudes and in close

proximity to roads and settlements, suitable ranges expand dramatically beyond major linear habitats for most species. Third, the greater the rate of habitat fragmentation and anthropogenic pressures, the more range expansion is predicted for all NIPS. And lastly, future suitable areas for species that currently behave like specialists relative to other NIPS in terms of establishment in certain habitats (i.e., *A. negundo* (in Maxent), *E. lobata*, *H. sosnowskyi*, and *I. glandulifera*) on average will cover smaller proportions of the entire study area and are more confined to major linear habitats. The differences in projections between Maxent and BIOMOD algorithms have nevertheless important implications for natural-resource management and must be discussed in detail.

6.5 Maxent vs. BIOMOD

As has been shown overall thus far, Maxent and BIOMOD best models attribute a similar relative importance to the predictor variables, and the logistic outputs in Maxent and the individual models in BIOMOD predict very similar spatial patterns of suitability for any given study species. For future projections however, the picture becomes more complicated. As Fig. 29 shows, BIOMOD algorithms appear to be more conservative than Maxent when projecting suitability to scenario iv as opposed to iii. At the same time, as can be seen from Table 6 and Fig. 22, projections based on the BIOMOD algorithms are highly variable, and for some species, binary suitability predictions determined by BIOMOD algorithms starkly overtake (in terms of area predicted as suitable) Maxent predictions. For example, both Maxent and BIOMOD –GLM predict very similar spatial patterns of suitable areas for establishment of *Helianthus tuberosus* for current conditions. However, by 2100, BIOMOD projections estimate almost twice as much of the study region to be suitable for establishment of the species than do Maxent projections (60% vs. 35%, see Table 6 above). Figs. 30 and 31 demonstrate how this translates to the spatial patterns of predictions.
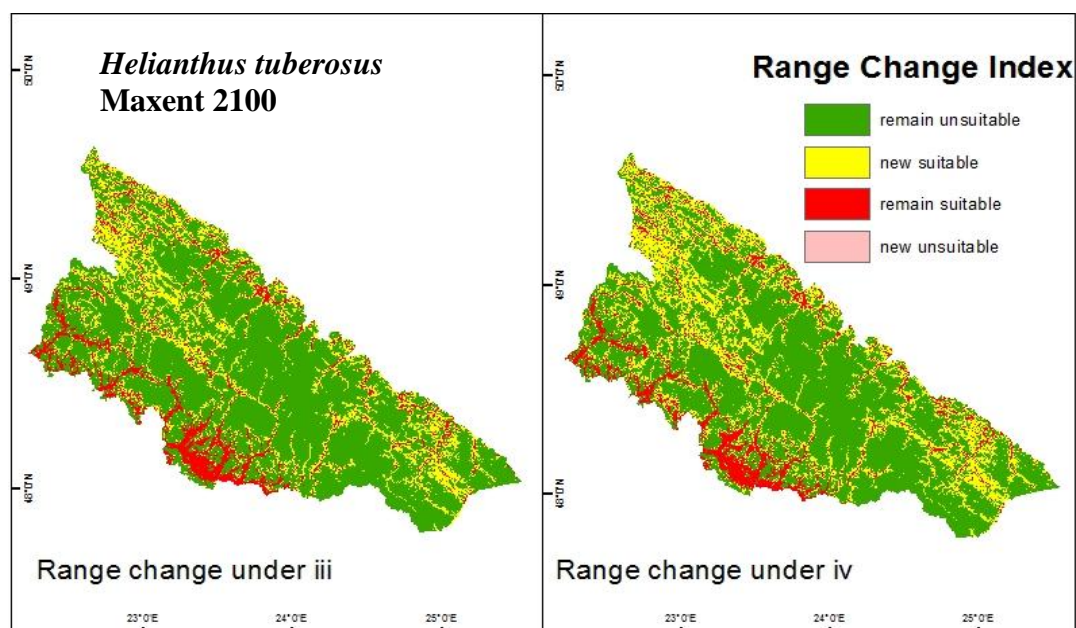
Figure 30: Binary Maxent predictions of suitable habitat within the Ukrainian Carpathians for *Helianthus tuberosus* by 2100
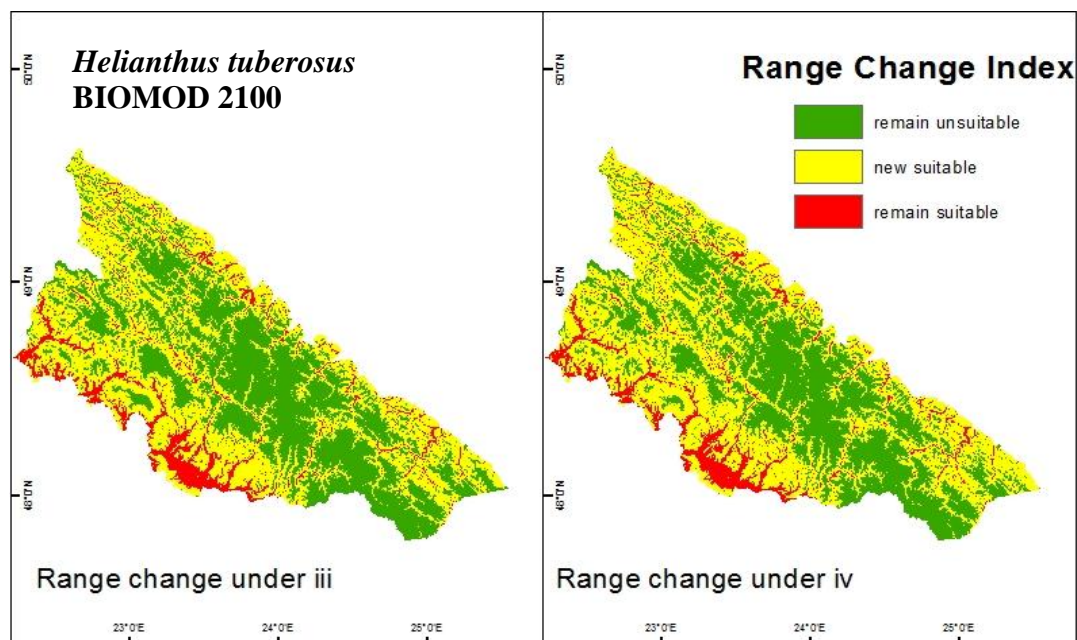
Figure 31: Binary BIOMOD predictions of suitable habitat within the Ukrainian Carpathians for *Helianthus tuberosus* by 2100

The BIOMOD projections not only predict the areas suitable for species establishment to migrate into the interior of the mountains but also project a stark lateral expansion. When looking at the relative contribution of the predictor variables to model calibration (Figs. 19 and 20) meanwhile, the relative contribution of each predictor seems similar between the Maxent model and BIOMOD-GLM. In both, average maximum temperatures of the warmest month (*maxtwarm*) decreases the performance of the models when permutated most, followed by distance to roads and settlements (*s_dist_sett_r*) and then slope (*slope)*. So why do the projections differ so much? It is because each algorithm creates slightly different response curves and bases projections on the model derived from them. Thus, seemingly small variations in model fitting can be exacerbated when values for predictors are changed. Two different models can give very similar statistical (in terms of AUC) and spatial (in terms of distribution patterns) results when calibrated on training data in part because very similar models can be fitted in a variety of ways depending on the weighing of predictors (particularly when variables are correlated); But these small differences in models can cause major divergences in projections under scenarios of change as the interactions or correlations between predictors are altered (see Thuiller 2003). A great example is *Acer negundo* (see Fig. 32).

In Maxent as well as BIOMOD-GLM, *maxtwarm* is given a strong weight (coefficient) during model calibration for *A. negundo*. However, while BIOMOD-GLM assumes that the higher the maximum temperature the likelier the presence of *A. negundo*, Maxent calibrates a tolerance limit of the species to high temperatures, i.e., temperatures above 25.5° C decrease suitability. Climate-change scenarios cause increases in temperatures beyond the maximum values determined by either algorithm for current conditions. These increases contribute to the projection of the loss of suitable areas in Maxent (0.2% of the total area) at locations where the predetermined tolerance limit is exceeded and which are otherwise not highly suitable (e.g., far

away from water or human structures).[12] If one now considers the response curves of all the predictors and their interactions modeled by individual algorithms, it becomes evident how small differences in model fitting can cause great variance in projections. In this sense, even a slightly higher weight (coefficient) assigned to *maxtwarm* by Maxent as opposed to BIOMOD, may results in more dependence of the model on climatic features and thus more conservative projections to scenario iv.
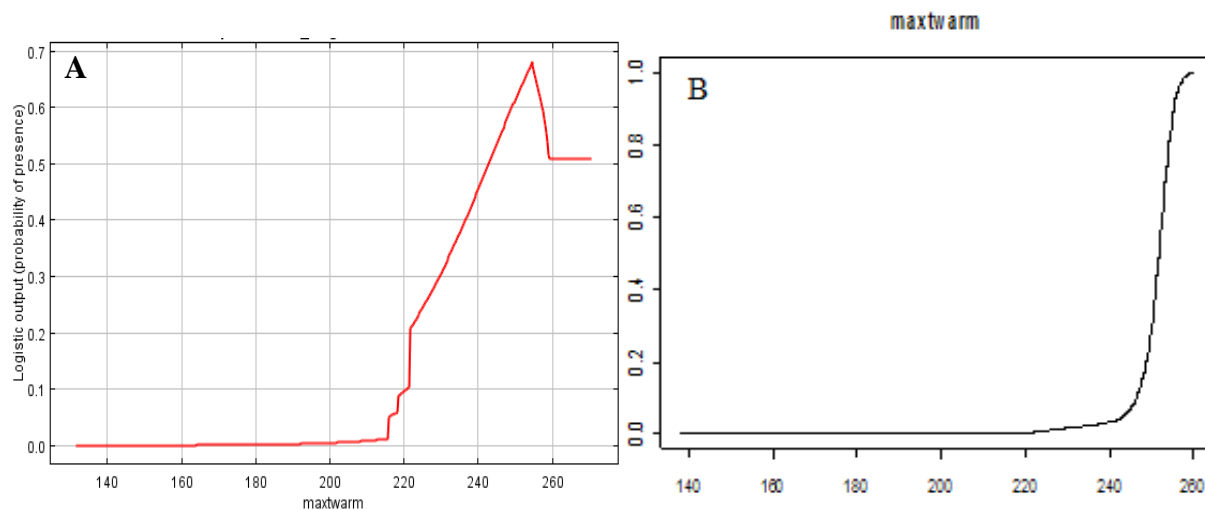
Figure 32: Probability of presence of *Acer negundo* in the Ukrainian Carpathians as a function of *maxtwarm* (in °C x 10) while the remaining five predictor variables are held at their average value; A - response curve determined by Maxent and B - response curve determined by BIOMOD-GLM;

For practical applications of the study results (see following chapter), projections for the outliers (i.e, species that seem to gain a disproportionally greater amount of novel habitats under one algorithm and compared to other, ecologically similar, species) must be interpreted with caution, particularly if the ecologies of these species in the invaded range contradict the projections.

Besides the different interpretations of responses between algorithms, the determination of an appropriate threshold to visualize certain levels of suitability is also a crucial factor to consider and depends on the purpose of the analysis. Here, a comparison between algorithms was the goal, so a threshold determination common to all algorithms was chosen. However, a threshold that maximizes correct predictions depicts only highly suitable areas and implies that the objective is to avoid false positives and false negatives. Such a threshold is appropriate when designating areas for protection (e.g., natural reserves) or working with scarce financial resources that limit monitoring to priority areas susceptible to establishment of NIPS. In reality, however, given the wide niches of the species and their successful "profiles" as invaders, it must be expected that the suitable habitats for species establishment cover a greater proportion of the study area than suggested by the binary maps. For example, Fig. 33 shows projections for 2100 (scenarios iii and iv) by BIOMOD-GBM for *Heracleum sosnowskyi*. The two maps at the top depict a logistic output of the projections and the two maps at the bottom are the corresponding binary transformations based on the optimized threshold of 0.627.

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[12] Ecologically, a tolerance limit to climatic conditions is highly reasonable. However, due to expected abundant precipitation in future, the presence of rivers, and expected increases in water-use efficiency in C_3 plants in response to higher CO_2 levels, higher temperatures are not expected to affect species tolerances strongly.
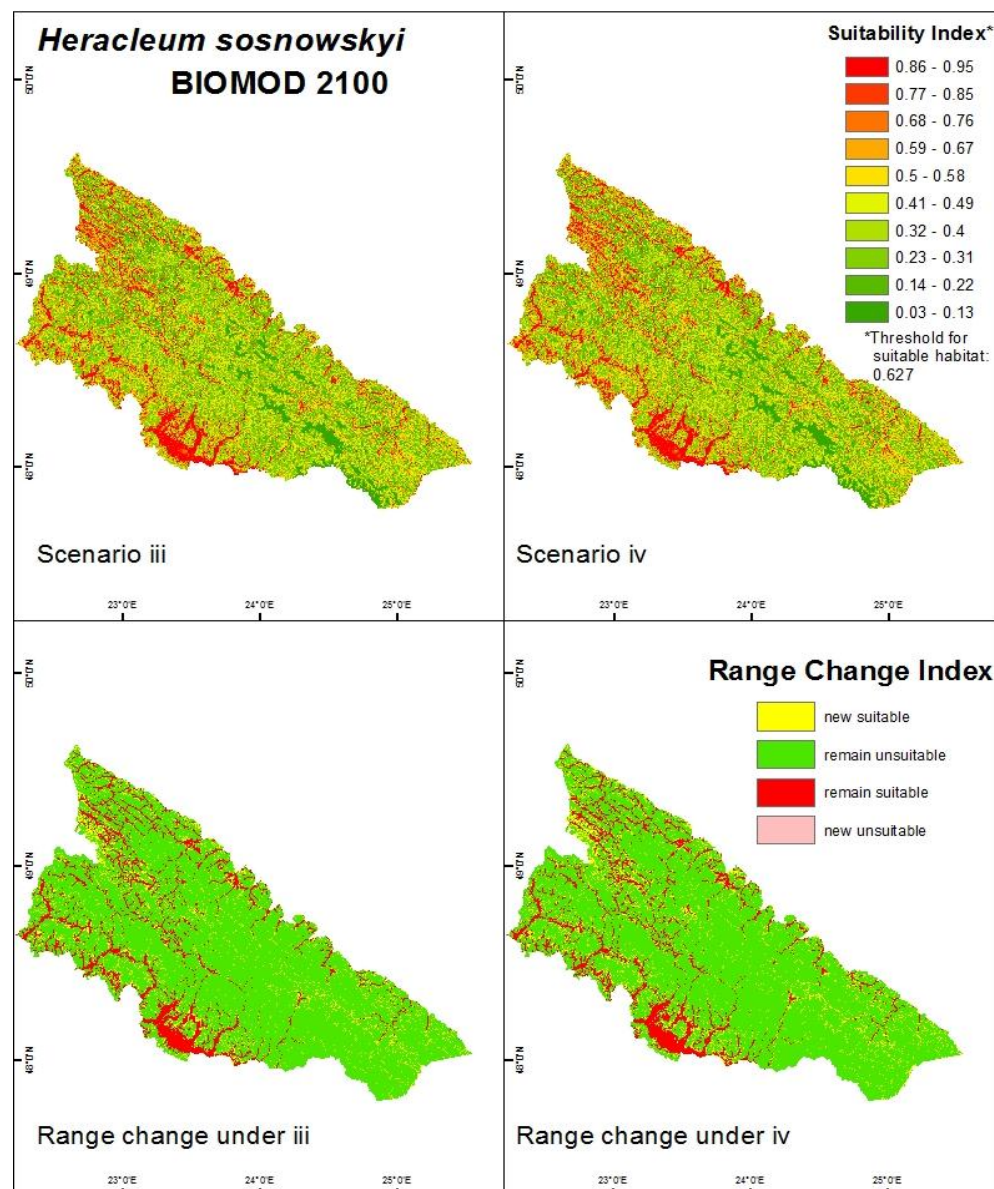
Figure 33: BIOMOD-GBM projections of the potential distribution of *Heracleum sosnowskyi* in the Ukrainian Carpathians by 2100

H. sosnowskyi is a particularly aggressive, highly adaptable NIPS that is spreading rapidly throughout the UA Carpathians and is negatively impacting not only biodiversity but also human health (Simpson *et al*. 2011b; Appendix B). Judging by the ecology of the species and its current rates of spread, the optimized threshold may very well underestimate the realistic possibility that this species becomes established along all major rivers and roads by 2100. As a precautionary measure, one would likely set a lower threshold, allowing for false positives but minimizing the risk of false negatives. In any case, a detailed analysis of the validity of thresholds is beyond the scope of this study. Regardless of threshold and differences between algorithms, it has been demonstrated that the NIPS analyzed here are likely to undergo range expansion under a warming climate and that anthropogenic vectors contribute to the current and future spatial distribution of NIPS. Having demonstrated the strong role of anthropogenic pressures, in

particular under climate change, one must now turn to the implications of the results for regional natural-resource management.

7. GENERAL IMPLICATIONS OF STUDY FOR NATURAL-RESOURCE MANAGEMENT

Regardless of algorithm, a majority of riparian habitats and major roads at lower elevations in general (up to approximately 600 m) and virtually all of these linear habitats at lower elevations in the southwest are currently at risk to become invaded by several aggressive NIPS. In addition, the presence of species in many habitats predicted as suitable means that further spread of the NIPS is imminent if current trends continue. Furthermore, future change scenarios clearly project a trend of upward migration of suitable habitats into higher elevations, until, by 2100, virtually all riparian habitats, major roads, and adjacent regions exposed to frequent disturbances are at risk of being invaded by at least one, and often several, NIPS. The questions become then: What does the potential spread of NIPS concretely mean for the ecoregion? And, how can the model predictions and projections be used for proactive management?

Given the negative impacts the NIPS presented in this study have on biodiversity, the impact of potential invasion of species-rich, protected landscapes is a major concern. Protected areas are landscapes designated and managed with the specific aim to protect biodiversity within them. In western Ukraine, protection of biodiversity has been brought to the foreground of environmental policy through design of and participation in several recent initiatives, including the Ukrainian Biodiversity Action Plan, Ecoregion Conservation Plan, the Kyiv Resolution on Biodiversity, the Convention on the Protection and Sustainable Development of the Carpathians, and the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) (WWF Carpathian Programme 2007; Maryskevych 2006). Today, the UA Carpathians are home to several nature reserves, including the trilateral (Poland, Slovakia, and the Ukraine) Eastern Carpathian UNESCO Biosphere Reserve which includes the Uzhanskyi National Nature Park and Nadsianskyi Regional Landscape Park on the Ukrainian side, the Carpathian Biosphere and Gorgany Nature Reserves, and six national parks (Carpathian, Synevir, Skolevski Beskydy, Vyzhnytskiy, Gutsulschyna, and Uzhotskiy). The total area covered by the reserves and other small parks such as botanical and zoological gardens is 220,000 ha, and over 17% of forests are protected in the UA Carpathians, the average in Western Europe being 5% (Oszlanyi *et al*. 2004; Keeton and Crow 2009). The value of such preserved areas is emphasized by Oszlanyi *et al*. (2004): "This natural heritage includes unique natural and semi-natural forest ecosystems, meadows, aquatic ecosystems, habitats and biotopes which are very important in many aspects: biodiversity preservation and protection, creation of a healthy environment, sources of natural renewable resources, place for recreation, research, science and education." Invasion by aggressive NIPS could be detrimental to the unique flora of the reserves.

Meanwhile, the results of this study illustrate that the NIPS have the potential to spread far into the mountain range. Figs. 34 and 35 below demonstrate the threats protected areas face by the highly adaptive and aggressive NIPS:
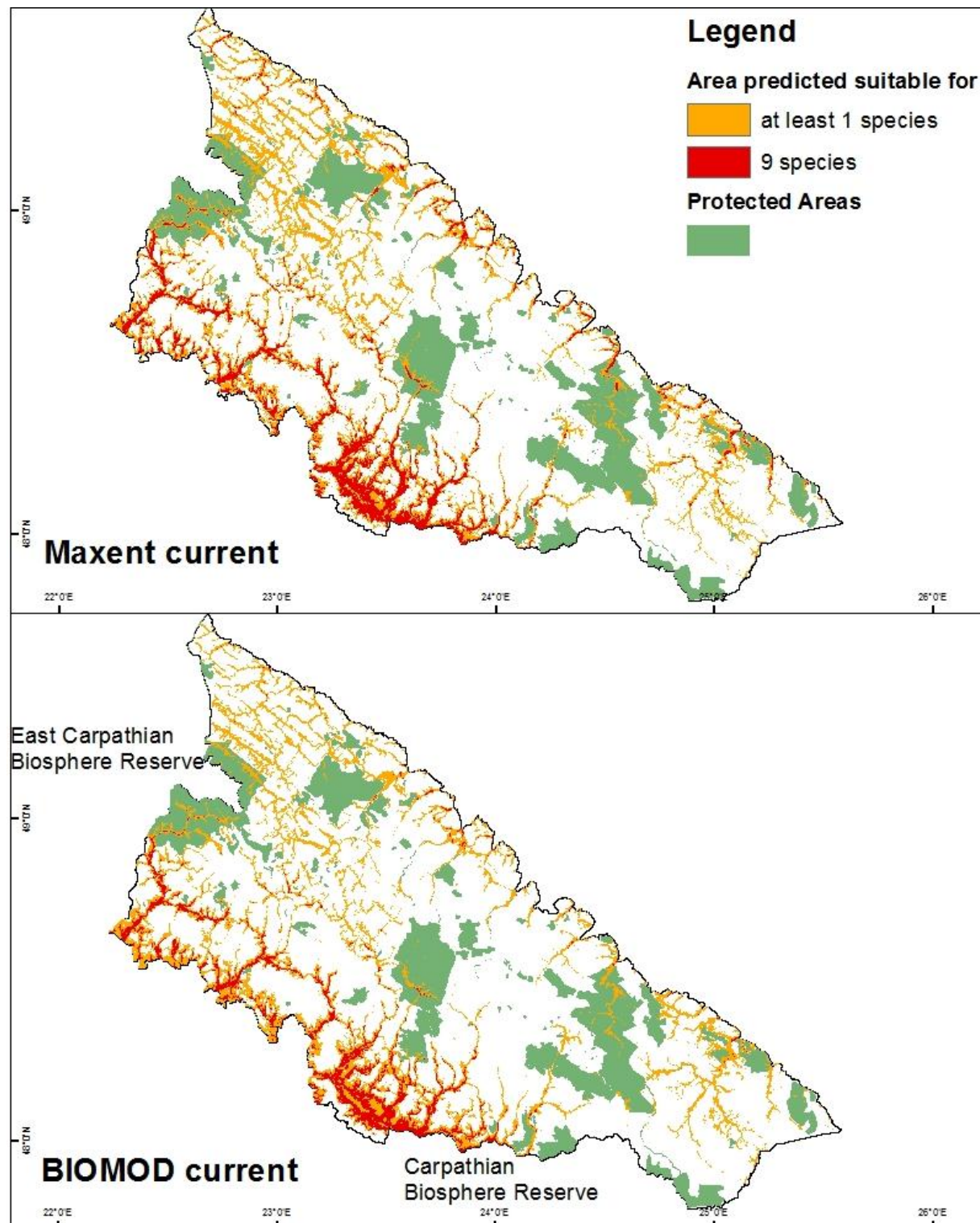
Figure 34: The range of potential impact of non-native invasive plants on biodiversity in the Ukrainian Carpathians under current environmental conditions; spatial distribution of suitable habitats for establishment of one or nine invasive plants/taxa within the region and within protected areas as determined by Maxent and BIOMOD algorithms;
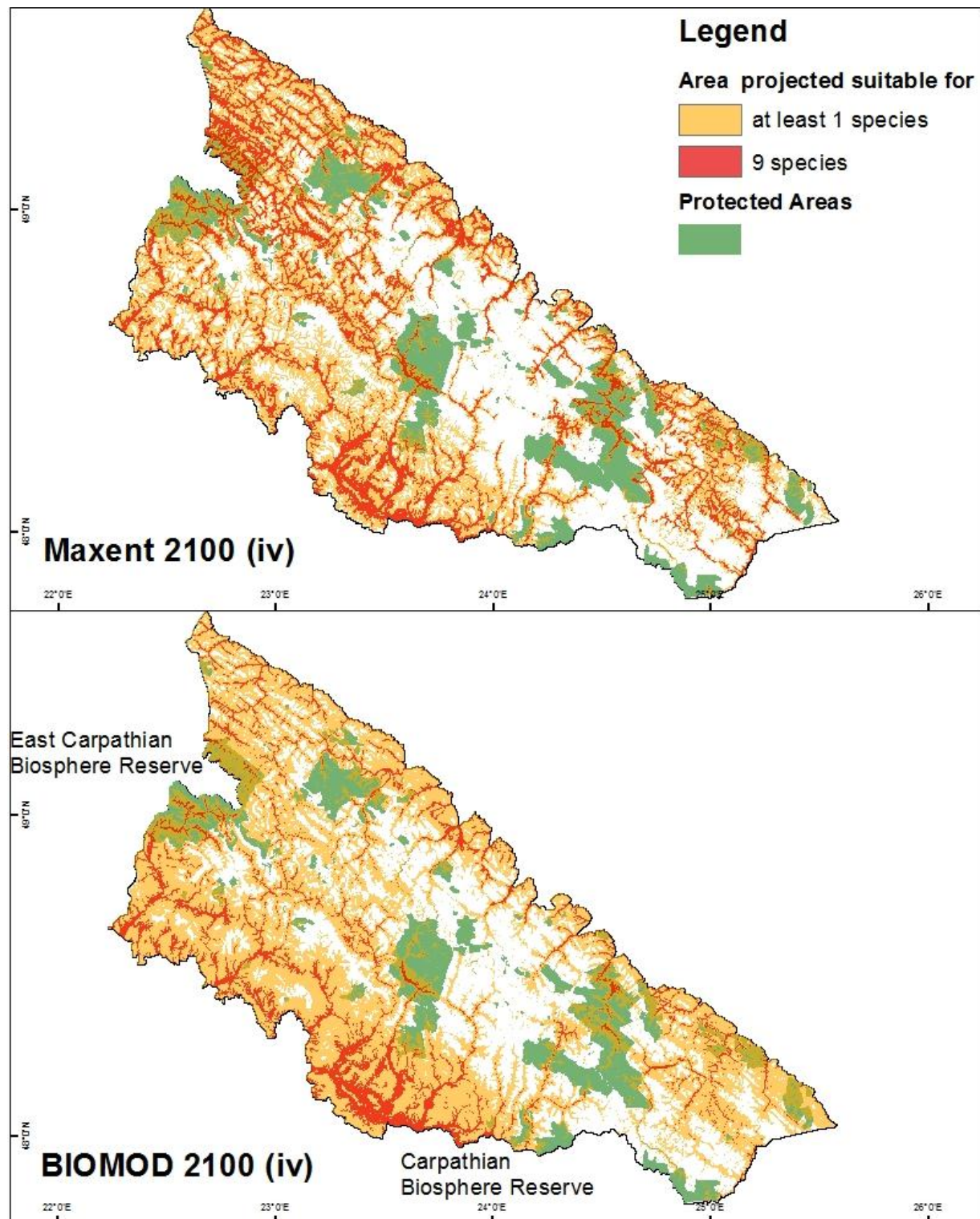
Figure 35: The range of potential impact of non-native invasive plants on biodiversity in the Ukrainian Carpathians by 2100 assuming climate change and high economic development/insufficient environmental protection; spatial distribution of suitable habitats for establishment of one or nine invasive plants within the region and within protected areas as projected by Maxent and BIOMOD algorithms under change scenario iv;

The four maps visualize the potential future (in the near and long term) distribution of the NIPS. Already today, all protected areas are at risk of being invaded by at least one of the nine species/taxa modeled. This is true for models fitted with Maxent and BIOMOD. Keeping in mind that the threshold for binary predictions is relatively conservative (see section 6.5), one can assume that the NIPS can potentially invade all major riparian habitats in the East Carpathian Biosphere Reserve and in all other nature reserves/protected areas at low elevations. If current trends continue, by 2100 (under scenario iv), only the most remote parts of protected areas at high elevations are projected to remain free of invasion. At the same time, protected areas at low elevations and under relatively greater anthropogenic pressure may become invaded by all nine species/taxa. In conclusion, protected areas are currently at a high risk of losing biodiversity to NIPS, losses that may be exacerbated by simultaneous invasions of ecosystems by several species and will most likely increase in future.

Therefore, analyses of potential introduction of NIPS into protected areas must be incorporated into strategies to protect biodiversity. In cooperation, ecologists, conservation biologists, and natural-resource managers can compare results obtained by Maxent and BIOMOD to determine the likelihood of invasion, which species are most likely to invade an area, and where these species are likely to come from. A clear understanding of the functioning of the algorithms, comparisons of predictive performances between models, and expert knowledge on the ecology of the species can be used to prioritize monitoring in order to achieve successful prevention and early detection of and quick response to invasion. For example, both Maxent and BIOMOD predict most suitable habitat for establishment under current conditions to be gained by *Heracleum sosnowskyi* (16 and 11% of the total area in Maxent and BIOMOD, respectively; see Table 6). The AUC values on predictions for this species are higher in BIOMOD than Maxent.

If a more broad-scale, long-term objective of preventing human-facilitated spread of this species is set, one would most likely focus on the more "lenient" Maxent predictions and/or determine a lower threshold for binary predictions, based on detailed ecological background knowledge of the already existing populations of this highly aggressive and rapidly spreading species. Fig. 36 below shows areas within the Uzhanskyi National Nature Park (NNP - part of the East Carpathian Biosphere Reserve) likely to be invaded by *H. sosnowskyi* according to Maxent predictions. As can be seen, *H. sosnowskyi* is already present along the main river, Ush, and suitable habitat for further local establishment of the species spreads out into the tributaries. Because *H. sosnowskyi* is an aggressive NIPS that is highly dangerous not only to biodiversity but also human heath (Appendix B), a program to eradicate current populations of this species within the Uzhanskyi NNP and monitor for possible novel introductions may utilize Fig. 36 (in cooperation with expert knowledge) to pinpoint locations in need of monitoring, starting with all riparian habitats determined to be highly suitable for *H. sosnowskyi* (red color in Fig. 36) and progressing further away from these areas along the suitability index until a predetermined threshold is reached.

Figure 36: Suitable areas for establishment of *Heracleum sosnowskyi* populations in the Uzhanskyi National Nature Park (NNP) based on logistic modeling results in Maxent

However, underfunding of the environmental protection sector often undermines efforts to protect biodiversity. The Ministry of Ecology and Natural Resources in the Ukraine and various other institutions such as State Agency for Forest Resources (Ministry of Agriculture of Ukraine) receive approximately 0.2% of the total annual GNP to implement and monitor environmental protection legislation (while equivalent institutions in Western Europe are typically allocated 1-2%). With state budgets shrinking due to stagnation of economic development in the last decade, the Ministry of Ecology cannot cope with widespread environmental issues (Nazarov *et al*. 2001). It is evident then that preventing the spread of NIPS must be, at least in the short term, extremely cost-effective. This may necessitate a focus on areas of highest, imminent risk of invasion. In such case, one could focus exclusively on the more reliable (higher AUC) BIOMOD predictions or on areas where the binary predictions for both algorithms overlap. Fig. 37 below shows areas within Uzhanskyi NNP highly suitable for invasion by *H. sosnowskyi* based on binary transformations of logistic BIOMOD-GBM outputs. Although similar to Fig. 36, predictions in BIOMOD are more conservative than in Maxent, and fewer areas on the periphery of major watersheds are predicted as suitable and may thus be eliminated from monitoring.

Figure 37: Suitable areas for establishment of *Heracleum sosnowskyi* populations in the Uzhanskyi National Nature Park (NNP) based on binary modeling predictions in BIOMOD

Meanwhile, effective monitoring of the spread of aggressive NIPS requires an understanding of the dominant factors causing particular patterns of distribution of suitable habitats for establishment. Coming back to the invasion of Uzhanskyi NNP by *H. sosnowskyi*, a key question is not only *where* the species is most likely to occur/become established but also *why* certain patterns of potential distribution are likely. To answer the latter question, one may look at the current distribution of *H. sosnowskyi* populations and at the importance the algorithms accorded to individual (or groups of) predictor variables. Populations of *H. sosnowskyi* are currently found clearly along rivers and moist road ditches and spread into adjacent open, disturbed habitats. *H. sosnowskyi* does not tolerate drought, and migration of populations is physically restricted by steep slopes and closed-canopy forests. Moreover, in both Maxent and BIOMOD-GBM, distance to settlements and roads contributes most to model fitting (closely followed by slope). Therefore, it must be assumed that disturbance and propagule pressure are critically important for the spread of this species along and away from linear habitats, and areas of high suitability are foremost close to large roads and settlements. More precisely, foci of introduction and local population

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growth of the species most likely coincide with high density of roads and settlements and, once established at these foci, long-distance seed dispersal by humans and water leads to establishment of new populations in the direction of water flow in riparian habitats and in the direction of traffic flow along roads. Fig. 38 below demonstrates this trend. The significance of disturbance and repeated introductions in overcoming otherwise unsuitable conditions for growth and reproduction is the most likely explanation for the presence of *H. sosnowskyi* populations in areas determined to be unsuitable by binary BIOMOD predictions (i.e., the eastern border of the NNP), as the density of settlements and roads is highest in these areas.

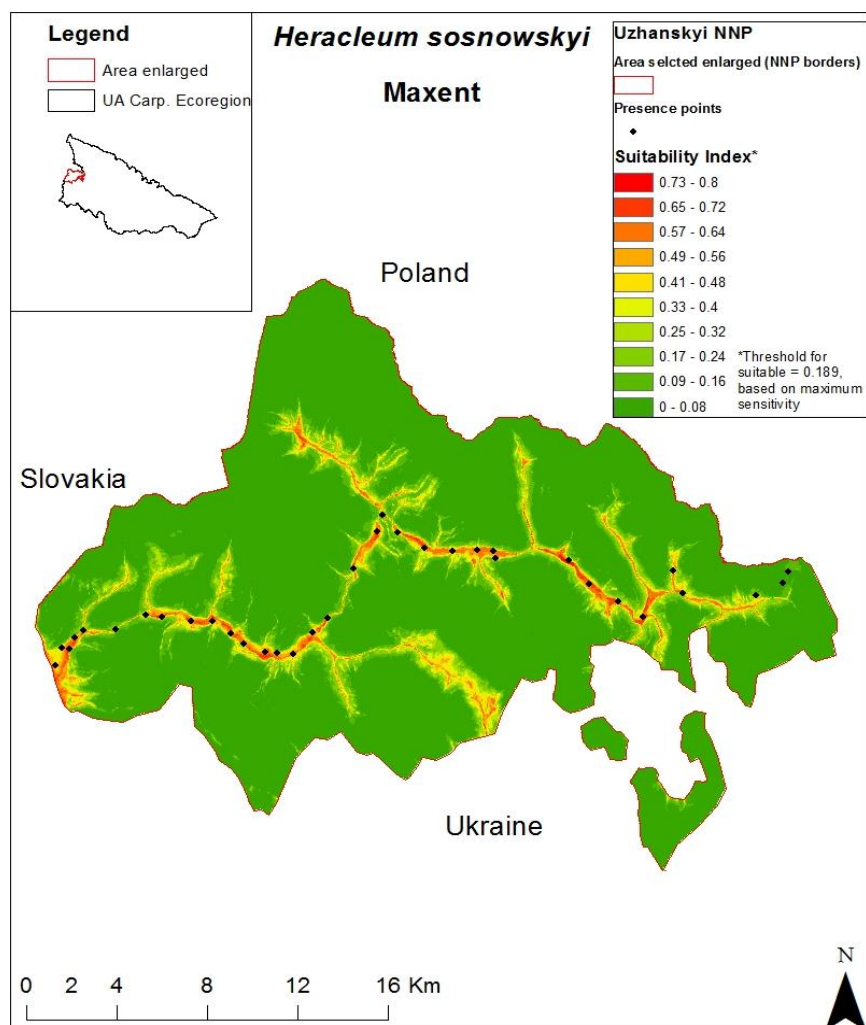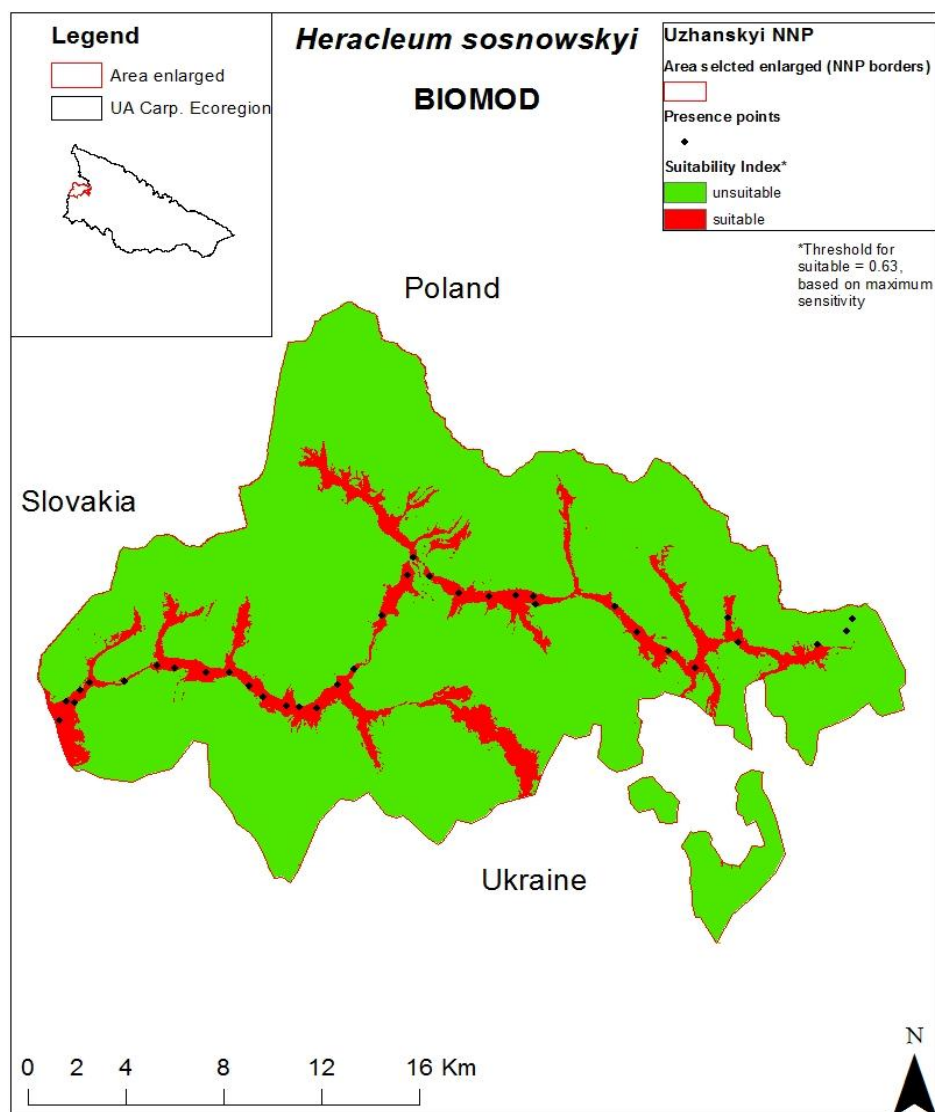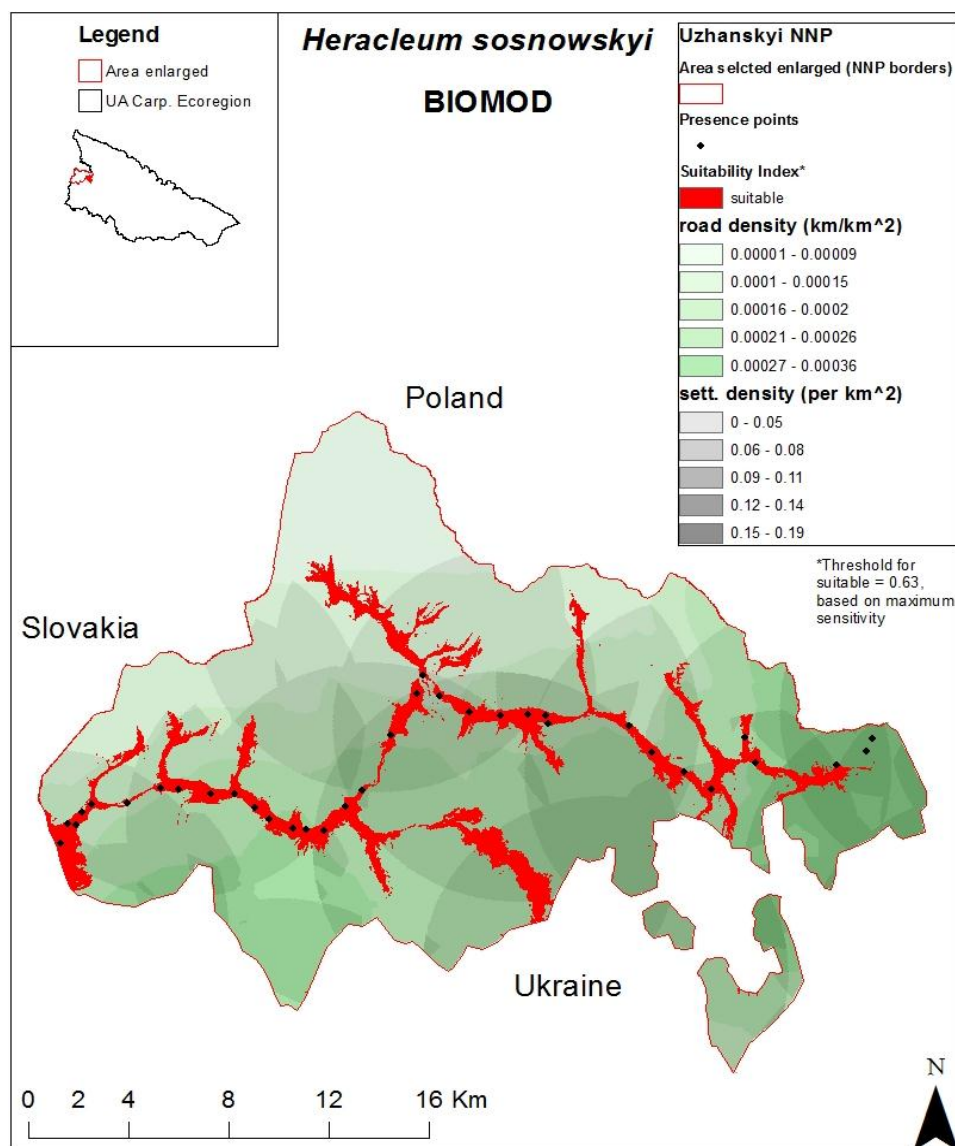**Figure 38:** Density of settlements and roads and suitable areas for establishment of *Heracleum sosnowskyi* populations in the Uzhanskyi National Nature Park (NNP); suitability based on BIOMOD binary model predictions;

For all species and models, knowledge of possible loci where NIPS are introduced and migrate from within the entire UA Carpathians is crucial for designing effective management programs.

In general, given the critical importance of anthropogenic influences on the distribution of NIPS, one must conclude that proactive management can only be accomplished by buffering linear habitats susceptible to invasion from anthropogenic pressures. However, in order to create proper buffer zones, natural-resource managers must understand the contribution of anthropogenic vs. climatic/environmental factors in determining the distribution of suitable habitats. This can be accomplished through interpretations of the variable importance analyses performed by each algorithm. For instance, linear habitats that are identified to be suitable only for a species that is strongly constricted by several predictors in its spread (e.g., *Echinocystis lobata*) may be considered of low monitoring and management priority, while habitats identified as suitable for one or several species that are highly adaptable and occur across gradients for several predictors, must be strongly buffered from human-caused disturbances; the more of these relative generalists one area is likely to contain, the bigger a protective buffer around the area is needed. This means concretely that particularly areas at low elevations and in close proximity to human structures must be protected from degradation and disturbances, as it is here where most NIPS are predicted to co-occur. This management objective may seem trivial and common knowledge but the outputs of this study provide a visualization of the threat NIPS pose to biodiversity and propose a link between this threat and anthropogenic pressures. In light of the results of this study and the already prevalent invasion of major linear habitats at low elevations, scientists may more effectively argue for more prudent forms of development in the mountains (Simpson *et al*. 2011a). Such a "transition to sustainable development, which would promote preservation and regeneration of ecosystems and thereby improve the living standards of people in the Ukrainian Carpathians" is assumed to become slowly accomplished within the next decades but must be pursued more aggressively if biodiversity preservation is a chief goal (Maryskevych 2006).

Meanwhile, protection of natural and semi-natural ecosystems from human-caused stresses cannot be accomplished without the support and involvement of local stakeholders (WWF Carpathian Programme 2007). When confronted with inefficient and slow bureaucracies, a large-scale dissemination of information and education of the local population are paramount. Children and adults must learn about the threats some popular ornamentals (e.g., *Helianthus tuberosus*) pose and that their own actions can have huge effects on ecosystems, effects that are not immediately visible such as favoring establishment of *Ambrosia artemisiifolia* due to pollution of soil through improper disposal of waste. People must thus be encouraged to pursue land-use practices that prevent the establishment of invasive species. Such practices include disposing waste properly, avoiding overgrazing in riparian zones, eradicating and avoiding planting of non-native ornamental plants on one's property, and communicating sightings of non-native species to local authorities. A cost-effective approach to awareness building is the development of campaigns that inform the general public about the ecological impacts of the most aggressive NIPS. Such campaigns cannot succeed without active involvement of the local/regional governments, but the financial burden can be carried by NGOs (see Nazarov 2001). Maps developed in this study are a great way to demonstrate the implications of the establishment of aggressive NIPS in the UA Carpathians.

Besides the general population, the forestry and tourism sectors are major stakeholders in biodiversity conservation in the UA Carpathians and must be involved in programs aiming at preventing the spread of NIPS in the mountains. Forestry practices must be adjusted to prevent the spread of aggressive invaders along corridors created by imprudent deforestation. That is,

logging must be selective in a way that maintains physical barriers between (potential) populations of NIPS. In doing so, two internationally accepted criteria of sustainable forest management would be achieved: preservation of biodiversity and maintenance of water resources (Keeton and Crow 2009). Maintaining riparian forest communities intact decreases the likelihood of invasion as the NIPS are shade-intolerant and do not proliferate in late-successional ecosystems. At the same time, severe flooding in recent years in the UA Carpathians has been shown to have been caused in part by forest clearing (Keeton and Crow 2009); and many of the NIPS established along rivers in the wake of forest clearings exacerbate risks of erosion and flooding (Appendix B). Therefore, maintenance of water resources and prevention of establishment of NIPS go hand in hand. In conclusion, certifications for sustainable forest management as proposed by WWF Carpathian Programme (2007) must incorporate criteria that evaluate the effectiveness of preventing the possible introduction of invasive plants into novel habitats.

Similarly, a lot of effort is currently put forward to establish sustainable forms of tourism (i.e., tourism that does not disturb natural ecosystems). Such efforts include evaluations of the number of tourists a particular landscape can carry without endangering the long-term health of natural systems (WWF Carpathian Programme 2007). The suitability predictions and projections that are results of this study can be used as a criterion for such evaluations. For example, a region under consideration for touristic development in the Transcarpathians may be inspected for the likelihood of being invaded by several NIPS under current conditions and future projections. In fact, Figs. 34 and 35 demonstrate that by 2100, under climate change and increased human development, all major riparian habitats in the southern and southwest UA Carpathians are likely to be invaded by at least one species in Maxent as well as BIOMOD. In addition, Fig. 39 on the next page demonstrates that already by 2050, increases in average monthly temperatures and human pressures cause an expansion of suitable habitat throughout the Transcarpathians for all NIPS. An opening of currently remote areas to tourists via infrastructure development (including illegal tourism in the Reserves or in core zones of National Nature Parks) will disturb ecosystems and increase propagule pressure for the NIPS – thus potentially creating high risks for protected areas to be invaded by several NIPS.
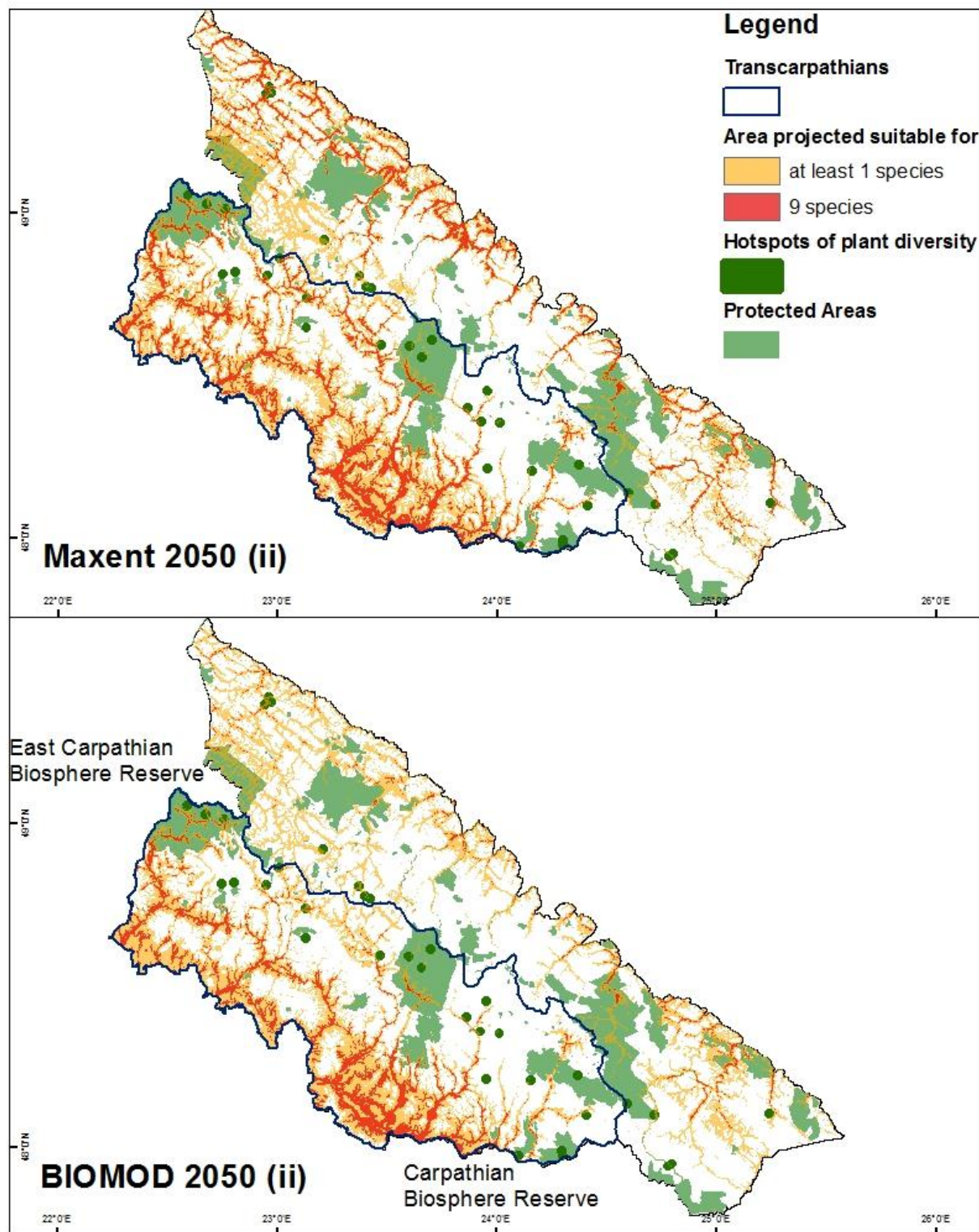
Figure 39: The range of potential impact of highly invasive plants on biodiversity in the UA Carpathians (with a focus on the Transcarpathians) by 2050 assuming climate change and high economic development/insufficient environmental protection; spatial distribution of suitable habitats for establishment of one or nine invasive plants within the region and within protected areas as projected by Maxent and BIOMOD algorithms under change scenario ii;

Based on the outputs of the study, the number of tourists any region or locality can carry is then in part determined by its location within suitability indices, i.e., areas of high invasion potential can carry fewer tourists and vice versa. In Fig. 39, for instance, major rivers within protected areas in the central UA Carpathians are projected to provide suitable habitat for all nine species/taxa by 2050. High number of tourists within or high rates of infrastructure development around these areas must be avoided. Furthermore, an important study by Lonsdale and Lane (1994) suggests that although seed transport through tourist vehicles is at least in part responsible for the establishment of invasive weed populations in natural parks, seeds are only found on few vehicles and effective control of these weeds should consist of monitoring of vulnerable sites and eradicate populations wherever possible. Such monitoring can be accomplished by overlaying major routes of tourist traffic with suitability analysis (made in Maxent or BIOMOD or both) for all or some selected species.

Lastly, despite the divergences of projections between algorithms and resulting uncertainties about the exact future distribution of suitable habitats for establishment, it is evident across algorithms that the potential distribution of the NIPS is highly dynamic and will most certainly increase in future. This has implications for the designation of protected areas and ecological networks connecting current and future protected areas. Fig. 39 clearly demonstrates that by 2050, major linear habitats in most protected areas at low elevations are predicted to be suitable for the establishment of several NIPS. If current trends continue, Fig. 35 illustrates that by 2100 virtually all protected areas are likely to be invaded by NIPS. Complete eradication of all aggressive NIPS from the UA Carpathians is not likely as many species have already established thriving populations. Assuming that further spread of the aggressive NIPS is inevitable (albeit the dependence of the intensity of the spread on the rate of climatic and land-use changes), designation of buffer zones within the protected areas and around them must take into account the possible future spread of NIPS. That is, there is little sense in protecting riparian habitats at low elevations while allowing higher touristic development at upper elevations because by 2050 climatic changes may create favorable habitat for NIPS at upper elevations while at the same time barring potential migration routes for native species. Similarly, when designing ecological networks connecting protected areas, care must be taken that these act as barriers for migration of NIPS under current and future climatic conditions.

In conclusion, the results of this study not only illustrate the threats biodiversity in the UA Carpathians faces from most commonly found NIPS in the region but also provide opportunities for ecologists, conservation biologists, and natural-resource managers to incorporate indices of the potential spread of these species into any regional management plan that targets the preservation of biodiversity. Expert knowledge and results of species distribution models can be used to optimize monitoring strategies by ranking suitable habitat for establishment of NIPS based on predetermined criteria (e.g., how many different species are likely to invade, distance from settlements, etc.), find likely foci of species introduction, educate the public, create appropriate buffer zones around high-risk areas (in terms of invasion), and define sustainability criteria for the forestry and tourism sector. These are just a few of the potential applications of the maps produced by this study. As was stated in the introduction, this study has above all contributed to an information database to be built on and improved (Simpson *et al*. 2011a); and improvement is particularly necessary in the accuracy of projections (i.e., more detailed future

change scenarios must be worked out). Meanwhile, one must keep in mind that the UA Carpathians are not an isolated entity, and any long-term management plans targeting NIPS must incorporate cross-border cooperation. Foci of species introduction do not necessarily lie within Ukrainian borders and populations established within the UA Carpathians are likely to migrate to neighboring countries. Thus, follow-up studies must incorporate the entire Carpathian Arc and adjacent lowlands.

8. CONCLUSIONS

The Ukrainian (UA) Carpathians stand out through the high levels of biodiversity found in the region. The richness of species and ecosystems is a result of the structurally complex and diverse geomorphology, the central geographic position within the Carpathian Arc, the moderate average annual temperatures and abundant precipitation, and centuries of extensive, environmentally-friendly land use. However, biodiversity in the mountain range is threatened by the introduction and spread of non-native invasive plant species (NIPS). Eleven species have been identified, by the Alien Plant Ranking System, as most dangerous invaders in the UA Carpathians and were the objects of this study: *Acer negundo* L., *Reynoutria japonica* Houtt., *Reynoutria x bohemica* Chrtek.& Chrtková, *Echinocystis lobata* (Michx.) Torr. & Grey, *Impatiens glandulifera* Royle, *Heracleum sosnowskyi* Manden, *Robinia pseudoacacia* L., *Helianthus tuberosus* L., *Solidago canadensis* L., *Solidago gigantea* Aiton, and *Ambrosia artemisiifolia* L.

The success of the NIPS in outcompeting native vegetation can be attributed to set of characteristic common to invasive plants in general: inherent competitive abilities, including fast growth, high seed production, and strong phenotypic plasticity, which the species can exhaust more so than native species because they are released from specialist and/or are under less pressure from generalist herbivores and parasites in their invaded range. At the same time, particular habitats, i.e., frequently disturbed (mostly by humans) linear habitats along rivers and roads and in close proximity to settlements, are used by all the NIPS for long-distance population migrations. Predicted intensification of natural-resource and land use within the UA Carpathians that permanently alters ecosystems or disrupts them at greater frequencies and intensities than are expected from natural disturbances may therefore promote further spread of NIPS. Furthermore, expected increases in atmospheric CO_2 levels will most likely benefit the NIPS, as the species will be able to accumulate more resources and expand their ranges to novel habitats created under a warming climate. The lack of information on the concrete patterns of future distributions of aggressive NIPS necessitated a study to determine suitable habitats within the UA Carpathians for introduction and establishment of NIPS and mechanisms explaining the particular (potential) distribution patterns under a variety of scenarios.

Two conceptually distinct distribution modeling software applications, Maxent (requires only data on species presence) and BIOMOD (requires info on absences), were used for modeling due to the realization that outcomes of habitat suitability models depend not only on the ecologies of the species but also on the algorithms used. The models were calibrated by describing the dependence of the likelihood of species occurrences on values of environmental predictor variables; and the functions obtained from locations of species presences were extrapolated to the entire study. The resulting predictions depict suitable habitats for establishment of the NIPS

in the UA Carpathians and were projected to four future change scenarios: (i) climate change/low economic development by 2050; (ii) climate change/high economic development by 2050; (iii) climate change/low economic development by 2100; and (iv) climate change/high economic development by 2100. Six predictor variables were chosen based on how accurately they approximate habitat suitable for the establishment of species within the realized niche of the NIPS. They are: minimum temperature of coldest month (*mintcold*), maximum temperature of warmest month (*maxtwarm*), sum of active temperatures > 10°C (*sat*), proximity to water (*s_dist_water*), proximity to settlements and roads (*s_dist_sett_r*), and slope (*slope*). The accuracy of the model predictions was measured with the threshold-independent ROC curve.

Despite uncertainties in model accuracy that arose from inherent uncertainties in obtaining and manipulating predictor variables and georeferencing presence locations, all model predictions are statistically significant, and, in part because presence/absence algorithms tend to fit predicted values closely to empirical averages, thus minimizing commission and omission errors, BIOMOD consistently outperforms Maxent in regards to AUC values. However, both applications produce excellent predictions with AUC values > 0.9. Under current climatic regimes and land-use patterns, habitats along large rivers and roads at elevations up to ca. 600 m above sea level, which correspond to the warm to moderately warm climatic zones, are predicted suitable for the eleven NIPS to become established. All eleven NIPS have already established populations in many of the areas predicted as suitable. Meanwhile, binary transformations of logistic outputs based on an optimized threshold suggest that there is a spatial aggregation of suitable habitats for establishment across species. Of the total area within the UA Carpathians predicted suitable for at least one species, 26% in Maxent and 20% in BIOMOD are predicted to be suitable for all nine species/taxonomic complexes. All species modeled are predicted to become established along major linear habitats in the southwest, west, and, at lesser frequencies, in the east and southeast. The likelihood of these habitats to be invaded by several highly aggressive NIPS is correlated ($p = 0.001$) to the density of settlements and roads in the regions of aggregation.

The factors causing the particular spatial distribution of suitable habitats are the predictor variables and their role in model fitting. Once scale dependencies and correlations between predictors have been accounted for, both Maxent and BIOMOD suggest that all predictors are important to model fitting, and that the clustering of suitable habitats in certain regions can be attributed to an aggregation of favorable values of the climatic, topographic, and land-use predictors in these regions. The significance of climatic variables explains why more species and suitable habitats are found in the warmer southwest as opposed to the colder northeast despite high population densities in both regions. Among the climatic variables, *maxtwarm* is of particular importance in all algorithms, which is plausible as the hydrophilic species adapted to moderate climates are more tolerant of occasional frost than of drought. Among the land-use and topographic variables, *s_dist_sett_r* influences model building the most and emphasizes the critical importance of anthropogenic disturbances and propagule pressure in predicting suitable habitats for the establishment of NIPS. Meanwhile, the relative importance of climatic vs. topographic/land-use variables differs more between species than between algorithms and indicates that the particular ecologies of the study species determine whether the species is more limited in its spread by climatic and topographic factors or human presence.

Projections of the models into future scenarios produce statistically significant gains of novel suitable habitats for all scenarios ($p < 0.001$). Some general trends for the future of the NIPS in the UA Carpathians are revealed across algorithms. Most importantly, with a warming climate, all NIPS gain novel suitable habitat for establishment along linear habitats in the interior of the mountain range in climatic zones currently unsuitable for establishment but projected to experience increases in the length of the growing season in the future. Meanwhile, the species lose only a few areas predicted to be suitable under current conditions. Furthermore, the high significance of human pressures on ecosystems as a predictor variable means that the greater the rate of future habitat fragmentation and destruction due to human development, the more the species are expected to expand their ranges beyond major linear habitats occupied today. The projected range changes under scenarios ii and iv, i.e., assuming high economic development in addition to increases of annual average temperatures, are significantly higher ($p = 0.002$) than under scenarios i and iii, i.e., assuming only climatic changes. By 2050, approximately 28 and 32% of the entire study area is projected to be suitable for at least one species across algorithms for scenario i and ii, respectively. By 2100, this proportion increases to 49 and 59% for iii and iv, respectively. In addition, for any given species, the extent of future suitable habitats varies based on the current distribution and establishment behavior of that species. Suitable habitats for a species that is currently distributed as specialist relative to other NIPS (i.e., *Acer negundo* (in Maxent), *Echinocystis lobata*, *Heracleum sosnowskyi*, and *Impatiens glandulifera*) will on average cover smaller proportions of the entire study area.

However, generalizations about potential future distributions of the NIPS based on their current niches are difficult to maintain because the projections suggest that there are marked differences between algorithms that cannot be attributed to the ecologies of the species alone. Divergences in projections between Maxent and BIOMOD models for any given species are a result of small differences in the calibration of response curves depicting the probability of species presence as a function of the predictor variables. If algorithms predict slightly different responses to certain values of predictors, changing the values of predictors during projections may exacerbate these differences.

As the eleven highly invasive species have already established viable populations throughout the region, further invasion is imminent. The co-occurrence of NIPS at locations of high suitability has already led to displacement of native species. Meanwhile, model predictions for current environmental conditions suggest that, at elevations up to approximately 600 m a.s.l., major linear habitats in all protected areas within the UA Carpathians, which are by definition of high conservation value, are at a risk of being invaded by several NIPS in the near future. By 2011, only the most remote parts of protected areas at high elevations are projected to remain free of invasion. Given the risks the NIPS pose to the native flora, the results of this study should be incorporated into strategies to protect biodiversity. Depending on the priorities of management, one can either choose to work with the more lenient predictions in Maxent (if a precautionary principle is applied) or the more conservative predictions in BIOMOD (if monitoring efforts must be concentrated). Expert knowledge on the ecologies of the NIPS and the model results can then be used to optimize monitoring strategies by determining highly suitable habitats for establishment of NIPS and to prioritize monitoring in these habitats based on criteria such as invasibility by several species or proximity to human settlements. In addition, analyses of variable importance can aid in finding likely foci of species introduction and creating buffer

zones around areas at high risk of invasion, i.e., areas that will potentially be invaded by several of the species that are predicted to behave like generalists and are not strongly constrained in their spread by individual predictor variables.

Lastly, the results of this study provide information that can be used to inform local and regional authorities and educate the public about invasive plants and how certain behaviors promote their proliferation. In addition, this study suggests that novel approaches to forestry and tourism are needed – approaches that redefine logging operation and infrastructure development with the goal to minimize the spread of NIPS as a result of increased propagule pressure, habitat fragmentation, and creation of linear dispersal corridors. Furthermore, any long-term projects aiming to protect biodiversity in the region must incorporate projections of the future spread of NIPS. Above all, this study provides an informational database that must be extended to include the entire Carpathian range in order to foster cross-border cooperation in preventing the introduction and spread of NIPS.

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9. REFERENCES

Alien Plant Ranking System (APRS) Implementation Team. (2000). *Alien Plants Ranking System Version 5.1.* Northern Prairie Wildlife Research Center: Maryland, USA. Retrieved April 22, 2011 from http://www.npwrc.usgs.gov/resource/literatr/aprs/index.htm.

Austin, M.P. (2002). Spatial predictions of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157, 101-118.

Baker, R.H.A., Sansford, C.E., Jarvis, C.H., Cannon, R.J.C., MacLeod, A., and Walters, K.F.A. (2000). The role of climatic mapping in predicting the potential geographical distribution of nonindigenous pests under current and future climates. *Agriculture, Ecosystems and Environment* 82, 57–71.

Bartha, D., Csiszar, A., and Zsigmond, V. (2008). Black locust (*Robinia pseudoacacia* L.). In *The Most Important Invasive Plants in Hungary*, (ed. Botta-Dukat, Z. *et al*.). HAS Institute of Ecology and Botany: Vacratot, Hungary, pp. 63-76.

Bartholy, J., Pongracz, R., Miklos, E., and Kis, A. (2011). Simulated regional climate change in the Carpathian Basin using ENSEMBLES model simulations. *American Meteorological Society 91st Annual Meeting*. Retrieved April 5, 2011 from http://ams.confex.com/ams/91Annual/webprogram/Paper185826.html.

Bartholy, J., Pongracz, R., Torma, C., Pieczka, I., Kardos, P., and Hunyady, A. (2009). Analysis of regional climate change modelling experiments for the Carpathian Basin. *International Journal of Global Warming* 1(1-3), 238-252.

Baumann, M., Kuemmerle, T., Elbakidze, M., Ozdogan, M., Radeloff. V.C., Keuler, N.S., Prishchepov, A.V., Kruhlov, I., and Hostert, P. (2011). Patterns and drivers of post-socialist farmland abandonment in Western Ukraine. *Land Use Policy* 28, 552-562.

Begon, M., Townsend, C.R., and Harper, J.L. (2006). *Ecology: From Individuals to Ecosystems*. Blackwell Publishing: Oxford, UK.

Berger, A.L., della Pietra, S.A., and della Pietra, V.J., (1996). A maximum entropy approach to natural language processing. *Comput. Linguist.* 22 (1), 39-71.

Bilz, M., Kell, S.P., Maxted, N., and Lansdown, R.V. (2011). *European Red List of Vascular Plants*. Publications Office of the European Union: Luxembourg, pp.144.

Brandes, D. and Nitzsche, J. (2006). Biology, introduction, dispersal, and distribution of common ragweed *(Ambrosia artemisiifolia* L.*)* with special regard to Germany. *Nachrichtenblatt Deutscher Pflanzenschutzdienst* 58(11), 286-291.

Broennimann, O. and Guisan, A. (2008). Predicting current and future biological invasions: both native and invaded ranges matter. *Biology Letters* 4, 585-589.

Broennimann, O., Treier, U.A., Mueller-Schaerer, H., Thuiller, W., Peterson, A.T, and Guisan, A. (2007). Evidence of climatic niche shift during biological invasion. *Ecology Letters* 10, 701-709.

Bouma, J., Varralyay, G., and Batjes, N.H. (1998). Principal land-use changes anticipated in Europe. *Agriculture, Ecosystems, and Environment* 67(2-3), 103-119.

Callaway, R.M. and Maron J.L. (2006). What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology and Evolution* 21(7), 369-374.

Chapin, F.S., III, Sala, E.O., Burke, I.C., Grime, J.P., Hooper, D.U., *et al*. (1998). Ecosystem consequences of changing biodiversity. *BioScience* 48(1), 45-52.

Chen, H, Chen, L., and Albright, T.P. (2006). Developing habitat suitability maps of invasive ragweed (*Ambrosia artemisiifolia*) in China using GIS and statistical modeling. In *GIS for Health and the Environment: Development in the Asia-Pacific Region* (ed. Lai, P.C.). Springer: New York, USA, pp. 105-121.

Chornesky, E.A. and Randall, J.M. (2003). The threat of invasive alien species to biological diversity. *Annals of the Missouri Botanical Garden* 90(1), 67-76.

Chytry, M., Maskell, L.C., Pino, J.. Pyšek, P., Vila. M., Font, X., and Smart, S.M. (2008). Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology* 45, 448-458.

Colautti, R., Grigorovich, I.A., and MacIsaac, H.J. (2006). Propagule pressure: a null model for biological invasions. *Biological Invasions* 8, 1023-1037.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A., and MacIsaac, H.J. (2004). Does the enemy release hypothesis predict invasion success? *Ecology Letters* 7, 721–733.

Deodatus, F. and Protsenko, L. (ed.). (2010). *Creation of Ecological Corridors in Ukraine: A Manual on Stakeholder Involvement and Landscape-Ecological Modelling to Connect Protected Areas, Based on a Pilot in the Carpathians*. State Agency for Protected Areas of the Ministry of Environmental Protection of Ukraine, Altenburg and Wymenga Ecological Consultants, InterEcoScience: Kyiv, UA.

Drake, B.G., Gonzalez-Meler, M.A., Long, S.P. (1997). More efficient plants: a consequence of rising atmospheric CO_2? *Annu Rev Plant Physiol Plant Mol Biol* 48, 609–639.

Dudik, M., Phillips, S.J., and Schapire, R.E. (2007). Maximum entropy density estimation with generalized regularization and an application to species distribution modeling. *Journal of Machine Learning Research* 8, 1217–1260.

Dukes, J.S. (2000). Will increasing atmospheric CO_2 concentration affect the success of invasive species? In *Invasive Species in a Changing World*. Ed Mooney, H.R. and Hobbs, R.J. Island Press: Washington, USA, Chapter 5.

Dukes, J.S. and Mooney, H.A. (1999). Does global change increase the success of biological invaders? *Trends in Ecology* 14, 135-139.

Dullinger, S., Kleinbauer, I., Peterseil, J., Smolik, M., and Essel, M. (2009). Niche based distribution modelling of an invasive alien plant: effects of population status, propagule pressure and invasion history. *Biol Invasions* 11, 2401–2414.

Elbakidze, M. and Angelstam, P. (2007). Implementing sustainable forest management in Ukraine's Carpathian Mountains: the role of traditional village systems. *Forest Ecology and Management* 249, 28-38.

Elith, J., Phillips, S.J., Hastie, T., Dudik, M., Chee, Y.E., and Yates, C.J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17, 43-57.

Elton, C.S. (1958). *The Ecology of Invasions by Animals and Plants*. The University of Chicago Press: Chicago, USA, and London, United Kingdom, 181 pp.

Evangelista, P.H., Sunil, K., Stohlgren, T.J., Jarnevich, C.S., Crall, L.W., Norman, J.B., and Barnett, D.T. (2008). Modelling invasion for a habitat generalist and a specialist plant species. *Diversity and Distribution* 14, 808-817.

Ficetola, G.F., Thiller, W., and Miaud, C. (2007). Prediction and validation of the potential global distribution of a problematic alien invasive species – the American bullfrog. *Diversity and Distributions* 13, 476-485.

Fielding, A.H. and Bell, J.F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24(1), 38-49.

Franklin, J. (2009). *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge University Press: Cambridge.

Freeman, E. (2011). PresenceAbsence package. *The R-Project - CRAN*. Available at http://cran.r-project.org/web/packages/.

Genton, B.J., Shykoff, J.A., and Giraud, T. (2005). High genetic diversity in French invasive populations of common ragweed, Ambrosia artemisiifolia, as a result of multiple sources of introduction. *Molecular Ecology* 14, 4275-4285.

Gotelli, N.J. (2008). *A Primer of Ecology* (4 ed.). Sinauer Associates Publishing: Massachusetts, USA.

Guisan, A., Zimmermann, N.E., Elith, J., Graham, C.H., Phillips, S., and Peterson, A.T. (2007). What matters for predicting the occurrences of trees: techniques, data, or species' characteristics? *Ecological Monographs* 77(4), 615–630.

Guisan, A. and Theurillat, J.P. (2000). Assessing alpine plant vulnerability to climate change: a modelling perspective. *Integrated Assessment* 1, 307–320.

Guisan, A. and Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8, 993-1009.

Guisan, A. and Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* 135, 147–186.

Haggett, P. (Ed.). (2002). *Encyclopedia of World Geography: Eastern Europe* (2 ed.). Andromeda Oxford Ltd: Oxford, United Kingdom, pp. 345.

Hastie, T., Tibshirani, R., and Friedman, J. (2009). *The Elements of Statistical Learning: Data Mining, Inference, Prediction*. Springer: New York, USA.

Herborg, L.M., Jerde, C.L., Lodge, D.M., Ruiz, G.M., MacIsaac, H.J. (2007). Predicting invasion risk using measures of introduction effort and environmental niche models. *Ecological Applications* 17(3), 663–674.

Herenchuk, K. I. (Ed.). (1968). *Pryroda Ukrayinskykh Karpat [Nature of the Ukrainian Carpathians]*. Vydavnytstvo Lvivskoho Universytetu: Lviv, UA. (in Ukrainian)

Hernandez, P.A., Graham, C.H., Master, L.L., and Albert, D.L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29, 773-785.

Hierro, J.L., Villarreal, D., Oezkan, E., Graham, J.M., and Callaway, R.M. (2006). Disturbance facilitates invasion: the effects are stronger abroad than at home. *The American Naturalist* 168(2), 144-156.

Hijmans, R.J. and Graham, C.H. (2006). The ability of climate envelope models to predict the effect of climate change on species distribution. *Global Change Biology* 12, 2272-2281.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978.

Holubets, M.A. (ed.), Honchar, M.T., Komendar, V.I., Kutsheravii, V.A., and Odinak, J.P. (1988). *Pryroda Ukrayinskykh Karpat [Nature of the Ukrainian Carpathians]*. Naykova Dumka: Kyiv, Ukraine. (in Ukrainian).

Hostert, P., Chaskovskyy, O., Knorn, J., and Kuemmerle, T. (2008). *Ukrainian Carpathians Land Cover Map – Final Report*. Geomatics Lab at Humboldt Universitaet zu Berlin: Berlin, Germany.

Hulme, P.E., Roy, D.B., Cunha, T., Larsson, T.-B. (2009). A pan-European inventory of alien species: rationale, implementations and implications of managing biological invasions. In

Handbook of Alien Species in Europe (Delivering Alien Invasive Species Inventories for Europe [DAISIE], ed.). Springer: Heidelberg, Germany, pp. 1-14.

Ibanez, I., Silander, J.A., Wilson, A.M., LaFleur, N., Tanaka, N., and Tsuyama, I. (2009). Multivariate forecasts of potential distributions of invasive plant species. *Ecological Applications* 19(2), 359-375.

Jacobs, G., Weber, E., and Edwards, P.J. (2004). Introduced plants of invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. *Diversity and Distributions* 10, 11-19.

Jeschke, J.M. and Strayer, D.L. (2008). Usefulness of bioclimatic models for studying climate change and invasive species. *Annals of the New York Academy of Sciences* 1134, 1-24.

Keane, R.M. And Crawley, M.J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17, 164-170.

Keeton, W. S. and Crow, S. M. (2009). Sustainable forest management alternatives for the Carpathian mountain region: providing a broad array of ecosystem services, 109-126. In Soloviy, I. and Keeton, W.S. (eds.). *Ecological Economics and Sustainable Forest Management: Developing a Trans-disciplinary Approach for the Carpathian Mountains*. Ukrainian National Forestry University Press: Lviv, Ukraine.

Kruhlov, I. (2008). Delimitation, metrization and classification of morphogenic ecoregions for the Ukrainian Carpathians. *Ukrainian Geographical Journal* 3, 59-68. (in Ukrainian)

Kubijovyč, M. (1984). Carpathian Mountains. *The Internet Encyclopedia of Ukraine*. Retrieved April 2, 2011 from http://www.encyclopediaofukraine.com/default.asp.

Kuemmerle, T., Chaskovskyy, O., Knorn, J., Radeloff, V.C. Kruhlov, I., Keeton, W.S., and Hostert, P. (2009). Forest cover change and illegal logging in the Ukrainian Carpathians in the transition period from 1988 to 2007. *Remote Sensing of Environment* 113, 1194-1207.

Kuemmerle, T., Hostert, P., Radeloff, V.C., van der Linden, S., Perzanowski, K., Kruhlov, I. (2008). Cross-border comparison of post-socialist farmland abandonment in the Carpathians. *Ecosystems* 11, 614–628.

Levine, J.M. and D'Antonio, C.M. (2003). Forecasting biological invasion with increasing international trade. *Conservation Biology* 17, 322–326.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J., Grigulis, K., and Lavorel, S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. Lond. B.* 270, 775-781.

Lobo, J.M., Jimenez-Valverde, A., and Real, R. (2007). AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 1-7.

Lonsdale, W.M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology* 80, 1522–1536.

Lonsdale, W.M. and Lane, A.M. (1994) Tourist vehicles as vectors of weed seeds in Kakadu National Park, Northern Australia. *Biological Conservation* 69: 277–283

Mack, R.N. and Lonsdale, W.M. (2001). Humans as global plant dispersers: getting more than we bargained for. *American Institute of Biological Sciences* 51(2), 95-102.

Maryskevych, O. (June 2006). *Policy Consultation on Sustainable Agriculture and Rural Development in the Carpathians*. UNEP: Vienna.

Morse, L.E., Randall, J.M., Benton, N., Hiebert, R., and Lu, S. (May 2004). *An Invasive Species Assessment Protocol: Evaluating Non-Native Plants for Their Impact on Biodiversity*. Nature Serve: Virginia, USA.

Nagel, J.M., Huxman, T.E., Griffin, K.L., and Smith, S.D. (2004). CO_2 enrichment reduces the energetic cost of biomass construction in an invasive desert grass. *Ecology* 85, 100-106.

National Research Council [NAS]: Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States. (2002). *Predicting Invasions of Nonindigenous Plants and Plant Pests*. National Academy of Sciences: Washington (DC), USA, pp.198.

Nazarov, N., Cook, H.F., and Woodgate, G. (2001). Environmental issues in the post-communist Ukraine. *Journal of Environmental Management* 63, 71-86.

Newbold, T. (2010). Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. *Progress in Physical Geography* 34, 3–22.

Nijnik, M. and van Kooten, G.C. (2000). Forestry in the Ukraine: the road ahead? *Forest Policy and Economics* 1, 139-151.

Oszlanyi, J., Grodzinska, K., Badea, O., and Shparyk, Y. (2004). Nature conservation in Central and Eastern Europe with a special emphasis on the Carpathian Mountains. *Environmental Pollution 130*, 127-134.

Pácskay, Z., Lexa, J., and Szákacs, A. (2006). Geochronology of Neogene magmatism in the Carpathian arc and intra-Carpathian area. *Geologica Carpathica* 57(6), 511 – 530.

Pearson, R.G., Dawson, T.P., Berry, P.M., and Harrison P.A. (2002). SPECIES: a spatial evaluation of climate impact on the envelope of species. *Ecological Modelling* 154, 289-300.

Peterson, A.T. (2006). Uses and requirements of ecological niche models and related distributional models. *Biodiversity Informatics* 3, 59-72.

Peterson, A.T. (2003). Predicting the geography of species invasions via ecological niche modeling. *The Quarterly Review of Biology* 78(4), 419-433.

Petit, R.J., Bialozyt, R., Garnier-Géré, P., and Hampe, A. (2004). Ecology and genetics of tree invasions: from recent introductions to Quaternary migrations. *Forest Ecology and Management* 197(1-3), 117-137.

Phillips, S.J. (2010). *A Brief Tutorial on Maxent.* AT&T Labs-Research: Princeton University, USA. Retrieved January 15, 2011 from http://www.cs.princeton.edu/~schapire/maxent/.

Phillips, S.J., Dudik, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J.,and Ferrier, S. (2009). Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19(1), 189-197.

Phillips, S.J., Anderson, R.P., and Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190, 231–259.

Poorter, H. (1993). Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. *Vegetation* 104/105, 77-97.

Protopopova, V.V., Shevera, M.V., and Mosyakin, S.V. (2006). Deliberate and unintentional introduction of invasive weeds: a case study of the alien flora of Ukraine. *Euphytica* 148, 17-33.

Prots, B.H. 2009. Invasive plant species in Transcarpathia: ecology, diffusion, and environmental effects. *Monograph (not published)*. [In Ukrainian].

Prots, B.H., Ivanenko, I.B., Yamelynets, T.S., and Stanchu, I. (2011). *Rapid Assessment and Prioritization of Protected Area Management (RAPPAM) in Ukraine*. World Wildlife Fund [WWF] Danube Program: Vienna, Austria & Lviv, Ukraine, pp. 40.

Pyšek, P., Lambdon, P.W., Arianoutsou, M., Kuehn, I., Pino, J., and Winter, M. (2009). Alien vascular plants of Europe. In *Handbook of Alien Species in Europe*. (Delivering Alien Invasive Species Inventories for Europe [DAISIE], ed.). Springer: Heidelberg, Germany, pp. 43-61.

Pyšek, P. and Prach, K. (1994). How important are rivers for supporting plant invasion? In *Ecology and Management of Invasive Riverside Plants,* (ed. de Waal, L.C. et al.). John Wiley and Sons: London, United Kingdom.

Pyšek, P. and Richardson, D.M. (2007). Traits associated with invasiveness in alien plants: where do we stand? In *Biological Invasions*. (W. Nentwig, ed.). Springer: Heidelberg, Germany, pp. 97-125.

Quattrochi, D.A. (ed.) and Goodchild, M.F. (ed.) (1997). *Scale in Remote Sensing and GIS*, Lewis Publishers: Washington (DC), USA, pp. 432.

R Development Core Team. (2011). Stats Package. *The R-Project - CRAN*. Available at http://cran.r-project.org/web/packages/.

Reinhart, K.O. and Callaway R.M. (2004). Soil biota facilitate exotic *Acer* invasion in Europe and North America. *Ecological Applications* 14(6), 1737-1745.

Richardson, D.M., Pyšek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D., and West, C.J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6, 93–107.

Rouget, M. and Richardson, D.M. (2003). Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *The American Naturalist* 162(6), 713-724.

Rounsevell, M.D.A., Reginster, I., Araujo, M.B., Carter, T.R., Dendoncker, N., *et al*. (2006). A coherent set of future land use change scenarios for Europe. *Agriculture, Ecosystems and Environment* 114, 57-68.

Sakai, A.K, Allendorf, F.W., Holt, J.S., and Lodge, D.M. (2001). The population biology of invasive species. *Annual Review Ecological Systems* 32, 305-332.

Shea, K. and Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17, 170–176.

Song, J.S. and Prots, B. (1998). Invasion of *Ambrosia artemisiifolia* L. (Compositae) in the Ukrainian Carpathians Mts. and the Transcarpathian Plain (central Europe). *Korean Journal of Biology* 2, 209-216.

State Statistics Service of Ukraine. (2011). *Population Census.* Retrieved May 10, 2011 from http://www.ukrstat.gov.ua/.

StatSoft, Inc. (2011). *Electronic Statistics Textbook*. StatSoft: Tulsa (OK), USA. Available at http://www.statsoft.com/textbook/.

Stern, K.R., Jansky, S., and Bidlack, J.E. (2003). *Introductory Plant Biology* (9 ed.). McGraw-Hill: Boston, USA, 624 pp.

Simpson, M., Prots, B., and Vykhor, B. (September 19-23, 2011a). Determining the potential distribution of highly invasive plants in the Carpathian Mountains of Ukraine: a species distribution modeling approach under different climate-land-use scenarios. *Proceedings of the 13th meeting of the Ukrainian Botanical Congress Lviv, Ukraine*, 80-81.

Simpson, M., Prots, B., and Vykhor, B. (2011b). Modeling of the invasive plant distribution: case study of Sosnowski's hogweed *Heracleum sosnowskyi* Manden. in the Ukrainian Carpathian Mts. *Biolologichni Systemy (Biological Systems)* 3(1), 80-89.

Sitko, I. and Troll, M. (2008). Timberline changes in relation to summer farming in the Western Chornohora (Ukrainian Carpathians). *Mountain Research and Development* 28, 263–271.

Süli-Zakar, I. (1998). Socio-geographical transition in the rural areas of the Carpathian Euroregion. *GeoJournal* 46, 193–197.

Suptelny, O. (2000). *Ukraine: A History* (4 ed.). University of Toronto Press Incorporated: Toronto, Canada, pp. 736.

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science* 240, 1285–1293.

Tasienkevych, L.O. (2008). *Natural Flora of the Carpathians: Checklist of Vascular Plants*. State Museum Lviv: Lviv, Ukraine, pp. 308. [in Ukrainian]

Thuiller, W., Lafourcade, B., Araujo, M.B. (2009a). *ModOperating Manual for BIOMOD*. Université Joseph Fourier – Laboratoire d'Ecologie Alpine: Grenoble, France.

Thuiller, W., Lafourcade, B., Engler, R., and Araujo, M.B. (2009b). BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography* 32, 369-373.

Thuiller, W., Richardson, D.M., and Midgley, G.F. (2007). Will climate change promote alien plant invasions? *Ecological Studies* 193, 198-211.

Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T., and Prentice, I.C. (2005). Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci USA [PNAS]* 102, 8245–8250.

Thuiller, W. (2003). BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global climate change. *Global Change Biology* 9, 1353-1362.

Thuiller, W., Richardson, D.M., Rouget, M., Proches, S., and Wilson, J.R.U. (2006). Interactions between environment, species traits, and human uses describe patterns of plant invasion. *Ecology* 87(7), 1755-1769.

Toeroek, K., Botta-Dukat, Z., Danczka, I., Nemeth, I., Kiss, J., *et al*. (2003). Invasion gateways and corridors in the Carpathian Basin: biological invasions in Hungary. *Biological Invasions* 5, 349-356.

Turnock, D. (2002). Ecoregion-based conservation in the Carpathians and the land-used implications. *Land Use Policy* 19, 47-63.

UNEP [United Nations Environment Programme] (2007). *Carpathians Environment Outlook*. Geneva United Nations Environment Programme. Retrieved January 06, 2011 from http://www.grid.unep.ch/activities/assessment/KEO/index.php.

Verburg, P.H., de Koning, G.H.J., Kok, K., Veldkamp, A., and Bouma, J. (1999). A spatial explicit allocation procedure for modelling the pattern of land use change based upon actual land use. *Ecological Modelling* 116, 45-61.

von der Lippe, M. and Kowarik, I. (2006). Long-distance dispersal of plants by vehicles as a driver of plant invasion. *Conservation Biology* 21(4), 986–996.

Walter, J., Essl, F., Englisch, T., and Kiehn, M. (2005). Neophytes in Austria: habitat preferences and ecological effects. *Neobiota* 6, 13-25.

Weber, E. (1998). The dynamics of plant invasion: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. *Journal of Biogeography* 25, 147-154.

Webster, R., Holt, S., and Avis, C. (2001). *The Status of the Carpathians: A Report Developed as Part of the Carpathian Ecoregion Initiative*. World Wildlife Fund for Nature [WWF]. Retrieved January 22, 2011 from http://www.carpates.org/docs/publications/status.pdf.

Wesolowski, T. (2005). Virtual conservation: how the European Union is turning a blind eye to its vanishing primeval forests. *Conservation Biology* 19, 1349−1358.

Williamson, M., Pyšek, P., Jarosik, V., and Prach, K. (2005). On the rates and patterns of spread of alien plants in the Czech Republic, Britain, and Ireland. *Ecoscience* 12(3), 424-433.

WWF [World Wildlife Fund] Norway and Danube-Carpathian Programme. January 2007. *Protection and Sustainable Use of Natural Resources in the Ukraine Carpathians*. Retrieved January 13, 2011 from http://wwf.panda.org/what_we_do/where_we_work/black_sea_basin/danube_carpathian/our_solutions/forests_and_protected_areas/carpathian_ecoregion/.

Yates, C.J., McNeill, A., Elith, J., and Midgley, G.F. (2010). Assessing the impacts of climate change and land transformation on *Banksia* in the South West Australian Floristic Region. *Diversity and Distributions* 16, 187–201.

Zingstra, H.L., Seffer, J., Lasak, R., Guttova, A., Baltzer, M., et al. (2009). *Towards an Ecological Network for the Carpathians*. Wageningen International: Wageningen, Netherlands, pp. 48.

Ziska, L.H. (2003). Evaluation of the growth response of six invasive species to past, present and future atmospheric carbon dioxide. *Journal of Experimental Botany* 54, 395–404.

Appendix A: Glossary – Definitions of Scientific Terms

Active growing season: the number of days with average temperatures above 10° C;

Alien: plants that arrived to an ecosystem that is not part of their natural range by means of intentional or unintentional introduction by humans;

Akaike Information Criterion: a statistic that tests how well values predicted by a model match the actual observed values at a specific location;

Archeophyte: a plant naturalized in a region but introduced to the region by humans in ancient times (before AD 1492);

Binomial test: a statistical test on presence/absence data; the hypothesis that the proportion of presences in a study area is not significantly different than would be expected by chance is tested;

Biodiversity: the diversity of naturally occurring life in a landscape; includes genetic, species, community, and ecosystem diversity;

C_3 plants: produce a 3-carbon molecule as the first isolated product during photosynthesis; use relatively large amounts of water during photosynthesis and are thus water-demanding plants;

Casual: introduced plants that do not form self-replicating populations;

Colonization: establishment of populations in a new area;

Dioecious: individual plants carry flowers of only one sex (male or female);

Entomogamous: a plant that depends on insects to pollinate its flowers;

Growing season: the number of days with average temperature above 5° C;

Invasibility: the susceptibility of a community or ecosystem to invasion by non-native plants;

Invasiveness: the degree of negative impacts an invasive plant has on the invaded range;

Long-day plants: plants that flower when day length is longer than the critical length of day for initiation of flowering (which is usually 12-14 hours in temperate climates);

Mesic habitat: rich in soil moisture;

Monocarpic: a plant that flowers, produces seeds, and then dies;

Monoecious: individual plants carry female and male flowers on one plant;

Native plants: species that arrived and became naturalized in a territory by natural means and before humans played a major role in dispersal;

Naturalized: a plant able to survive, reproduce, and maintain populations without human interference in an alien range (not yet invasive);

Neophyte: alien plant naturalized in a region and introduced by humans after AD 1492;

Nitrogen-fixing plants: species that enter symbiotic relationships with soil bacteria (diazotrophs) able to transform atmospheric nitrogen to forms that can be taken up by plants;

Pearson's r statistic: measures the correlation between two variables; ranges from -1 to +1; the closer r approaches -1 or +1, the more correlated two variables are, i.e. the actual values as both variables increase (or the dependent variable decreases), lie in close proximity to or on the trendline;

Phenotypic plasticity: the ability of a plant to express a different phenotype (the visible result of genes) under a different set of environmental conditions

Predictor variable: the independent variable which determines the distribution of the species, in this study the climatic, topographic, and human-impact variables;

Propagule pressure: the number of individuals introduced and the number of introduction attempts; in areas where plants or their reproductive parts are continuously introduced (e.g. through vehicles, water, etc.), propagule pressure is high and establishment of species might be the results of propagule pressure and not solely suitable habitat;

Response variable: the dependent variable that responds to the parameters given by the dependent variable(s); in this study, the response variable is the occurrence of the species (as points with geographic coordinates)

Rhizome: an underground stem that, when separated from its mother plant, can produce new daughter/clone plants;

Saturated: communities in which all possible environmental niches are occupied;

Short-day plants: flower when day length is shorter than the critical length of day for initiation of flowering (which is usually 12-14 hours in temperate climates)

Species occurrence: the locations within a study area where a species is present; knowledge of species absences is not needed;

Species prevalence: the number of sampling units a species occupies in the study area; knowledge of species absences is needed

Stomata: minute pores (openings) in the outer tissue of leaves and stems which regulate transpiration (H_2O out) and gas exchange (CO_2 in and O_2 out);

Succession: orderly progression of community composition from primary (early) succession (appearance of vegetation after disturbance) to secondary (late) succession (establishment of complex communities maximizing species diversity and niche occupancy);

Sustainable/sustainability: long-term maintenance of the health and stability of a system, which means resource exploitation at or below the level of natural regeneration;

Unsustainable (resources)**:** exploitation of resources above the level of natural regeneration;

Unsustainable land management: forms of human development that disturb natural ecosystems at frequencies far greater than would occur naturally, fragment and/or permanently alter habitats, decrease biodiversity, and alter ecosystem functions;

Vegetative reproduction: asexual reproduction in which plants produce clones of themselves;

Appendix B: Ecology of the 11 Most Aggressive Non-Native Invasive Plant Species in the UA Carpathians

Acer negundo L., box-elder (Aceraceae)

Morphology/biology: This relatively short-lived (up to 100 years) perennial woody species shows high phenotypic plasticity, is **dioecious**[13] and among the earliest pollen producers in spring (flowering begins before the development of leaves). Pollination occurs mainly by wind, and the fruits (the typical double samaras of maples) are released in spring but require frost to germinate (Udvardy 2008). Wind is the most important dispersal agent, but seeds can also be transported by water particularly over long distances, as they can survive for six weeks in water and germinate without touching the ground (Medrzycki 2007). In mesic soils and ample sunlight, *A. negundo* can reach sexual maturity in five years – earlier than native floodplain tree species (Medrzycki 2007). The tree also reproduces vegetatively by growing outward and producing secondary roots and shoots where primary shoots touch the ground. However, because seeds are produced in high number, are easily dispersed, and germinate under a variety of environmental conditions, reproduction via seed dispersal is the most common way of population growth (Udvardy 2008). The varieties cultivated and then naturalized in Eastern Europe did not support extreme frost, and their descendants today are commonly found below 1000 m a.s.l (Medrzycki 2007).

A. negundo possesses high genetic variability and ubiquitous ecology. In its native as well as invaded range, *A. negundo* occurs in a variety of habitat types. The species tolerates some shade and is highly tolerant to soil water and soil nutrient deficits (Rosario 1988, Udvardy 2008). Because *A. negundo* is more resistant to flooding than other woody species in **mesic habitats**, it has been able to become established predominantly in upper floodplain terraces. The species is shade-intolerant and absent from mature closed-canopy forest communities (Udvardy 2008). In addition, *A. negundo* is an early successional tree species and is usually replaced by shade-tolerant species in late successional stages. Flooding, however, provides a level of disturbance that hampers succession (Medrzycki 2007).

Figure B40: *Acer negundo* profile: A – *A. negundo* infestation along river in UA Carpathians and distribution in Europe (green = present) (Medrzycki 2007); B – *A. negundo* seedlings along road in UA Carpathians;

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[13] Unless otherwise specified, terms in bold are defined in Appendix A.

History of introduction: *A. negundo* extends its native range continuously throughout the entire United States and the temperate climates of Canada, and can be found in mountains of Mexico and in Guatemala (Mędrzycki 2007; Rosario 1988). This ubiquitous species occurs in 13 ecosystem types in North America, including swamps, mesic deciduous forest, and mesic to dry coniferous forests. The woody plant was intentionally introduced to Western Europe in the wake of the exploration of the New World in the 17th century (Udvardy 2008). Variants of the species from the northern parts of the native range found their way to Eastern Europe in the late 18th century. In the early 20th century, *A. negundo* then spread promptly in parks and gardens due to the rapid initial growth of the plant and thus increasing popularity as ornamental, wind-breaker, and shelter-belt tree (Mędrzycki 2007; Petit *et al*. 2004). By mid-20th century, *A. negundo* escaped controlled cultivation in many Eastern European countries, including Ukraine, and **naturalized** populations can be found on a massive scale along river valleys and in (other) habitats disturbed by human activities.

Impacts: Adverse impacts of this weedy tree are most evident in riparian habitats. The vegetative reproduction of *A. negundo* prevents regeneration of poplars and willows in riparian habitats. With the displacement of these species, *A. negundo* diminishes biodiversity and alters ecosystem functions.

Ambrosia artemisiifolia (L.), common ragweed (Asteraceae)

Morphology/biology: This erect annual herb reaches heights of 70-200 cm and grows very fast early in the growing season, thus achieving a competitive advantage (Brandes and Nitzsche 2006). *A. artemisiifolia* spreads exclusively by seeds and is very successful in doing so as small plants produce more than 3000 and large ones can produce up to 62,000 seeds per plant (Bassett and Crompton 1975). The plant is **monoecious** and anemophilous (wind-pollinated). Flowering and maturation of seeds of this **short-day** species occur relatively late in the season, August-October, and seeds are dispersed mainly by water, animals, and human vectors such as cars (Brandes and Nitzsche 2006; Kasprzyk *et al*. 2010).

Temperature is the most important environmental factor determining the survival of seeds and thus distribution of the species. Seeds are tolerant of inundation but sensitive to frost and require mild spring temperatures to germinate (optimal are alternating temperatures of 7-28 °C). However, they can remain dormant for up to 30 years until conditions for germination are right. Cold temperatures, -4 °C to -10 °C for Approximately 15 weeks, are required to break dormancy (Brandes and Nitzsche 2006; Bassett and Crompton 1975). In addition, *A. artemisiifolia* grows on mesic as well as xeric soils but prefers a moderate soil moisture content as it is not efficient at storing water in tissues and thus does not tolerate long periods of drought (Kasprzyk *et al*. 2010; Brandes and Nitzsche 2006). The herb is a pioneer species that can accumulate large amounts of trance elements (e.g., lead) in its tissues, exhibits phenotypic plasticity (adaptability to a range of biotic and abiotic factors), and is thus highly tolerant of disturbances (Brandes and Nitzsche 2006, Genton *et al*. 2005). It rarely occurs in late-successional habitats such as woodlands (Bassett and Crompton 1975).

Figure B41: *Ambrosia artemisiifolia* profile: A - Distribution of *A. artemisiifolia* in Europe (green = present) and enlarged photo of inflorescence (Flora Italiana 2010); B - *A. artemisiifolia* infestation along a major road in the Transcarpathians;

History of introduction: *A. artemisiifolia* is native to the southwestern plains in the U.S. and extends its range into Mexico (Brandes and Nitzsche 2006). Among the species studied here, *A. artemisiifolia* is the only one that has been introduced largely accidently, usually hitchhiking in transports of American corn, sunflower, and birdfeed seeds. Transport of soils contaminated with reproductive parts of the weed has also become an important dispersal vector (Csontos *et al*. 2010; Brandes and Nitzsche 2006). First reports of naturalized populations of the species in Central and Eastern Europe date back to the early 1900s (Csontos *et al*. 2010). Today, the Carpathian Basin is one of the three European centers of *A. artemisiifolia* infestation (Kasprzyk *et al*. 2010). Within its invasive range, the species is found on open disturbed habitats (Bassett and Crompton 1975). It relies on water as a long-distance seed transport agent, although it is not found exclusively along riparian habitat. In general, the species is a common pest in well-irrigated grain and cultivated fields and in open disturbed habitat (Genton *et al*. 2005; Kasprzyk *et al*. 2010).

Impacts: As a persistent agricultural pest, *A. artemisiifolia* can contribute to losses in crop harvest and requires intensive chemical control (Genton *et al*. 2005; Bassett and Crompton 1975). However, the species is of far greater concern to public health due to its high production of allergenic pollen. *A. artemisiifolia* is a major cause of hay fever in the eastern United States, with Approximately 26% of the population sensitive to pollen of this species; in Europe, sensitivity to Ambrosia pollen is on the rise (Kasprzyk *et al*. 2010). Also, contact with the inflorescences can lead to dermatitis (Brandes and Nitzsche 2006; Csontos *et al*. 2010).

Echinocystis lobata (Michx.) Torr. & Gray., wild cucumber (Cucurbitaceae)

Morphology/biology: This annual vine can climb up to 12 m. *E. lobata* grows very fast and branches out rapidly in its invaded range. The relatively large leaves (5-8(-15) cm) of the plant cover the shoots of the plants which this species uses as support structures (Klotz 2007, Bagi and Boeszoermenyi 2008). Flowers typically develop from July to September and are monoecious. *E. lobata* is pollinated by insects but can self-fertilize under stressful conditions. Approximately 1-6 seeds are produced per fruit

(Bagi and Boeszoermenyi 2008). Because the seeds are relatively heavy but stress-tolerant (can be dormant for over a year), water is the most important long-distance dispersal agent (Klotz 2007). Dormancy of seeds is broken by low temperatures (5-10° C) for 3-6 weeks (Bagi and Boeszoermenyi 2008).The vine is shade-intolerant and sensitive to early fall and late spring frosts, and plants can become severely damaged by extreme temperatures (Klotz 2007). In addition, soil temperatures must be relatively high for seeds to germinate in spring. Frost sensitivity thus determines the latitudinal gradient of the vine, and the species most often invades riverbanks in lowlands.

Figure B42: *Echinocystis lobata* profile: A – *E. lobata* inflorescence and distribution in Europe (Klotz 2007) (red stripes = known in country, red points = surveyed populations); B - *E. lobata* invading riparian community at the Tisza along the Ukrainian/Romanian border

History of introduction: *E. lobata* is native to North America where it grows in woodland fringes with abundant sunlight and along the littoral zone of freshwater bodies (banks of rivers or lakes) (Silvertown 1988; Bagi and Boeszoermenyi 2008). The vine was introduced to Austro-Hungary in the late 19th and early 20th century, more recently than the other invaders studied here. The pathway of introduction was however not unique. *E. lobata* was traded as ornamental and medicinal plant and was planted in botanical gardens across the continent (Bagi and Boeszoermenyi 2008; Vasic 2005). In Eastern Europe, the first reports of uncontrolled population growth of *E. lobata* appeared in the early 20th century in Slovakia, and the vine has been expanding its range eastwards along major rivers ever since (Vasic 2005; Bagi and Boeszoermenyi 2008). Thus, in its invaded range, the vine occupies mostly riparian habitats but can also occur at margins of woodlands and clearings (Klotz 2007). Due to its sensitivity to frost, *E. lobata* is only found in areas with an average January temperature of 0 to -5° C and an associated average July temperature of 18-25° C (Bagi and Boeszoermenyi 2008).

Impacts: Because *E. lobata* rapidly branches out horizontally, it can cover large areas and overshadow native vegetation. Growing upward using poplars and willows (or any other riparian tree species) as support structures, the plant can also overgrow and shade the trees (Vasic 2005). In addition, the vine contains toxins (cucurbitacines) that can adversely impact human health (Klotz 2007).

Helianthus tuberosus L., Jerusalem artichoke (Asteraceae)

Morphology/biology: This perennial species can grow as tall as 4 m, with an average height of 2 m (Cardina *et al*. 2010; Swanton *et al*. 1992). Rapid growth of above-ground tissue begins in April/May, but this short-day species flowers late in the growing season, from August to October (Cardina *et al*. 2010; Swanton *et al*. 1992). *H. tuberosus* is pollinated by insects and plants are self-incompatible (Swanton *et al*. 1992). The plant produces rhizomes and edible tubers. In fact, *H. tuberosus* produces relatively few seeds and the main way of population growth is by means of vegetative reproduction from the **rhizomes** and tubers (Swanton *et al*. 1992). A single plant can produce up to 200 tubers (the average being 75) and each tuber supports the growth of as many as 6 shoots (Cardina *et al*. 2010; Feher and Concekova 2009). Nutrients are stored in the tubers and rhizomes in winter and allow for fast growth in the following season (Walter *et al*. 2005). Temperatures below 5° C for 2-3 months are required to break dormancy in the rhizomatous tubers (Swanton *et al*. 1992). As a result of vegetative reproduction, *H. tuberosus* can form dense colonies in which the relatively large leaves of the plants (10-25 cm long and 4-12 cm wide) shade out other vegetation (Swanton *et al*. 1992). *H. tuberosus* is moderately frost-tolerant and adapted to grow on most soil types and in a wide range of climates (dry to moist). The species does, however, prefer moist soils and is limited in its distribution by extreme temperatures and rainfall as it does not tolerate long periods of drought or cool dry winters (Swanton *et al*. 1992).

Figure B43: *Helianthus tuberosus* profile: A – *H. tuberosus* inflorescence and distribution in Europe (green = present) (PLANTS database); B – *H. tuberosus* infestation along agricultural fields and channels in UA Carpathians;

History of introduction: *H. tuberosus* is native to North America and has a long tradition as agricultural crop among Native Americans. In North America, the species can be found from the East Coast (southern Canada to Georgia) to the Midwest, preferring nutrient-rich and moist soils (Swanton *et al*. 1992). It was introduced to Europe in the 17th century as food resource for humans and animals (Cardina *et al*. 2010). *H. tuberosus* escaped cultivation in the 18th century and established naturalized populations in Western Ukraine by the early 19th century. The species is most often found along riparian corridors (Walter *et al*. 2005) due to its hydrophilic characteristics and because water is a major long-distance dispersal agent for the rhizomes and tubers.

Impacts: Due to the high efficiency of energy allocation to tuber growth and vegetative reproduction, *H. tuberosus* can form high-density, monospecific stands, once introduced to a novel habitat. Local biodiversity is diminished as a result. Moreover, *H. tuberosus* has been reported to form hybrids with native *Helianthus* species in Western Ukraine (Protopopova *et al*. 2006; see also Swanton *et al*. 1992). Hybridization potentially decreases the health of native *Helianthus* populations. In Canada, the species has also been reported as an agricultural pest, reducing seed yields by 16-25% when invading corn fields (Swanton *et al*. 1992).

Heracleum sosnowskyi Manden, Sosnowskyi's hogweed (Apiacea)

Morphology/biology: This **monocarpic** perennial plant reaches heights of up 130 cm. Studies have determined that new shoots of *H. sosnowskyi* survive -4 to -7 °C in their first year, down to -25 °C from their second year on, and even down to -45 °C under snow cover. Seeds do not tolerate extremely low temperatures and require moderately cold and wet conditions in order to break dormancy. Once dormancy is broken, seeds germinate very rapidly, usually earlier in spring than native vegetation, and with germination potential as high as 80% (Nielsen *et al*. 2005). Flowering and seed production occur rapidly, but plants can postpone flowering (become dormant) under stressful environmental conditions. Furthermore, *H. sosnowskyi* is a shade-intolerant plant, particularly at the beginning of the growth phase (Kabuce and Priede 2010a). *H. sosnowskyi* can self-fertilize, reproduces exclusively from seeds, but has tuberous roots which aid in regeneration of shoots after disturbance events (Nielsen *et al*. 2005; Pyšek and Prach 1994). The reproductive potential of the plant is enormous as "an average plant bears about 20,000 seeds (almost half of them on the terminal umbel), but individual plants with over 100,000 seeds have been reported" (Nielsen *et al*. 2005).

Figure B44: *Heracleum sosnowskyi* profile: A – Field along road and close to a river in UA Carpathians infested by hogweed and distribution of *H. sosnowskyi* in Europe (grey = species observed, points = species counts taken) (Nielsen *et al*. 2005); B – closer look at the inflorescence;

History of introduction: The species is native to the central and eastern Caucasus, western, central, eastern and southwestern Transcaucasia, and northeastern Turkey (Kabuce and Priede 2010a). Because *H. sosnowskyi* is frost-tolerant, it was introduced as a crop to northwestern Russia in 1944. From then on, the hardiness of the plant led to its deliberate introduction as fodder plant in Latvia, Estonia, Lithuania, Belarus, the former German Democratic Republic, and the Ukraine (Nielsen *et al.* 2005). However, because *H. sosnowskyi* is anise scented, consumption of the plant by agricultural animals affected the taste of meat and milk, and *H. sosnowskyi* quickly became unsuitable as fodder plant (Kabuce and Priede 2010a). With introduction efforts fading in the 1950s, few populations were observed in Europe until the 1980s, but after this initial lag phase, the species experienced an exponential population growth and is now considered an aggressive weed in most of its invaded territory (Kabuce and Priede 2010a). As is common for many invasive plants, in its non-native range *H. sosnowskyi* is most commonly found in disturbed human-created (e.g., roadsides, riparian areas) and semi-natural habitats (e.g., shrublands, pastures) (Kabuce and Priede 2010a). In the Ukraine, the species establishes along disturbed riparian habitats, with water acting as a major agent for long-distance seed dispersal, and can propagate into adjacent suitable habitats such as pastures (Prots 2009).

Impact: Due to the early germination of seeds and the large size and leaf area of individual plants, *H. sosnowskyi* is a strong competitor for light and often forms dense stands along rivers, displacing native species and leading to a stark decline in species richness (Kabuce and Priede 2010a, Nielsen *et al*. 2005). It is estimated that in stands where *H. sosnowskyi* is dominant, 80% of incoming sunlight is absorbed by the species (Nielsen *et al*. 2005). In addition, *H. sosnowskyi* is highly phototoxic, excreting photosensitising furanocoumarins which cause, in combination with ultraviolet light, irritation and burning when the chemicals come in contact with human skin (Kabuce and Priede 2010a; Jahodova *et al*. 2007).

Impatiens glandulifera Royle, Himalayan balsam (Balsaminaceae)

Morphology/biology: This annual species is considered the largest herbaceous plant in Europe as it can grow up to two and a half meters in shaded areas. The plant is not known to reproduce vegetatively but most often reproduces through seeds. *I. glandulifera* is gregarious, which means that all seeds germinate synchronously in early spring with a yield of approximately 1000 seeds per plants and a germination potential of 80%. Germination can occur under water and requires breaking of dormancy (ca. +4-5ºC for 1-1.5 months) (Balogh 2008a; Beerling and Perrins 1993). The seeds do not tolerate temperature below -10ºC. *I. glandulifera* produces large flowers in July that are highly **entomogamous**, i.e., compete successfully for pollinators, attracting more than 33 species of insects (Balogh 2008a). The flowers, however, are capable of self-fertilization. Similar to *E. lobata*, seedlings and mature plants are very sensitive to frost and do not survive the first autumn frosts in temperate climates. Due to its frost-sensitivity, *I. glandulifera* is also highly sensitive to the length of the growing season (Beerling and Perrins 1993). Furthermore, *I. glandulifera* requires high soil moisture content but cannot withstand long periods of floods, grows best in nutrient-rich soils at various slopes, and only tolerates direct sunlight in habitats with ample water supply. Therefore, the plant is often found in riparian habitats and can spread into forests due to its shade tolerance (Balogh 2008a; Beerling and Perrins 1993; Pyšek and Prach 1995).

Figure B45: *Impatiens glandulifera* profile: A **-** Invasion along river in UA Carpathians and distribution of *I. glandulifera* in Europe (Hejda 2006) (red stripes = known in country, red points = surveyed populations); B – flowers of *I. glandulifera*;

History of introduction: The species is native to the temperate and humid regions of the Western Himalayas. In its native range, *I. glandulifera* grows at high altitudes, between 1800 and 3200 m, reaching up to 4300 m (Beerling and Perrins 1993). Because of its attractive flowers, *I. glandulifera* was intentionally introduced to England as an ornamental plant in the early 19th century and escaped controlled cultivation within 20 years of introduction there (Balogh 2008a). By the early 20th century, the plant was introduced as an ornament across Europe and reached Ukraine approximately in 1938, where it quickly acclimatized to the temperate climate and followed a similar invasion history as in England, i.e., exponential population growth after a lag phase of a few decades (Balogh 2008a; see Fig. 2). Today, *I. glandulifera* is found mostly along rivers in the Ukrainian Carpathians, due to the habitat preferences of the plant and to water being the most important long-distance transport agent for seeds (Protopopova and Shevera 1998).

Impacts: In habitats where *I. glandulifera* reaches high population densities, the plant impedes the regeneration of forest communities after events of disturbance, e.g., flooding or deforestation, thus diminishing habitat diversity. Furthermore, high-density communities of *I. glandulifera* destabilize riverbanks because the shallow roots of the plants (10-15 cm) do not hold soil efficiently (Beerling and Perrins 1993; Heyda 2006). In addition, the quick growth and large size of individual plants and entomogamous flowers displace native plants from riparian communities. However, when intact riparian communities are invaded, *I. glandulifera* has been shown to affect the cover hierarchies of the communities more so than the total number of species present, i.e., the species becomes dominant but does not permanently eradicate native species (Hejda and Pyšek 2006).

Reynoutria spp., knotweed: *R. japonica* Houtt., and *R. x bohemica* Chrtek & Chrtková (Polygonaceae)

Morphology/biology: Because the two *Reynoutria* species used in the study utilize very similar habitats in their invaded range, their traits and invasive behavior are discussed under a single heading. These herbaceous perennial species can tolerate a wide range of climatic and soil conditions, grow up to 4 m, and form dense stands due to clonal growth (Rhoads and Timothy 2002, Balogh 2008b). *Reynoutria* spp. are dioecious, and interestingly, only one female clone of *R. japonica* was introduced to and spread across Europe (Pyšek 2006). Because no male plants were available, this spread was

accomplished exclusively via the extensive system of rhizomes that can reach 15-20 m in length per plant (Rhoads and Timothy 2002). Transport of rhizome fragments occurs via anthropogenic agents or water (Pyšek 2006). Clones are known to persist more than 130 years in suitable habitat. *R. x bohemica* is the hybrid of *R. japonica* and *R. sachalinensis* (not commonly found in the Ukrainian Carpathians) and is competitively stronger than either of the two parent species (Pyšek 2006; Tiebre *et al*. 2008). *R. x bohemica* spreads through seed dispersal, but the main mode of reproduction remains vegetative (Pyšek 2006; Sirbu and Oprea 2008). The distribution of *Reynoutria* spp. is limited primarily by the length of the growing season and minimum temperature (Beerling 1993).
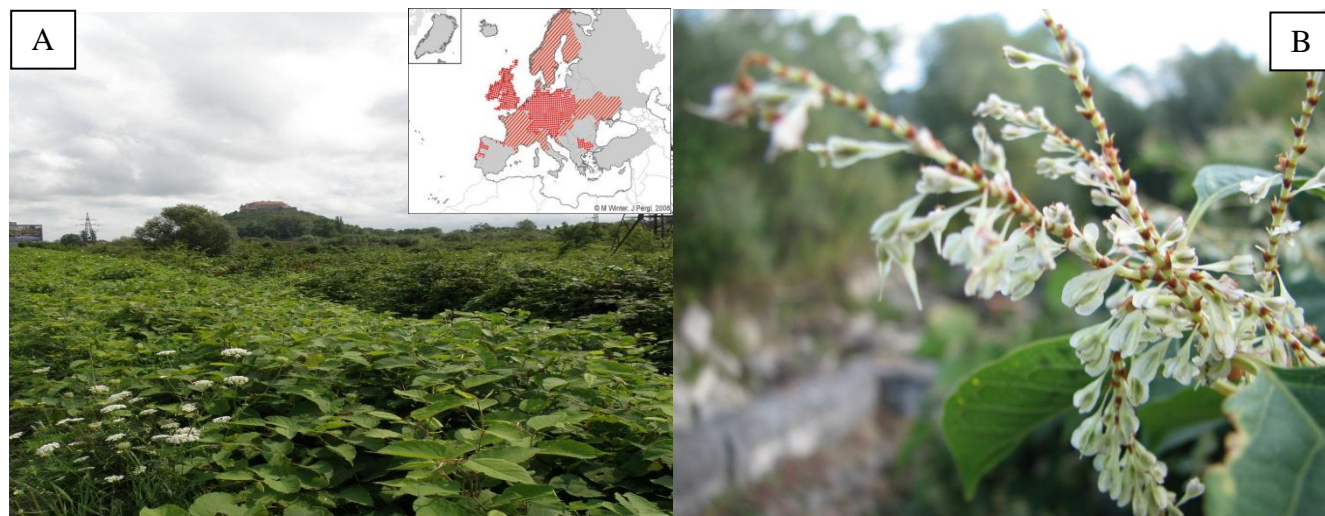

Figure B46: *Reynoutria* spp. profiles: A - *Reynoutria* spp. infestation along major road and close to a river in AU Carpathians and distribution in Europe (red stripes = known in country, red points = surveyed populations) (Pyšek 2006); B – *R. japonica* seeds;

History of introduction: The *Reynoutria* taxon is native to East Asia where it is a wide-spread pioneer taxon that is mostly found on recent volcanic features (Balogh 2008b; Rhoads and Timothy 2002). *Reynoutria* spp. have been intentionally introduced to Europe as garden ornamentals in the 19th century. The plants escaped cultivation shortly after introduction to the invaded range, and today naturalized populations can be found across the continent, profiting strongly from anthropogenic disturbances to natural habitats (Tiebre *et al*. 2008; Beerling 1991). *R. x bohemica* is only found in the invaded range (Pyšek 2006). In their invaded range in the Ukrainian Carpathians, the species grow in disturbed habitats in moist soil, particularly along rivers, and prefer, similar to *I. glandulifera*, relatively steep slopes and mountainous areas (Sirbu and Oprea 2008).

Impacts: *Reynoutria* spp. alter riparian habitat by reducing light availability for native species, releasing allelopathic compounds that can suppress the growth of native plants, and changing the chemical composition of soils (Rhoads and Timothy 2002). Soils containing *Reynoutria* spp. have a higher potassium (K) and manganese (Mn) concentration than surrounding soils (Pyšek 2006). In addition, *F. japonica* has been found to decrease soil bulk density and increase the organic matter, water, and nutrient content in soils (Pyšek 2006). Lastly, just as is the case for all the other invasive species producing extensive rhizome networks, *Reynoutria* spp. can increase risk of flooding by increasing resistance of herbaceous riparian habitat to water flow (Pyšek 2006).

Robinia pseudoacacia L., black locust (Fabaceae)

Morphology/biology: This deciduous tree species can grow up to 30 m and individual trees can live up to 200-250 years (Basnou 2006; Bartha *et al*. 2008). *R. pseudoacacia* is a **nitrogen-fixing**, leguminous pioneer species. Flowers of the entomogamous tree appear in May/June, are large, and produce a great amount of nectar and pollen, thus successfully competing for pollinators (Wieseler 1998). Fruits of the tree remain attached to the plant and only split open in winter; seeds are dispersed by wind and water (Basnou 2006). Germination of seeds begins early in the growing season and requires the breaking of dormancy by prolonged periods of frost (Bartha *et al*. 2008). Although seeds are produced in high abundance (Approximately 0.28 kg/year/individual in closed stands), germination rate is low, but seedlings that manage to become established in suitable habitat (open, disturbed areas) grow very rapidly – up to 2 m in their 2nd-5th year. Although their distribution is limited by frosts in May and early fall as these damage young plants (Bartha *et al*. 2008). In addition to seed production, *R. pseudoacacia* also spreads vegetatively via root suckering (Basnou 2006). *R. pseudoacacia* is shade intolerant but tolerates drought and is adapted to growing in acidic and or polluted soils as it enters symbiotic relationships with soil bacteria that fix nitrogen and provide it to the plant (Basnou 2006). In addition, the species does not tolerate excessive soil moisture (i.e., prolonged periods of flooding), has high evaporation rates at the roots, and thus grows best in well-drained moderately mesic soils (Bartha *et al*. 2008).

Figure B47: *Robinia pseudoacacia* profile: A – Close-up look at *R. pseudoacacia* inflorescence and distribution of in Europe (red stripes = known in country, red points = surveyed populations) (Basnou 2006); B – *R. pseudoacacia* along road in UA Carpathians;

History of introduction: *R. pseudoacacia* is native to the Appalachian Mountains in the Southeastern United States (Wieseler 1998, Bartha *et al*. 2008). In its native range, the species is a forest tree that grows in moist calcareous soils (Basnou 2006) at an optimal elevation of 500-1500 m (Bartha *et al*. 2008). It was intentionally introduced to Western Europe in the early 17th century to use for reforestations, erosion control, and as an ornamental tree to gardens as it grows quickly and tolerates drought and poor soils (Basnou 2006). *R. pseudoacacia* was introduced in the Ukraine in 1804 as an ornamental and honey plant (Protopopova *et al*. 2006). By the mid-1800s, *R. pseudoacacia* reached

Eastern Europe where it became a popular species for reforestation projects (Bartha *et al*. 2008). Once the tree escaped cultivation, it established along rivers and linear habitats altered by anthropogenic disturbance (e.g., roads, forest edges along roads, recently felled forest, etc.) (Basnou 2006).

Impacts: In addition to shading out native species through quick growth and clonal reproduction, *R. pseudoacacia* outcompetes native entomogamous species as do *I. glandulifera* and *Solidago* spp. (Basnou 2006; Wieseler 1998). Because the species enriches soils with nitrogen and has high evaporation rates, it also significantly changes soil chemistry and moisture and thus functional relationships between species in invaded habitats. Furthermore, the tree uses allelopathic compounds to suppress the growth of native plants. All of these characteristics have led to reduced species richness of herbaceous plants in habitats invaded by *R. pseudoacacia* (Bartha *et al*. 2008).

Solidago spp., goldenrod: *S. canadensis* L. and *S. gigantea* Aiton (Asteraceae)

Morphology/biology: Because the two *Solidago* species used in the study utilize very similar habitats in their invaded range, their traits and invasive behavior are discussed under a single heading. The herbaceous perennial species grow 50-250 cm, *S. gigantea* reaching relatively larger sizes (Jacobs *et al*. 2004; Botta-Dukat and Dancza 2008). *Solidago* spp. flower between July and October and produce a larger number of flower heads per shoot (1500 on average) (Weber 1998). Accordingly, one shoot can produce up to 10,000 seeds (Kabuce and Priede 2010b). Sexual reproduction occurs exclusively through pollination (plants cannot self-fertilize), and the flowers are highly attractive to pollinators due to their color, odor, and high amount of nectar and pollen (Weber 1998). Similar to *I. glandulifera* therefore, *Solidago* spp. are strong competitors for pollinators. The plants are rhizomatous and thus reproduce vegetatively in addition to producing seeds, and the high population densities typical of local invasions can be attributed to clonal reproduction. Clones can live up to 150 years (Kabuce and Priede 2010b). Long-distance dispersal of seeds occurs mainly by wind and water. In addition, rivers can introduce rhizome fragments to novel habitats downstream (Jacobs et al. 2004; Kabuce and Priede 2010b).

While in their native range, *S. gigantea* and *S. canadensis* prefer moist and dry soils, respectively, *Solidago* spp. are morphologically highly variable and tolerate a wide range of soil fertility, texture, and moisture conditions in their invaded ranges (Jacobs *et al*. 2004). The plants do not tolerate excessive summer heat or winter frost but are able to withstand environmental stress as seeds and can remain dormant in soil for several years (Jacobs *et al*. 2004). While *S. canadensis* is shade intolerant in both its native and introduced ranges, *S. gigantea* has been reported to tolerate shade in its invaded range but prefers open habitats (Weber and Jacobs 2005). In addition, *Solidago* spp. produce allelopathic (toxic) compounds that are hypothesized to suppress growth of native plants in an invaded habitat (Kabuce and Priede 2010b).
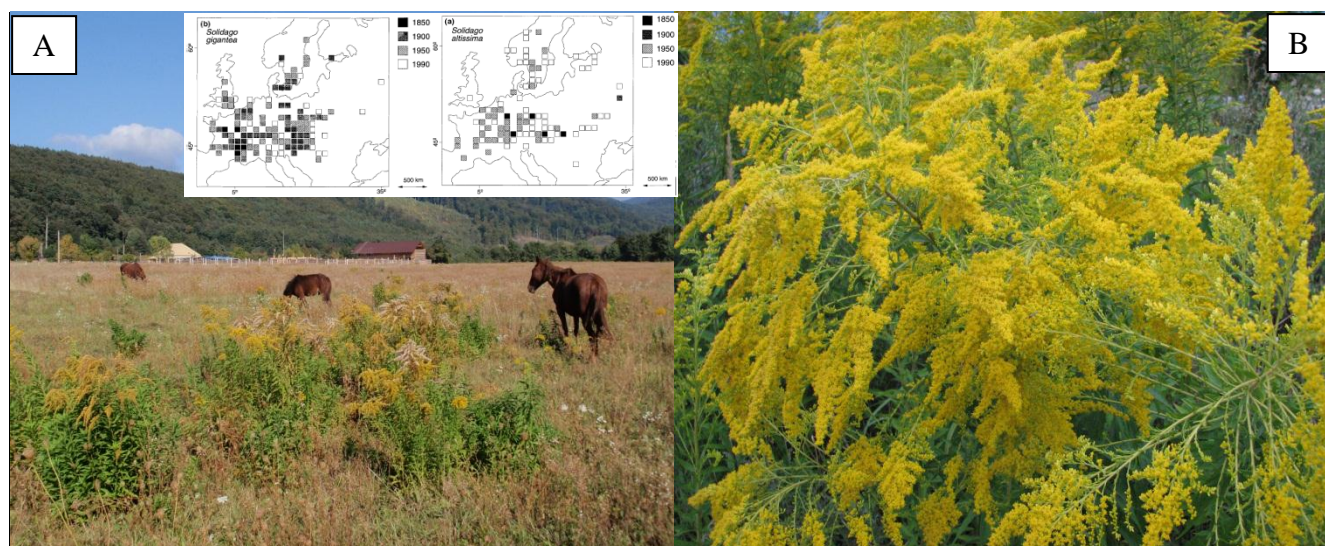
Figure B48: *Solidago* spp. profiles: A - *S. gigantea* on pasture in UA Carpathians and spread of *Solidago* spp. in Europe (*S. altissima = S. canadensis*, each square is 100 x 100 km grid cell with at least one locality of *Solidago*) (Weber 1998); B – *S. gigantea* inflorescence**;**

History of introduction: *Solidago* spp. are native to North America and have an extensive range between 26° N and 45° N latitude, reaching higher latitudes (up to 65° N) in western Canada. In their native range, the species colonize abandoned croplands, pastures, and disturbed natural areas, and can be a nuisance in forest nurseries (Botta-Dukat and Dancza 2008; Kabuce and Priede 2010b). *S. canadensis* was favored as ornamental plant by gardeners in England as early as 1645 (Kabuce and Priede 2010b). *S. gigantea* became a popular ornamental plant in central Europe in the 18th century (Jacobs *et al*. 2004). By the end of the 19th century, *Solidago* spp. established naturalized populations in most Eastern European nations including the Ukraine (Weber 1998; Botta-Dukat and Dancza 2008). Today, the species are found close to human settlements and form dense populations in grasslands and forest edges along roads, railway tracks, and waterways (Jacobs *et al*. 2004). Due to its intolerance to frost and requirements for a relatively long growing season (as flowering is late in the season), *Solidago* spp. are rarely found above 1200 m a.s.l. (Weber and Jacobs 2005).

Impacts: Quick growth, large seed banks, clonal reproduction, allelopathic compounds, and attractiveness to pollinators give *Solidago* spp. a high competitive advantage over native species and lead to homogenization of habitats invaded by the taxon. Once established, the plants form dense stands which are detrimental to biodiversity in invaded habitats (Jacobs *et al*. 2004; Botta-Dukat and Dancza 2008). Furthermore, *S. canadensis* is a host of insect larvae that are vectors of crop pathogens, and the species can thus have negative economic effects on crop productions (although research quantifying the exact impacts is needed) (Kabuce and Priede 2010b).

References

Bagi, I. and Boeszoermenyi, A. (2008). Wild cucumber (*Echinocystis lobata* Torr. et Gray). In *The Most Important Invasive Plants in Hungary*, (ed. Botta-Dukat, Z. *et al*.). HAS Institute of Ecology and Botany: Vacratot, Hungary, pp. 103-114.

Balogh, L. (2008a). Himalayan balsam (*Impatiens glandulifera* L.). In *The Most Important Invasive Plants in Hungary*, (ed. Botta-Dukat, Z. *et al*.). HAS Institute of Ecology and Botany: Vacratot, Hungary, pp. 129-137.

Balogh, L. (2008b). Japanese, giant, and Bohemian knotweed (*Fallopia japonica* Houtt., *Fallopia sachalinensis* Frdr. Schmidt, *Fallopia x bohemica* Chrtek et Chrtkova). In *The Most Important Invasive Plants in Hungary*, (ed. Botta-Dukat, Z. *et al*.). HAS Institute of Ecology and Botany: Vacratot, Hungary, pp. 13-33.

Bartha, D., Csiszar, A., and Zsigmond, V. (2008). Black locust (*Robinia pseudoacacia* L.). In *The Most Important Invasive Plants in Hungary*, (ed. Botta-Dukat, Z. *et al*.). HAS Institute of Ecology and Botany: Vacratot, Hungary, pp. 63-76.

Basnou, C. (2006). Robinia pseudoacacia. *Delivering Alien Invasive Species Inventory Europe [DAISIE]*. Retrieved January 13, 2011 from www.europe-aliens.org.

Bassett, I.J. and Crompton, C.W. (1975). The biology of Canadian weed: *Ambrosia artemisiifolia* L. and *A. psilostachya* DC. *Canadian Journal of Plant Sciences* 55, 463-476.

Beerling, D.J. (1993). The impact of temperature on northern distribution limits of the introduced species *Fallopia japonica* and *Impatiens glandulifera* in north-west Europe. *Journal of Biogeography* 20, 45-53.

Beerling, D.J. (1991). The effect of riparian land use on the occurrence and abundance of Japanese knotweed *Reynoutria japonica* on selected rivers in South Wales. *Biological Conservation* 55, 229-333.

Beerling, D.J. and Perrins, J.M. (1993). Biological flora of the British Isles: *Impatiens glandulifera* Royle (*Impatiens roylei* Walp.). *Journal of Ecology* 81, 367-382.

Botta-Dukat, Z. and Dancza, I. (2008). Giant and Canadian goldenrod (*Solidago gigantea* Ait., *Solidago canadensis* L.). In *The Most Important Invasive Plants in Hungary*, (ed. Botta-Dukat, Z. *et al*.). HAS Institute of Ecology and Botany: Vacratot, Hungary, pp. 167-177.

Brandes, D. and Nitzsche, J. (2006). Biology, introduction, dispersal, and distribution of common ragweed *(Ambrosia artemisiifolia* L.) with special regard to Germany. *Nachrichtenblatt Deutscher Pflanzenschutzdienst* 58(11), 286-291.

Cardina, J., Herms, C., Koch, C., and Webster, T. (2010). Helianthus tuberosus. *Ohio Perennial and Biennial Weed Guide*. Retrieved March 4, 2011 from http://www.oardc.ohio-state.edu/weedguide/singlerecord.asp?id=870.

Csontos, P., Vilatos, M., Barina, Z., and Kiss, L. (2010). Early distribution and spread of *Ambrosia artemisiifolia* in Central and Eastern Europe. *Botanica Helvetica* 120, 75-78.

Feher, A. and Concekova, L. (2009). Evaluation of mechanical regulation of invasive Helianthus tuberosus populations in agricultural landscape. *Journal of Central European Agriculture* 10, 245-250.

Flora Italiana (2010). Ambrosia artemisiifolia *L.: nomencl. ref.: Sp. Pl.: 988. 1753*. Retrieved April 27, 2011 from http://luirig.altervista.org/flora/taxa/index1.php?scientific-name=ambrosia+artemisiifolia.

Genton, B.J., Shykoff, J.A., and Giraud, T. (2005). High genetic diversity in French invasive populations of common ragweed, Ambrosia artemisiifolia, as a result of multiple sources of introduction. *Molecular Ecology* 14, 4275-4285.

Hejda, M. (2006). Impatiens glandulifera. *Delivering Alien Invasive Species Inventory Europe [DAISIE]*. Retrieved January 13, 2011 from www.europe-aliens.org.

Hejda, M. and Pyšek, P. (2006). What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biological Conservation* 132, 143-152.

Jacobs, G., Weber, E., and Edwards, P.J. (2004). Introduced plants of invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. *Diversity and Distributions* 10, 11-19.

Jahodová S., Froeberg L., Pyšek P., Geltman D., Trybush S. and Karp A. (2007). Taxonomy, identification, genetic relationships and distribution of large *Heracleum* species in Europe. In *Ecology and Management of Giant Hogweed (*Heracleum mantegazzianum*), (ed. Pyšek P., *et al*.). CAB International: Wallingford, United Kingdom, pp. 1-19.

Kabuce, N. and Priede, N. (2010a). *Heracleum sosnowskyi*: invasive alien species fact sheet. *Online Database of the North European and Baltic Network on Invasive Alien Species [NOBANIS]*. Retrieved January 13, 2011 from www.nobanis.org.

Kabuce, N. and Priede, N. (2010b). *Solidago canadensis*: invasive alien species fact sheet. *Online Database of the North European and Baltic Network on Invasive Alien Species [NOBANIS]*. Retrieved February 10, 2011 from www.nobanis.org.

Kasprzyk, I., Myszkowska, D., Grewling, L., Stach, A., Šikoparija, B., Skjøth, C.A., and Smith, M. (2010). The occurrence of Ambrosia pollen in Rzeszów, Kraków, and Poznań, Poland: investigation of trends and possible transport of Ambrosia pollen from Ukraine. *International Journal of Biometeorology*, 1-12.

Klotz, S. (2007). *Echinocystis lobata*. *Delivering Alien Invasive Species Inventory Europe [DAISIE]*. Retrieved January 20, 2011 from www.europe-aliens.org.

Mędrzycki, P. (2007): *Acer negundo*: invasive alien species fact sheet. *Online Database of the North European and Baltic Network on Invasive Alien Species [NOBANIS]*. Retrieved January 15, 2011 from www.nobanis.org.

The PLANTS Database. *National Plant Data Team*. U.S. Department of Agriculture [USDA]: Greensboro, USA. Available at http://plants.usda.gov.

Petit, R.J., Bialozyt, R., Garnier-Géré, P., and Hampe, A. (2004). Ecology and genetics of tree invasions: from recent introductions to Quaternary migrations. *Forest Ecology and Management* 197(1-3), 117-137.

Protopopova, V. and Shevera, M. (1998). Expansion of alien plants in settlements of the Tisa river basin. *Thaiszia Journal of Botany* 8, 33-42.

Protopopova, V.V., Shevera, M.V., and Mosyakin, S.V. (2006). Deliberate and unintentional introduction of invasive weeds: a case study of the alien flora of Ukraine. *Euphytica* 148, 17-33.

Pyšek, P. (2006). Fallopia japonica. *Delivering Alien Invasive Species Inventory Europe [DAISIE]*. Retrieved January 20, 2011 from www.europe-aliens.org.

Pyšek, P. and Prach, K. (1994). How important are rivers for supporting plant invasion? In *Ecology and Management of Invasive Riverside Plants,* (ed. de Waal, L.C. et al.). John Wiley and Sons: London, UK.

Rhoads, A.F. and Timothy, A.B. (2002). Japanese knotweed and giant knotweed: invasive species fact sheet. *Morris Arboretum of the University of Pennsylvania*. Retrieved April 10, 2011 from http://www.paflora.org.

Rosario,L.C. (1988). Acer negundo. In: *Fire Effects Information System.* U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, USA. Retrieved May 23, 2011 from http://www.fs.fed.us/database/feis/.

Silvertown, J. (1988). Survival, fecundity, and growth of wild cucumber, *Echinocystis lobata*. *Journal of Ecology* 73(3), 841-849.

Sirbu, C. and Oprea, A. (2008). Two alien species in the spreading process in Romania: *Reynoutria x bohemica* Chrtek & Chrtková and *Grindelia squarrosa* (Pursh) Dunal. *Cercetări Agronomice în Moldova* 134(2), 41-50.

Swanton, C.J., Cavers, P.B., Clements, D.R., and Moore M.J. (1992). The biology of Canadian weeds 101: *Helianthus tuberosus* L. *Canadian Journal of Plant Sciences* 72, 1367-1382.

Tiebre, M.S., Saad, L., and Mahy, G. (2008). Landscape dynamics and habitat selection by alien invasive *Fallopia* (Polygonaceae) in Belgium. *Biodiversity Conservation* 17, 2357-2370.

Udvardy, L. (2008). Boxelder (*Acer negundo* L.). In *The Most Important Invasive Plants in Hungary*, (ed. Botta-Dukat, Z. *et al*.). HAS Institute of Ecology and Botany: Vacratot, Hungary, pp. 115-120.

Vasic, O. (2005). *Echinocystis lobata* (Michx) Torrey et A. Gray in Serbia. *Acta Bot. Croat.* 64 (2), 369–373.

Walter, J., Essl, F., Englisch, T., and Kiehn, M. (2005). Neophytes in Austria: habitat preferences and ecological effects. *Neobiota* 6, 13-25.

Weber, E. (1998). The dynamics of plant invasion: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. *Journal of Biogeography* 25, 147-154.

Weber, E. and Jacobs, B. (2005). Biological flora of central Europe: *Solidago gigantea* Aiton. *Flora* 200, 109-118.

Weber, E. and Schmid, B. (1998). Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. *American Journal of Botany* 85(9), 1110-1121.

Wieseler, S. (1998). Black locust. *Plant Conservation Alliance*. Retrieved March 2, 2011 from http://www.nps.gov/plants/alien/fact/rops1.htm

Appendix C: Overview of BIOMOD Functions (see Thuiller *et al*. 2009; Franklin 2009; Hastie *et al*. 2009)**:**

Linear regression models (LR): LR predicts the response variable Y as a function f(X) of a vector of multiple predictor variables, $X = (X_1, ..., X_n)$, with the formula:

$$F(X) = Y = \alpha + \beta_1 X_1 + \ldots + \beta_n X_n + \varepsilon,$$

where β are the coefficients, ε is the error term and α the intercept. The linear model assumes normal distribution of the response variable (and the error term) with respect to the environmental variables.

Machine learning models: Unlike traditional statistical approaches where an analyst determines the form of response (e.g., linear, curvilinear, binomial) of a species to the predictor variables, machine learning methods "learn," via several algorithms, the response function based on the distribution of the response variables in the sample space.

Generalized Linear Models (GLM): GLMs are an extension of the LRs that can handle non-normal distributions of the response variable. They use a link function to "link" the mean of the response variable to the predictor variables. In such, they can incorporate binomial distributions (the type of distribution of the response variable in this study). The simple equation for GLMs is:

$$g(E(Y)) = LP = \alpha + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n + \varepsilon$$

where the linear predictor, LP, is the result of linear regression. The expected values of Y, defined as E(Y), or the probability of species presence given certain values for predictor variables, are related to LP through the link function. For a binomial distribution, this link function is logistic regression, with the formula:

$$g(\ ) = \ln \left(\frac{p}{1 - p} \right).$$

where $p = E(Y) =$ probability of presence, and $1 - p =$ probability of absence.

Generalized Additive Models (GAM): GAMs are very similar to GLMs, but unlike GAMs, they are able to characterize the nature of the response function between predictors and response. The formula for GAMs is written as follows:

$$g(E(Y)) = LP = \alpha + f_1(X_1) + f_2(X_2) + \ldots + f_n(X_n) + \varepsilon$$

The β coefficients/parameters in GLMs are replaced by a smoothing function, f(). This function smoothes the data by taking a local (neighborhood) average of the data.

Multivariate Adaptive Regression Splines (MARS): MARS split the plot produced by a response function into sections of diverse responses (e.g., one subset are the values below and another above a certain threshold) and produce linear response functions, called "basis functions", for each subset. The basis functions are then added, producing a large model. In a final step, the model is generalized by removing the least important basis functions. Fig. 1AC below is a graphic representation of MARS. Here the response to a predictor X has been divided into two subsets, and basis functions for each were

developed. Evidently, the response to X below the threshold chosen for the split into two subsets is negative and then positive above that threshold.
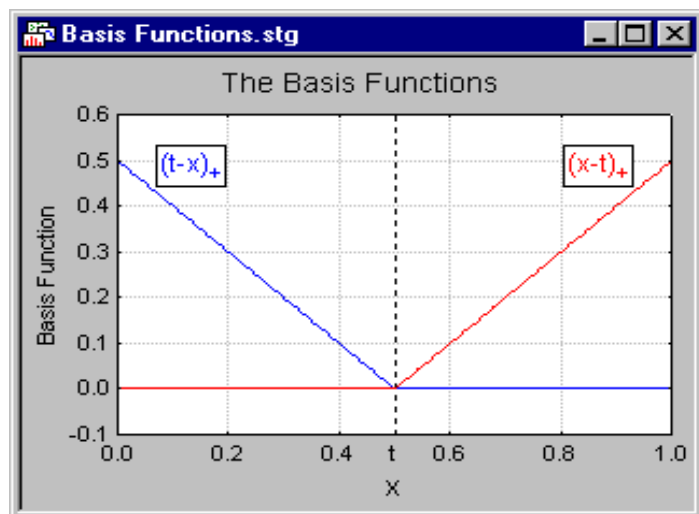

Figure C49: Graphic demonstration of Multivariate Adaptive Regression Splines (MARS) (StatSoft 2011)

Generalized Boosted Models (GBM): GBMs are a more complex form of MARS and divide the data into several homogeneous subgroups repeatedly (cross-validation) and fit the data of the subgroups to simple or transformed (i.e., log-link for binomial distribution) regression models. The many models are then weighted and averaged to produce a result that is less biased on a particular split. Because a potentially complex response function is split into groups of simple, linear response functions based on the distribution of the data, GBM is a machine learning technique that does not require a prior definition of the response function (e.g., linear, quadratic, polynomial, etc. in the case of GLM). An example of a GMB response curve for the probability of presence for *Impatiens glandulifera* modeled on simple distance from settlements and roads is shown below:
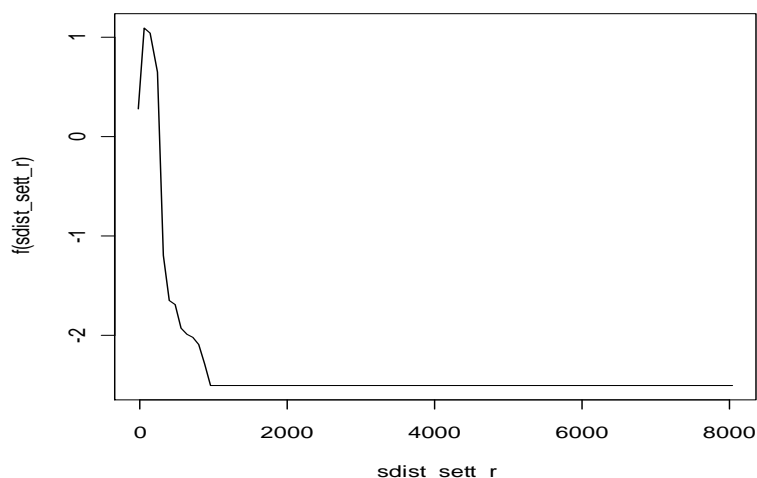

Figure C50: BIOMOD Generalized Boosted Models (GBM) graph for simple distance to roads and settlements (predictor) and species presence (response)

The thresholds for dividing the response curve into different subgroups are evident from the linear subdivisions of the graph. The entire graph is the averaged and weighted result of the subset data models.

<u>Functional Discriminant Analysis (FDA)</u>: This is a form of analysis is particularly suited for multivariate data (i.e., more than one response variable). The response variable(s) is(are) divided into groups, in this case presence and absence, and the analysis consists of determining which predictor variables best discriminate between the groups. This is done by creating logistic regression terms in which the β parameters for each predictor determine the influence of that predictor.

<u>Classification and Regression Tree analysis (CTA)</u>: Decision trees are machine learning methods and work in a similar fashion to a dichotomous key. They use optimal thresholds based on the range of values extracted on the sample space (presence/pseudo-absence locations) to divide the values of predictor variables into homogeneous groups (similar values or classes). Based on these divisions, predictions are made on the presence of a species by working down the branches (i.e., predictor variables with thresholds). Because CTA is highly data-driven and non-parametric, different choices of training data can produce different models/thresholds. The following figure is the result of a CTA analysis performed in BIOMOD:
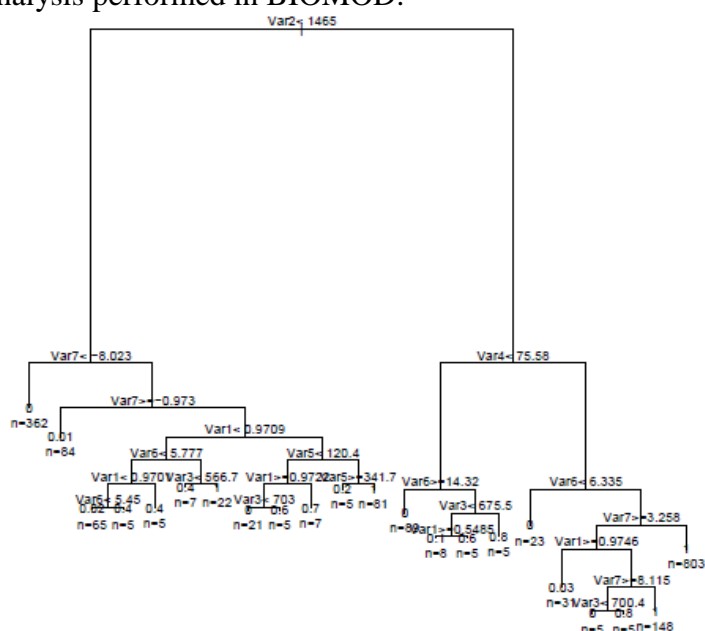

Figure C51: Example of Classification and Regression Tree analysis (CTA); branches are based on thresholds of predictor values and the endpoints show the number (n) of locations for which a particular path is true (Thuiller *et al*. 2009)

<u>Random Forests (RF)</u>: RFs are a more complex and computationally intensive form of decision trees. In order to minimize the instability of CART (i.e., dependence of predictions on choice of training data), RFs repeatedly sample the data with replacement and creating trees for each sample. The part of the data that is withheld from analysis is used to test the accuracy of the model. Finally, the predictions based on all the trees are averaged.

<u>Artificial Neural Networks (ANN)</u>: The main concept of ANNs is to create linear combinations of the predictor variables, derive "features," or new composite variables, from these combinations, and finally model the response variable as a non-linear function of the features. The schematic diagram below (developed for a study in Great Britain) demonstrates the computing steps in ANN:
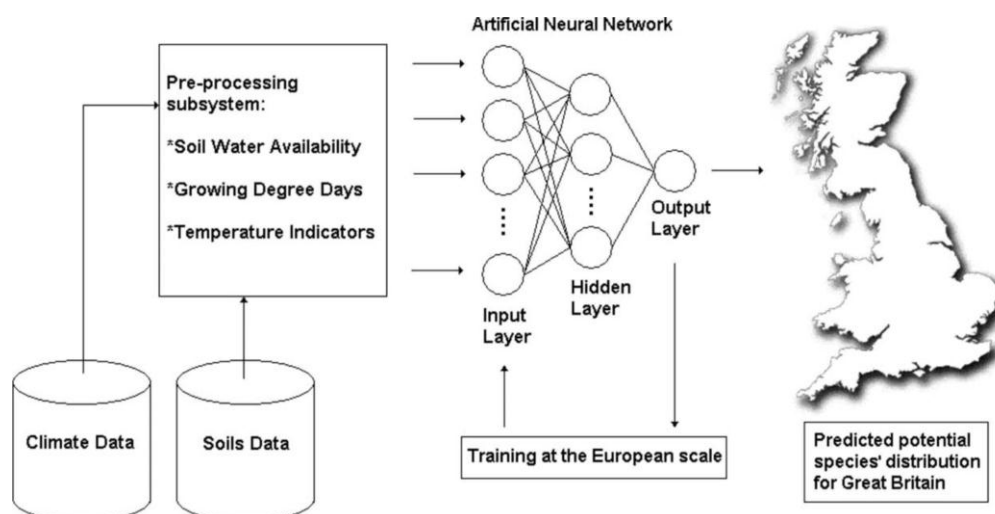
Figure C52: Model building process in Artificial Neural Networks (ANN) (Pearson *et al*. 2002)

In the diagram, the hidden layers are the features. In essence, ANNs are non-linear statistical models which create linear regression models (features) and use a type of link function to model non-linear outputs (probability of species occurrence).

Rectilinear Envelope (SRE): An envelope defines the potential range of a species as a multidimensional space (each predictor variable represents one dimension) that is bounded by the minimum and maximum value of each predictor variable at the presence locations. Suitable habitat is therefore given as a binary prediction: suitable within and unsuitable outside the envelope. Fig. 5AC demonstrates the main idea behind climatic envelopes (the main type of envelope models):
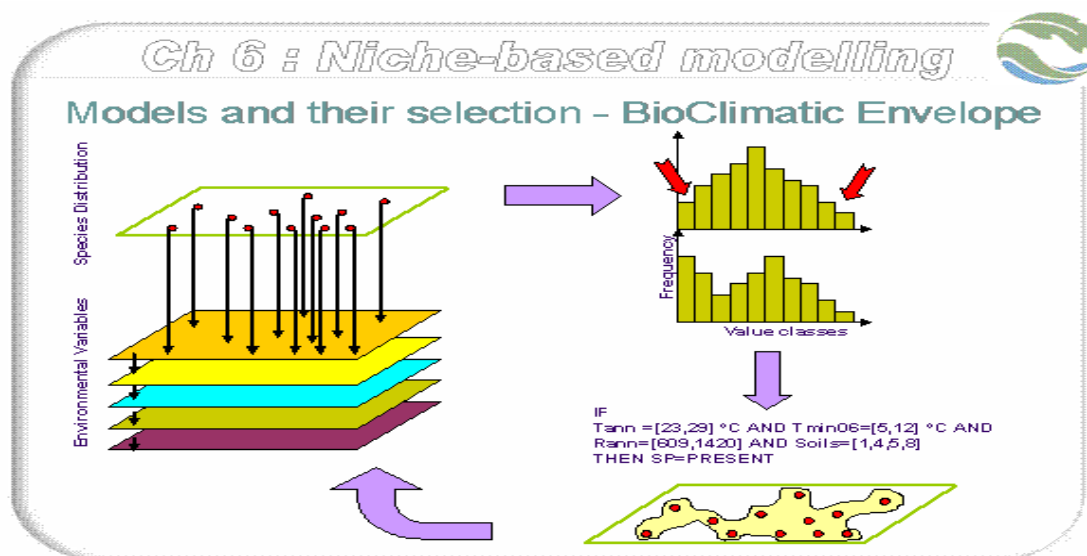

Figure C53: The process behind climatic envelope models; Values at species presence locations are taken for a set of predictor variables, and minimum and maximum values are defined for each predictor; species presence is then modeled based on the constraints set by these values (Council for Scientific and industrial Research 2005);

References

Council for Scientific and Industrial Research [CSIR]. (2005). *Assessment of Impacts and Adaptations to Climate Change in Multiple Regions and Sectors [AIACC].* South African National Biodiversity Institute [SANBI]: South Africa. Retrieved March 3, 2011 from http://planet.botany.uwc.ac.za/nisl/Climate_change/page_02.htm.

Franklin, J. (2009). *Mapping Species Distributions: Spatial Inference and Prediction.* Cambridge University Press: Cambridge.

Hastie, T., Tibshirani, R., and Friedman, J. (2009). *The Elements of Statistical Learning: Data Mining, Inference, Prediction.* Springer: New York, USA.

Pearson, R.G., Dawson, T.P., Berry, P.M., and Harrison P.A. (2002). SPECIES: a spatial evaluation of climate impact on the envelope of species. *Ecological Modelling* 154, 289-300.

Thuiller, W., Lafourcade, B., Araujo, M.B. (2009a). *ModOperating Manual for BIOMOD.* Université Joseph Fourier – Laboratoire d'Ecologie Alpine: Grenoble, France.

Appendix D: BIOMOD Best Model Based on AUC Values (Thuiller *et al*. 2009)

Explanation of rows:
PA1 and PA2: Final model (fitted on all presence points) for pseudo-absence run 1 and run 2, respectively;
PA1_rep1-5 and PA2_rep1-5: As the occurrence data are split into five groups, or folds, and models are fitted reserving a different portion of the data as test localities in each group, rep(lication) 1 through 5 represent each of the five folds for pseudo-absence run 1 and run 2, respectively;

Explanation of columns:
Best.Model: Depicts the model with the highest training and test AUC scores and the highest sensitivity and specificity.
Cross.validation: For PA1 and PA2 – the average test AUC scores of the five repetitions for each pseudo-absence run; For PA1_rep1-5 and PA2_rep1-5 – average AUC values determined based on test data for each of the cross validation runs and random pseudo absences 1 and 2;
Indepdt.data: Presence or absence of independent test data;
Total.score: For PA1 and PA2 – AUC based on all presence records and random pseudo absences 1 and 2; For PA1_rep1-5 and PA2_rep1-5 – the average AUC scores from combined calibration and test scores of the five repetitions for each pseudo-absence run;
Cutoff: Optimized threshold AUC value (x 1000);
Sensitivity: Percentage of presence locations correctly predicted to overlay suitable habitat based on cutoff;
Specificity: Percentage of pseudo-absence locations correctly predicted to overlay unsuitable habitat based on cutoff;

Choice of "best model":
Where BIOMOD determined the best model to be RF, a closer examination of the final models (row PA1 and row PA2) reveals that RF tends to overfit, as is indicated by an unrealistically high AUC when calibrating the model on all presence records; by the relatively large performance decrease from calibration to evaluation data; and by the unusually large sensitivity and specificity scores. Whenever data on model performance indicate overfitting, the best model that does not overfit is chosen. The chosen "best" models for projections are highlighted.

Acer negundo L.

	Best.Model	Cross.validation	indepdt.data	total.score	Cutoff	Sensitivity	Specificity
PA1	RF	0.989	none	1	609	100	100
PA1_rep1	RF	0.991	none	0.999	133	98.82	98.81
PA1_rep2	RF	0.991	none	0.999	124	98.525	98.63
PA1_rep3	RF	0.992	none	0.999	109	98.525	98.52
PA1_rep4	GLM	0.985	none	0.989	613.386	95.575	95.55
PA1_rep5	RF	0.991	none	0.999	129	98.82	98.75
PA2	RF	0.989	none	1	608	100	100
PA2_rep1	GLM	0.985	none	0.989	584.415	95.575	95.58
PA2_rep2	RF	0.99	none	0.999	97	98.23	98.34
PA2_rep3	RF	0.995	none	0.999	136	98.82	98.83
PA2_rep4	GBM	0.988	none	0.989	603.396	95.575	95.57

Ambrosia artemisiifolia L.

	Best.Model	Cross.validation	indepdt.data	total.score	Cutoff	Sensitivity	Specificity
PA1	GBM	0.989	none	0.991	549.45	94.583	94.75
PA1_rep1	GLM	0.988	none	0.992	501.498	95	95.08
PA1_rep2	RF	0.997	none	1	117	99.167	99.21
PA1_rep3	RF	0.993	none	0.999	48	98.333	98.33
PA1_rep4	GBM	0.993	none	0.992	521.478	94.583	94.64
PA1_rep5	GAM	0.99	none	0.991	559.44	95	94.89
PA2	GLM	0.989	none	0.992	548.451	95	95
PA2_rep1	GLM	0.985	none	0.992	426.146	94.583	94.77
PA2_rep2	RF	0.994	none	0.999	62	98.333	98.38
PA2_rep3	GAM	0.99	none	0.991	548.451	94.583	94.67
PA2_rep4	RF	0.995	none	0.999	138	99.167	99.16
PA2_rep5	GLM	0.988	none	0.992	480.519	94.583	94.52

Echinocystis lobata (Michx.) Torr. & Grey

	Best.Model	Cross.validation	indepdt.data	total.score	Cutoff	Sensitivity	Specificity
PA1	GBM	0.985	none	0.989	597.402	95.64	95.62
PA1_rep1	RF	0.99	none	0.992	620.418	96.458	96.42
PA1_rep2	GAM	0.986	none	0.988	619.38	95.64	95.58
PA1_rep3	GLM	0.983	none	0.989	577.422	95.64	95.52
PA1_rep4	GBM	0.988	none	0.992	628.779	96.458	96.4
PA1_rep5	RF	0.984	none	0.998	92	97.82	97.83
PA2	GBM	0.988	none	0.992	629.984	96.458	96.46
PA2_rep1	RF	0.99	none	0.999	114	98.365	98.38
PA2_rep2	RF	0.99	none	0.989	627.372	95.913	95.78
PA2_rep3	GBM	0.987	none	0.992	590.69	96.458	96.46
PA2_rep4	GLM	0.987	none	0.989	586.413	95.368	95.63
PA2_rep5	GAM	0.991	none	0.989	653.346	95.913	95.75

Helianthus tuberosus L.

	Best.Model	Cross.validation	indepdt.data	total.score	Cutoff	Sensitivity	Specificity
PA1	RF	0.983	none	0.987	620.379	95.044	95.04
PA1_rep1	GLM	0.983	none	0.986	626.373	95.044	95.05
PA1_rep2	RF	0.99	none	0.999	90	98.251	98.2
PA1_rep3	GLM	0.982	none	0.985	612.387	94.461	94.52
PA1_rep4	GBM	0.985	none	0.99	529.425	95.627	95.51
PA1_rep5	RF	0.986	none	0.998	106	98.251	98.27
PA2	RF	0.984	none	0.987	607.392	95.044	95.04
PA2_rep1	GLM	0.983	none	0.986	590.409	94.752	94.75
PA2_rep2	GLM	0.988	none	0.987	592.407	94.752	94.78
PA2_rep3	RF	0.993	none	0.999	116	98.542	98.54
PA2_rep4	GAM	0.981	none	0.987	581.418	95.044	95.01
PA2_rep5	GBM	0.984	none	0.99	568.109	95.627	95.63

Heracleum sosnowskyi **Manden**

	Best.Model	Cross.validation	indepdt.data	total.score	Cutoff	Sensitivity	Specificity
PA1	RF	0.973	none	1	593	100	100
PA1_rep1	RF	0.963	none	0.996	136	97.336	97.33
PA1_rep2	GBM	0.979	none	0.977	616.506	92.718	92.68
PA1_rep3	RF	0.971	none	0.997	137	97.336	97.31
PA1_rep4	RF	0.975	none	0.998	161	97.869	97.86
PA1_rep5	RF	0.977	none	0.998	142	97.513	97.52
PA2	RF	0.969	none	0.977	634.81	92.54	92.6
PA2_rep1	RF	0.968	none	0.996	149	97.691	97.71
PA2_rep2	RF	0.971	none	0.996	116	96.98	96.98
PA2_rep3	RF	0.972	none	0.978	613.773	92.54	92.6
PA2_rep4	GBM	0.972	none	0.977	602.39	92.54	92.54
PA2_rep5	RF	0.965	none	0.996	120	96.803	96.7

Impatiens glandulifera **Royle**

	Best.Model	Cross.validation	indepdt.data	total.score	Cutoff	Sensitivity	Specificity
PA1	RF	0.976	none	1	597.394	100	100
PA1_rep1	MARS	0.967	none	0.98	17.982	93.585	93.59
PA1_rep2	RF	0.978	none	0.997	120.274	98.491	98.47
PA1_rep3	MARS	0.979	none	0.98	17.982	93.585	93.24
PA1_rep4	RF	0.981	none	0.998	73.408	97.358	97.35
PA1_rep5	RF	0.979	none	0.997	81.426	97.736	97.72
PA2	GLM	0.981	none	0.982	620.756	93.962	93.97
PA2_rep1	RF	0.983	none	0.998	77.578	97.736	97.73
PA2_rep2	GLM	0.969	none	0.981	599.4	93.585	93.75
PA2_rep3	RF	0.985	none	0.998	67.184	97.358	97.23
PA2_rep4	GLM	0.987	none	0.981	636.363	93.585	93.77
PA2_rep5	RF	0.984	none	0.998	103.376	98.113	98.09

Reynoutria spp. (*Reynoutria japonica* Houtt. and *Reynoutria x bohemica* Chrtek.& Chrtková)

	Best.Model	Cross.validation	indepdt.data	total.score	Cutoff	Sensitivity	Specificity
PA1	RF	0.985	none	1	602	100	100
PA1_rep1	GBM	0.981	none	0.987	585.226	94.32	94.4
PA1_rep2	RF	0.989	none	0.999	132	98.279	98.14
PA1_rep3	RF	0.988	none	0.999	185	98.623	98.62
PA1_rep4	RF	0.988	none	0.999	128	98.107	98.11
PA1_rep5	GAM	0.983	none	0.983	595.404	93.804	93.79
PA2	RF	0.984	none	1	594	100	100
PA2_rep1	RF	0.985	none	0.998	152	98.451	98.42
PA2_rep2	RF	0.982	none	0.998	116	97.762	97.7
PA2_rep3	RF	0.984	none	0.998	120	97.935	97.96
PA2_rep4	RF	0.981	none	0.997	118	97.935	97.88
PA2_rep5	RF	0.987	none	0.999	150	98.279	98.29

Robinia pseudoacacia L.

	Best.Model	Cross.validation	indepdt.data	total.score	Cutoff	Sensitivity	Specificity
PA1	RF	0.978	none	0.986	603.39	94.521	94.55
PA1_rep1	GBM	0.985	none	0.986	584.672	94.521	94.47
PA1_rep2	RF	0.982	none	0.998	109	98.082	97.95
PA1_rep3	RF	0.975	none	0.997	88	97.534	97.46
PA1_rep4	RF	0.981	none	0.998	89	97.26	97.28
PA1_rep5	GBM	0.973	none	0.985	543.893	94.247	94.13
PA2	RF	0.977	none	1	601	100	100
PA2_rep1	RF	0.984	none	0.998	84	97.26	97.25
PA2_rep2	RF	0.977	none	0.997	93	97.534	97.65
PA2_rep3	RF	0.979	none	0.998	93	97.26	97.29
PA2_rep4	RF	0.982	none	0.986	565.668	94.521	94.39
PA2_rep5	GBM	0.97	none	0.985	530.786	94.247	94.16

Solidago spp. (*Solidago canadensis* L. and *Solidago gigantea* Aiton)

	Best.Model	Cross.validation	indepdt.data	total.score	Cutoff	Sensitivity	Specificity
PA1	GLM	0.99	none	0.991	632.367	96.061	96.06
PA1_rep1	RF	0.99	none	0.999	110	98.788	98.63
PA1_rep2	RF	0.994	none	0.999	101	98.485	98.5
PA1_rep3	GBM	0.991	none	0.994	525.954	96.667	96.72
PA1_rep4	GBM	0.987	none	0.99	638.361	96.061	96.06
PA1_rep5	GLM	0.992	none	0.991	626.373	96.061	95.96
PA2	GLM	0.99	none	0.992	628.371	96.061	96.06
PA2_rep1	GLM	0.988	none	0.992	588.411	95.758	95.76
PA2_rep2	GLM	0.99	none	0.992	628.371	96.061	96.06
PA2_rep3	RF	0.996	none	1	137	99.091	99.1
PA2_rep4	RF	0.99	none	0.999	96	98.485	98.49
PA2_rep5	GBM	0.987	none	0.991	575.424	95.758	95.86

Reference

Thuiller, W., Lafourcade, B., Araujo, M.B. (2009). *ModOperating Manual for BIOMOD*. Université Joseph Fourier – Laboratoire d'Ecologie Alpine: Grenoble, France.

Appendix E: Predictions for Current Conditions

For each species, three maps are displayed: Maxent – logistic suitability for current conditions determined by the Maxent final model; BIOMOD - logistic suitability for current conditions determined by the BIOMOD best model; and Combined – areas of overlap and differences between binary predictions (based on indicated threshold) in Maxent and BIOMOD.

In addition, the locations of the presence points used for model calibration and evaluation are displayed on each map.

Acer negundo L.
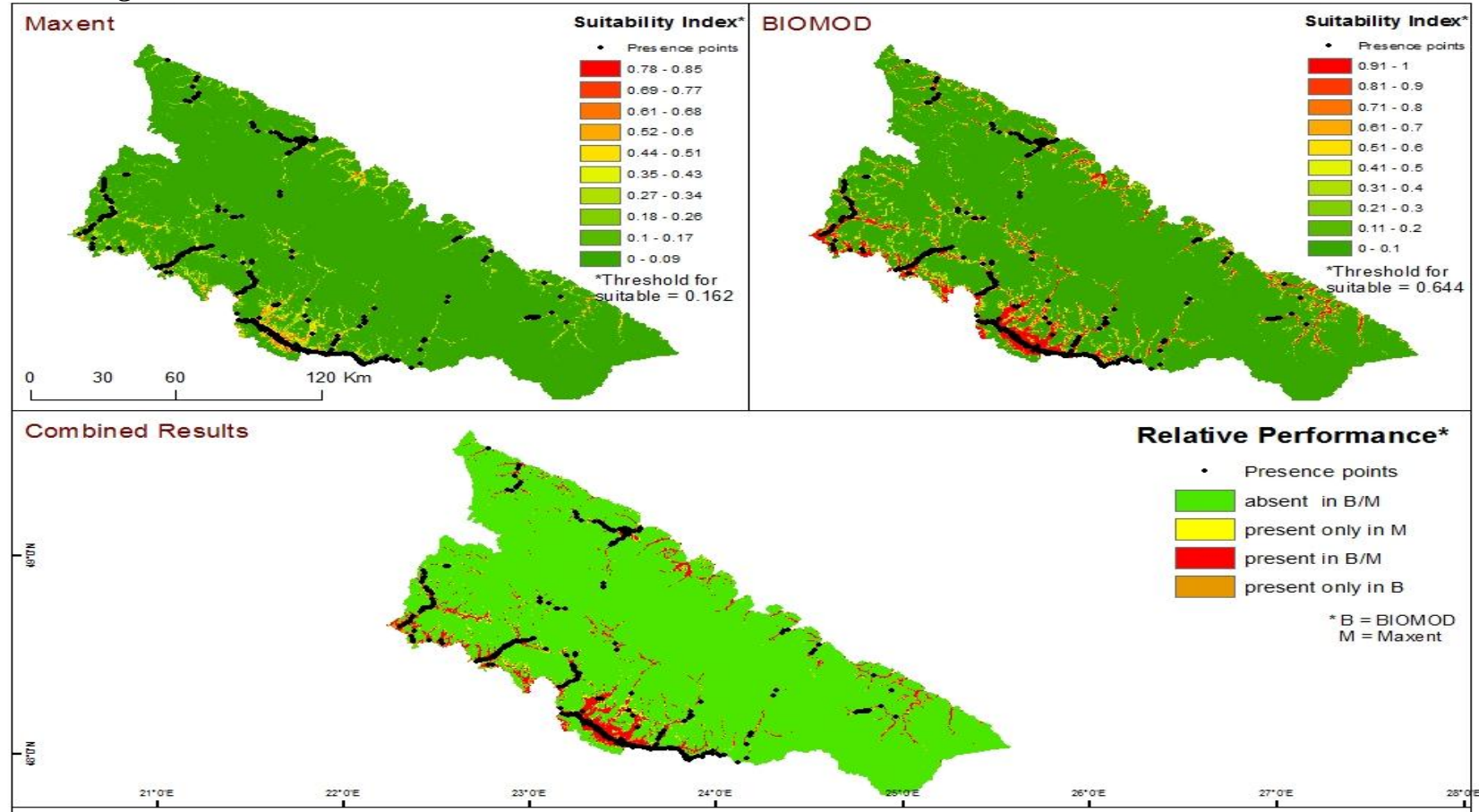
Ambrosia artemisiifolia **L.**
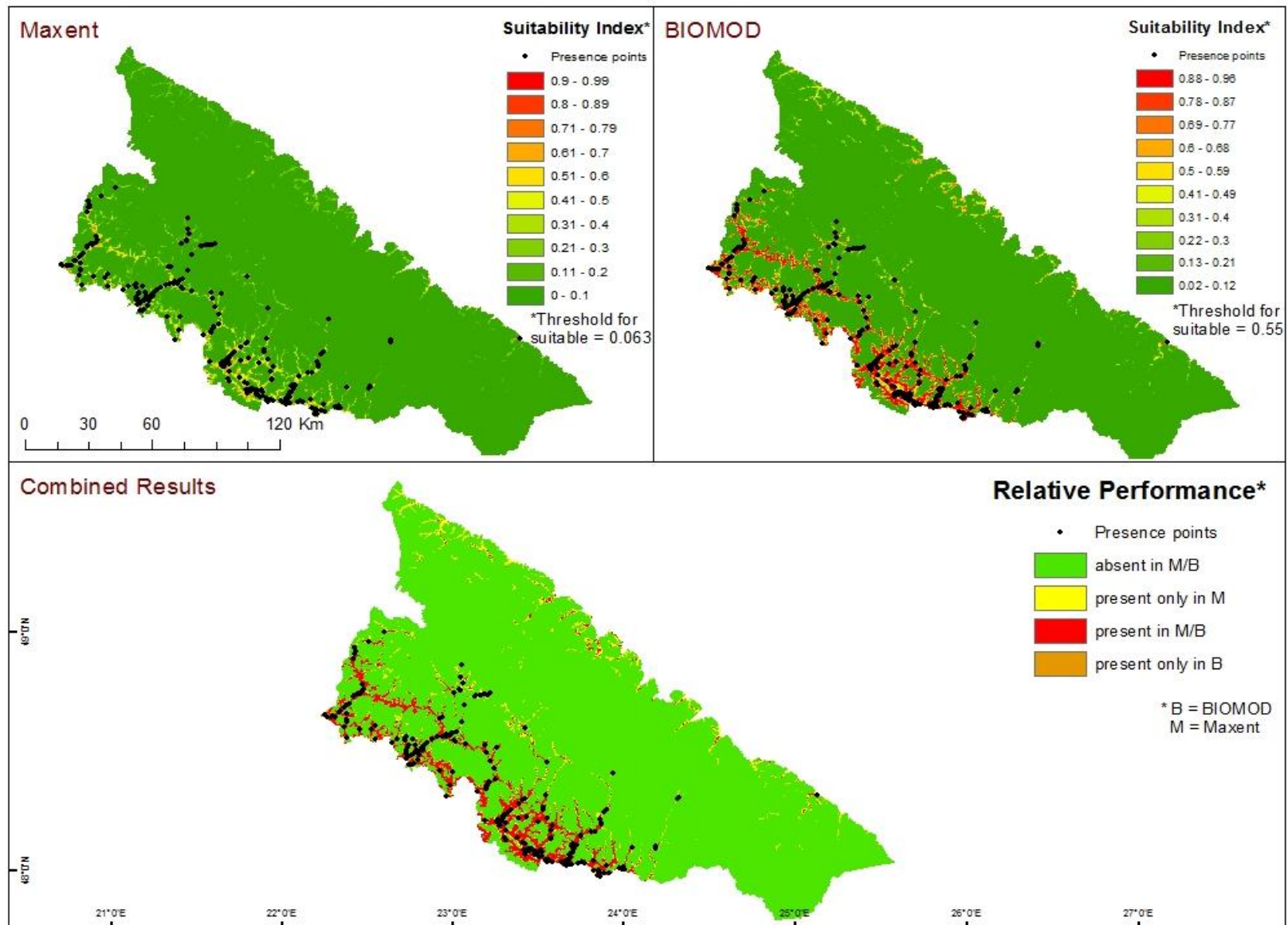
Echinocystis lobata (Michx.) Torr. & Grey
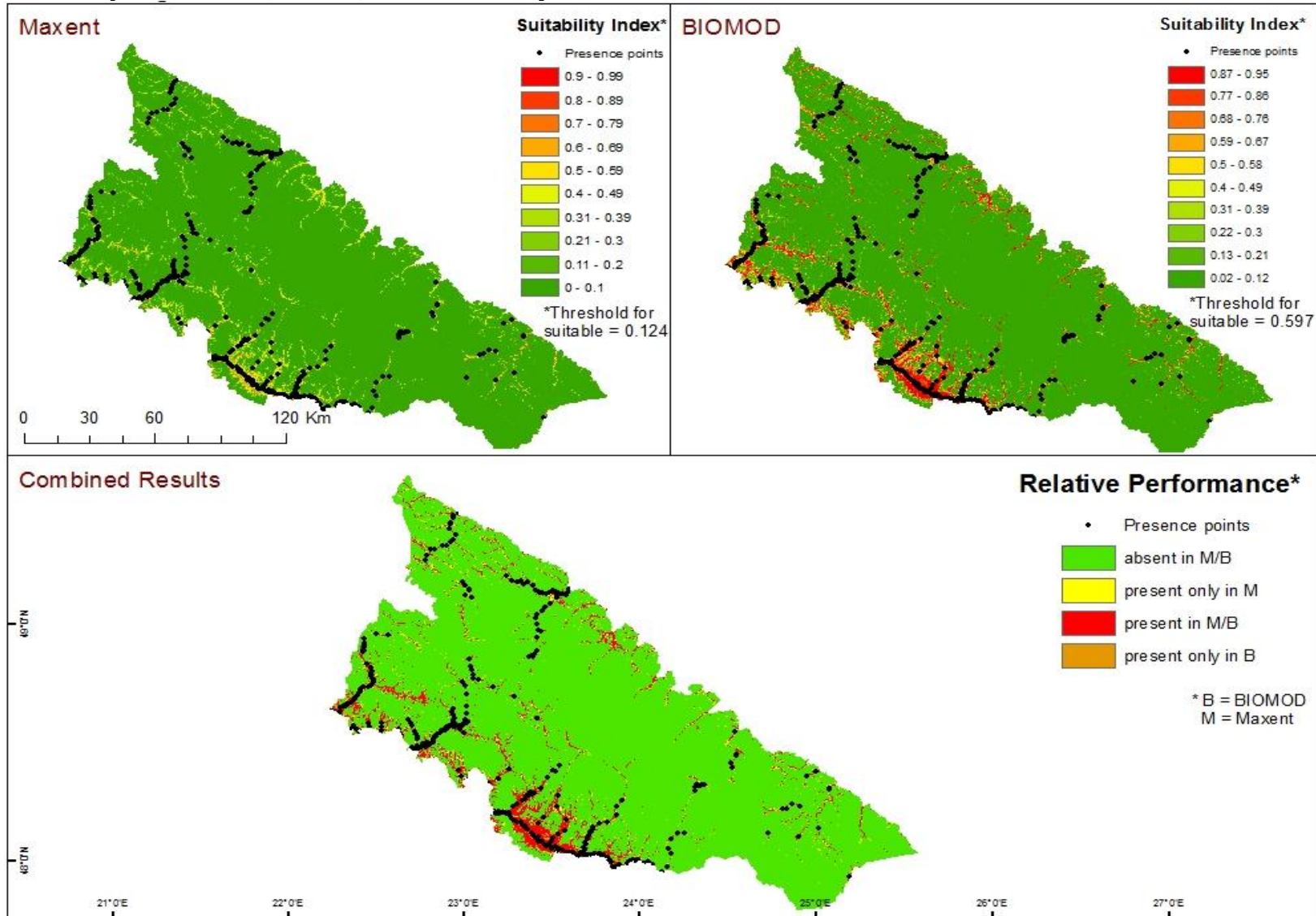
Helianthus tuberosus **L.**
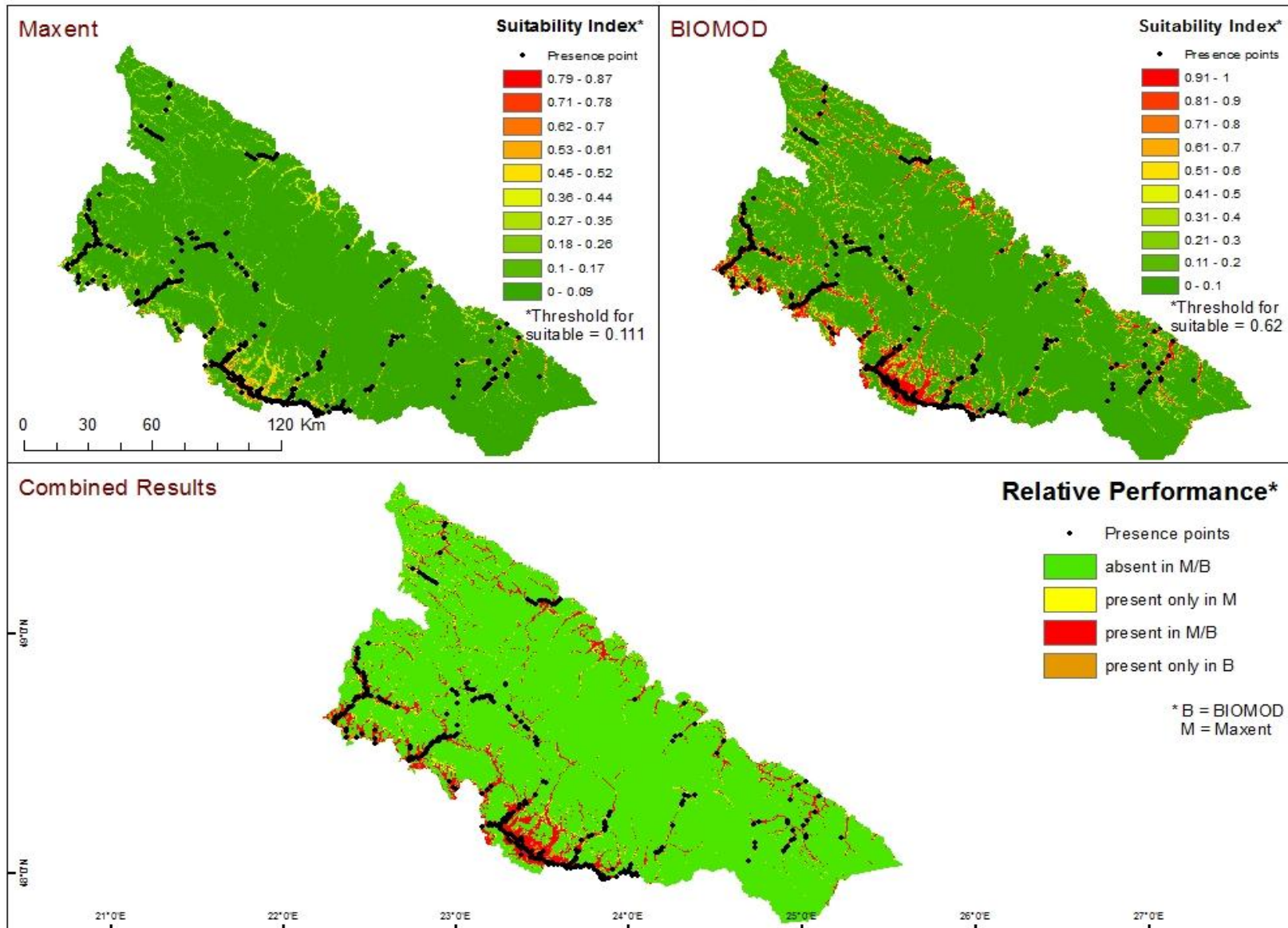
Heracleum sosnowskyi Manden
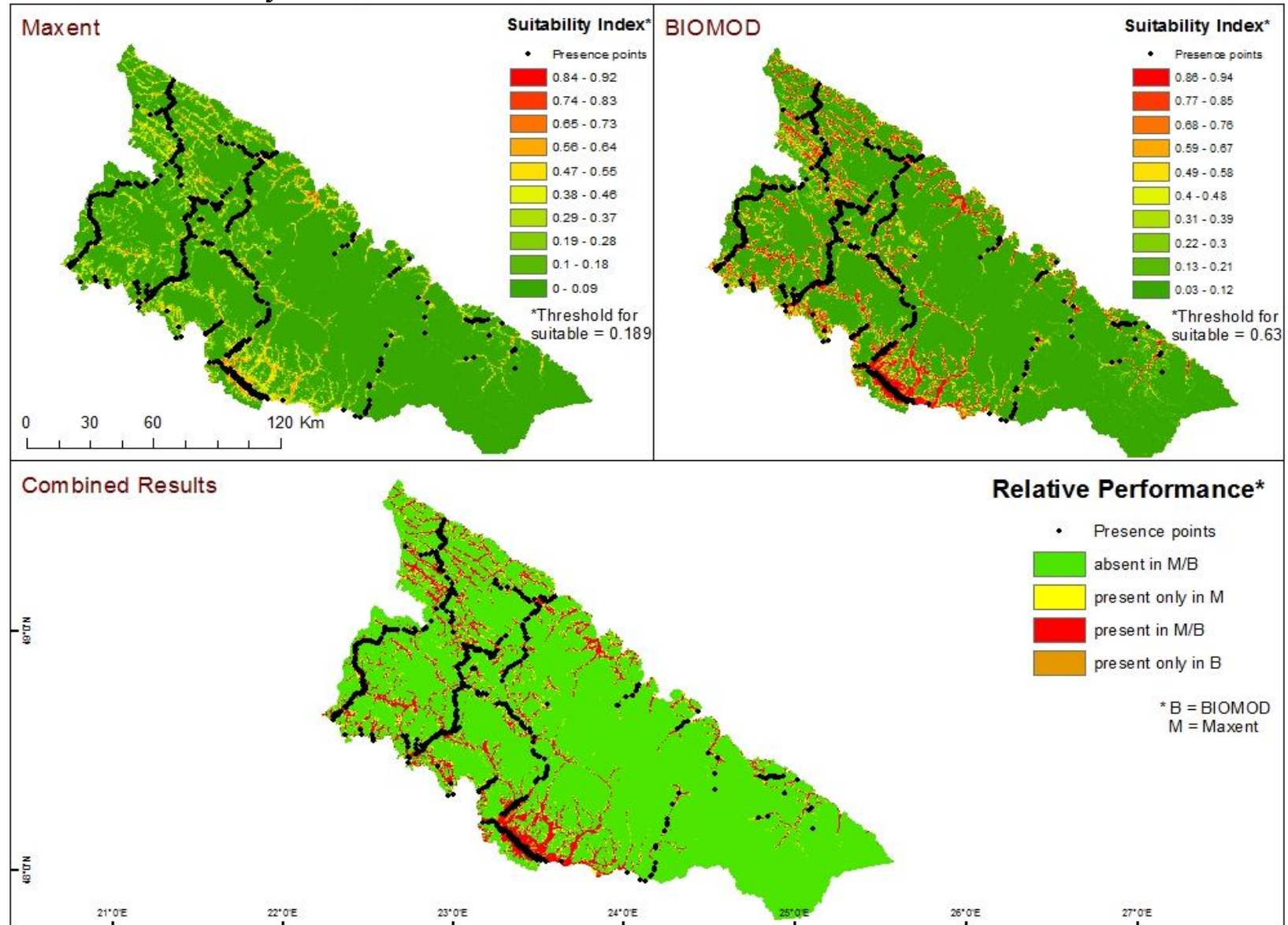
Impatiens glandulifera **Royle**
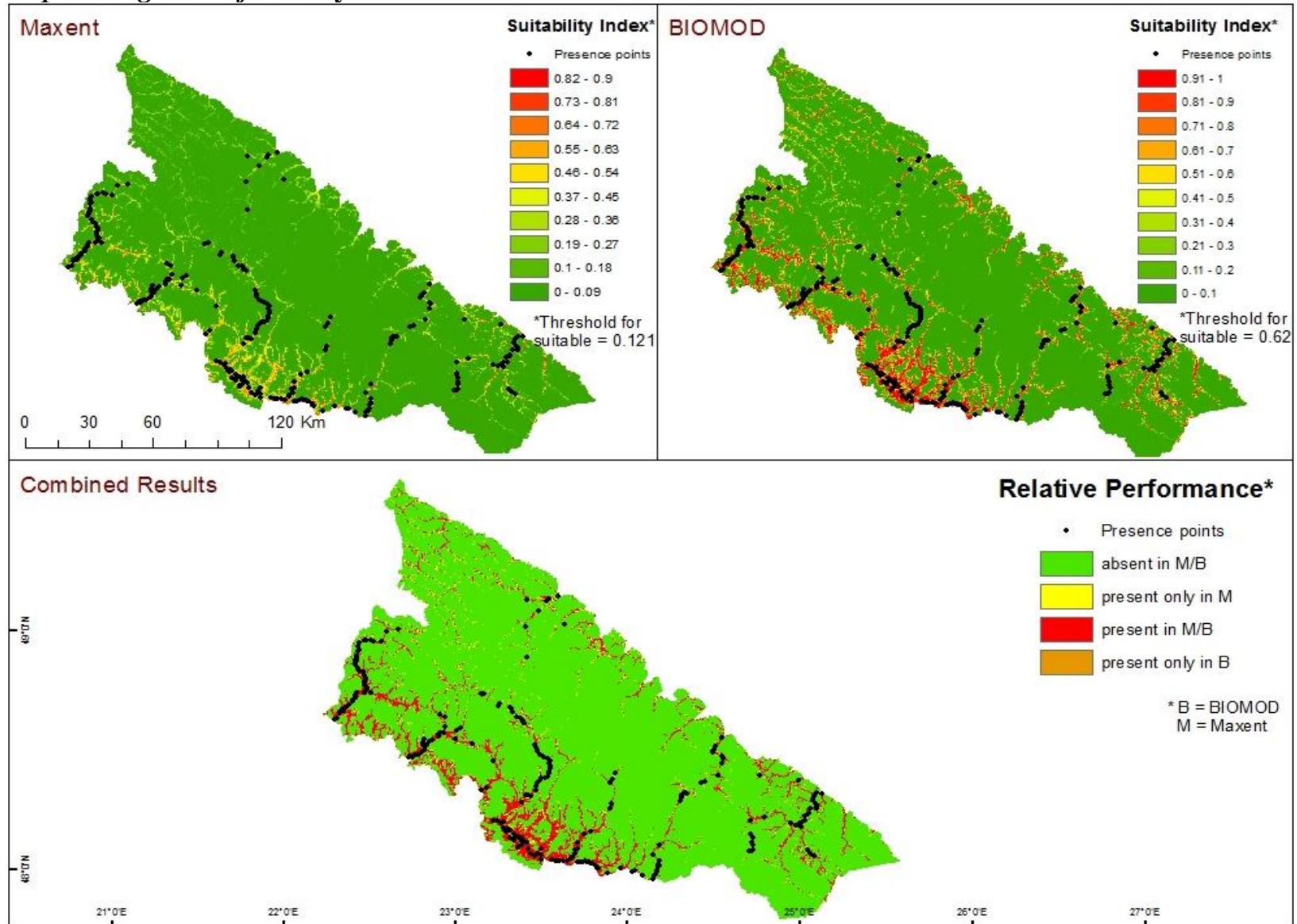
Reynoutria spp. (_Reynoutria japonica_ Houtt. and _Reynoutria x bohemica_ Chrtek.& Chrtková)
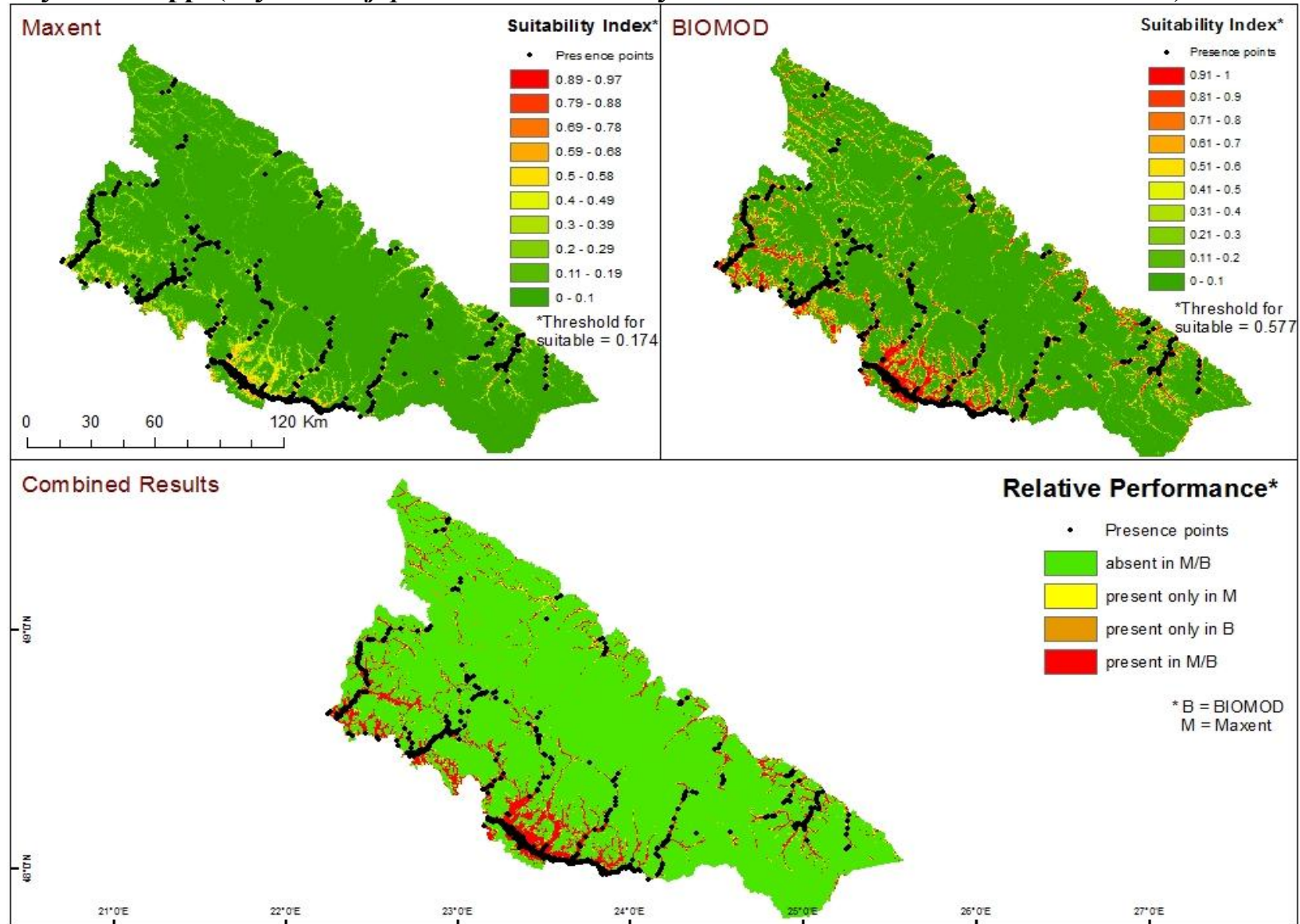
Robinia pseudoacacia L.
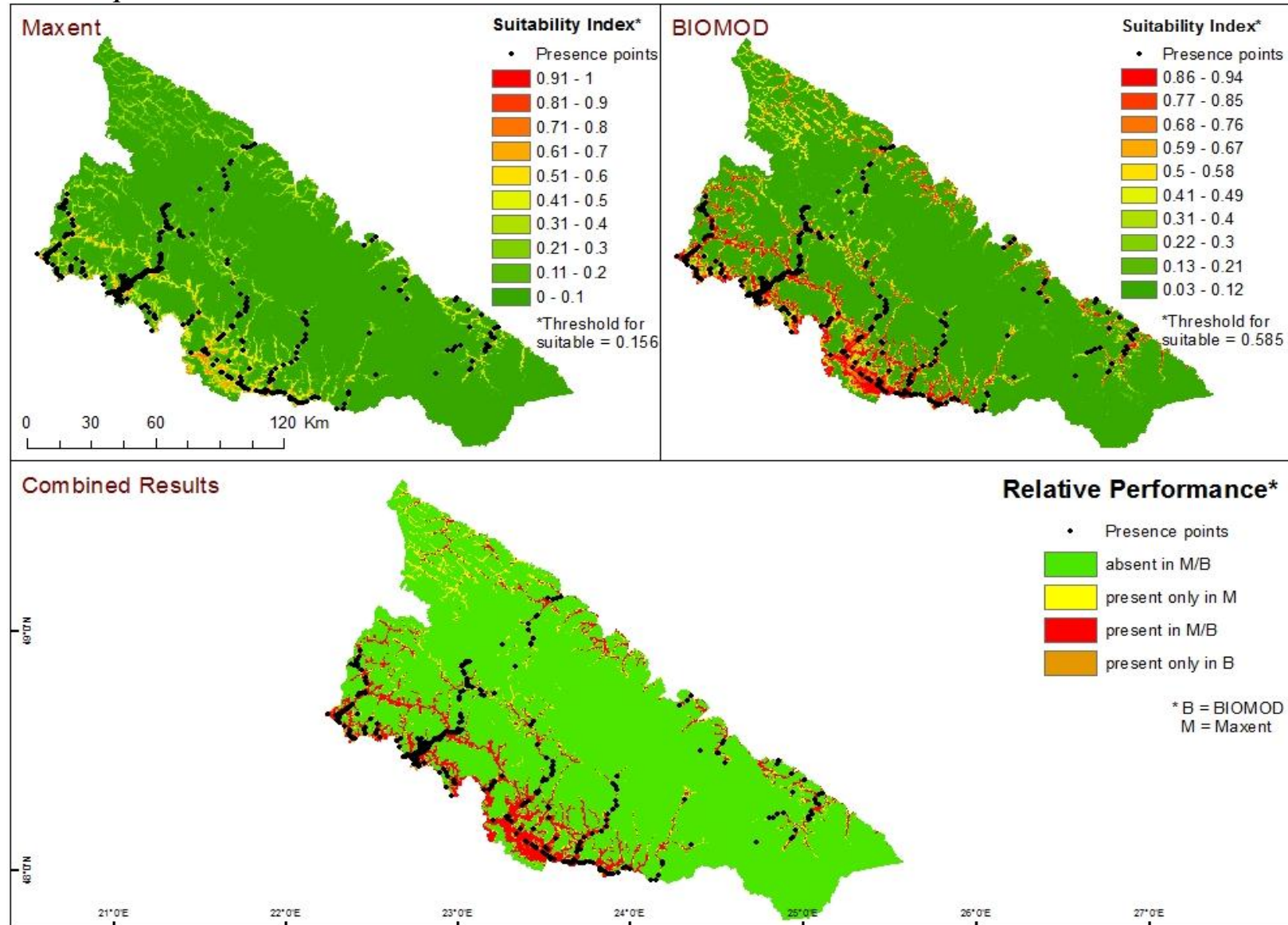
Solidago spp. (*Solidago canadensis* L. and *Solidago gigantea* Aiton)
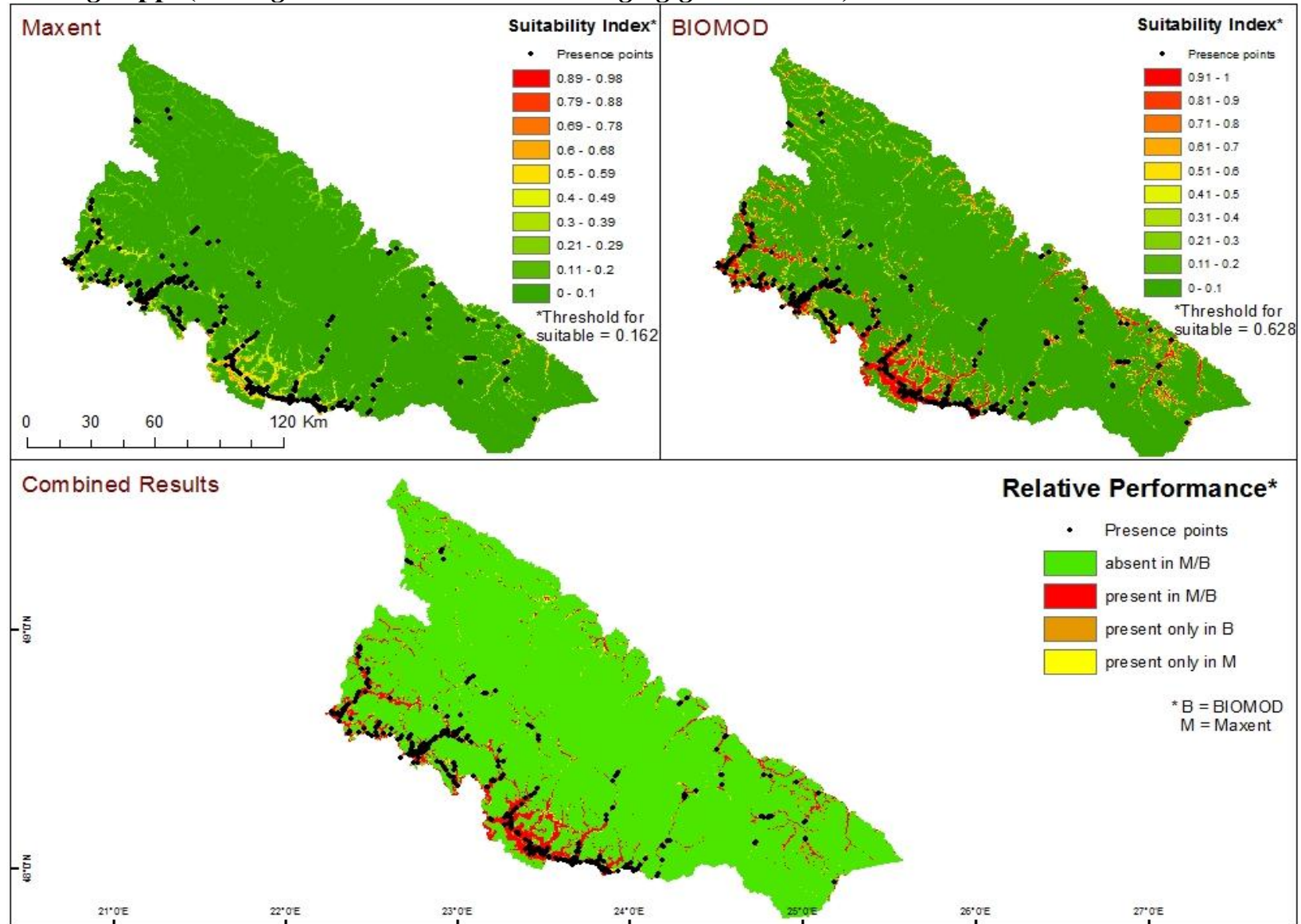
Appendix F: Measures of Variable Importance in Maxent and BIOMOD

Maxent (Phillips 2010)

Gain: a measure of goodness-of-fit of the model, i.e. how well predicted values fit empirical values; the higher the gain, the better the fit;

Jackknife test of variable importance: tests the contribution of a variable to the gain of the model in several steps: (a) by excluding each variable in turn; (b) creating a model with only the excluded variable; and (c) cretaing a model with all the variables; Caution must be taken interpreteting the results of step (a) when predictors are correlated because the calculation of contribution is dependent on the path a model takes – for example, if a model is first calibrated with "maxtwarm", then the correlated variable "mintcold", if picked thereafter, might contribute little to model performance;

Percent contribution: the contribution of each variable to the gain; must be interpreted with caution because it is defined heuristically; That is, values depend on the path the algorithm takes to get an optimal solution, and another algorithm, for example generilzed boosting models (GBM), can get to the same solution using a different path assigning different percent contributions to predictors;

Permutation importance: after the final model has been calibrated, each predictor is permutated in turn, and the decreases in the AUC on training data are recorded as percent;

BIOMOD (Thuiller *et al*. 2009; StatSoft 2011)

Akaike Information Criterion (AIC): statistic that tests the goodness-of-fit of a model, i.e. how well the predicted values match the observed ones; the formula is: $AIC = 2k - 2\ln(L)$, where k is the number of parameters in the model and L is the maximum value of the likelihood function (probability) of the estimated model; just like with the principle of a small desired deviance between actual and observed values, the model with the lowest AIC should be chosen;
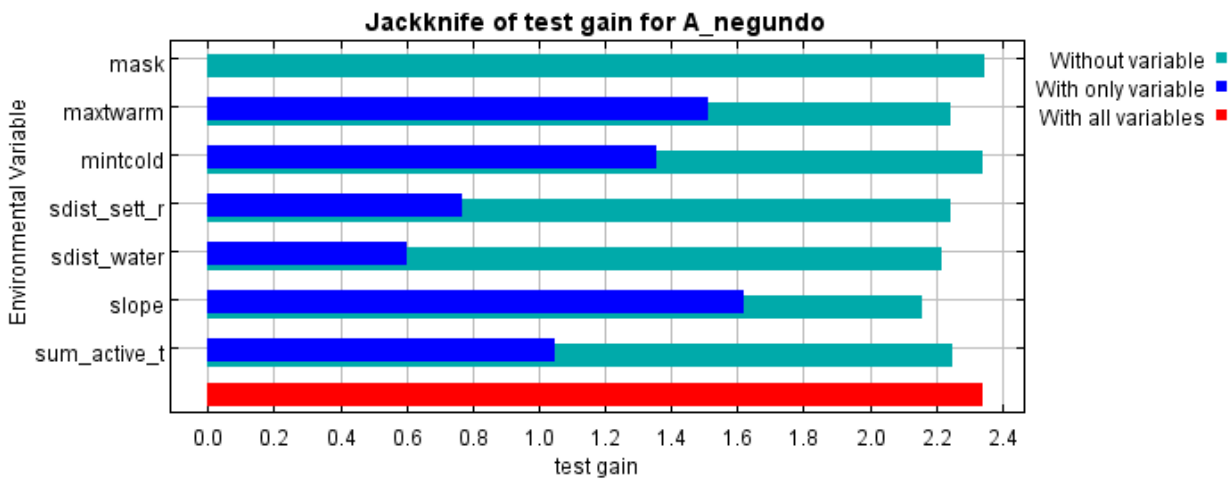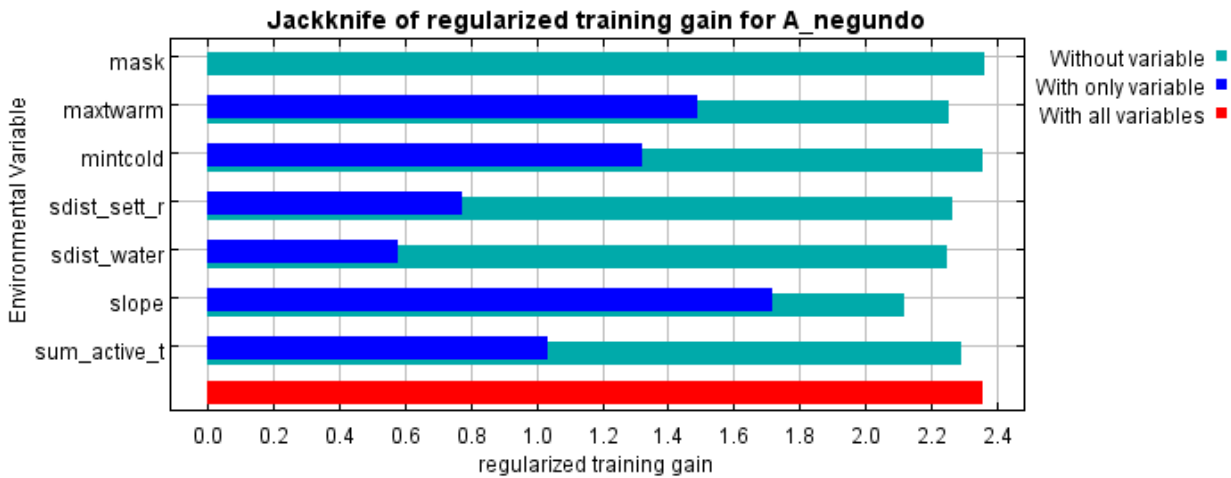
GAM/GLM stepwise regression: enhances the model in steps until lowest AIC is achieved; (a) the model is run with a contant term; (b) variables are tried out one by one as linear (1), quadratic (2), and polynomial (3) terms and picked in order of their importance to decrease the AIC; (c) variables that do not improve model performance are left out;

GBM relative influence: very similar to "percent contribution" in Maxent, including the limitations of this method (see above);

VarImportance: calculates the correlation score between prediction made with final model and model where a particular variable is permutated; shows results as 1 - correlation score; corresponds to "permutation importance" in Maxent;

Acer negundo **L.**

Maxent:

Jackknife of regularized training gain for A_negundo

Jackknife of test gain for A_negundo

Variable	Percent contribution	Permutation importance
slope	50	24.6
maxtwarm	30.9	40
sdist_water	8	5.7
sdist_sett_r	7	23
sum_active_t	3.2	5.9
mintcold	0.9	0.7
mask	0	0

BIOMOD_GLM:

```
> A.negundo_GLM_PA1$anova
Stepwise Model Path
Analysis of Deviance Table

Initial Model:
A.negundo ~ 1

Final Model:
A.negundo ~ poly(maxtwarm, 3) + poly(slope, 3) + sdist_sett_r +
    sdist_water + poly(sat, 3)


                  Step Df  Deviance Resid. Df Resid. Dev        AIC
1                                      10338   939.9076 471.95379
2 + poly(maxtwarm, 3)  3 604.13906     10335   335.7685 151.63077
3    + poly(slope, 3)  3 111.66312     10332   224.1054 115.56013
4      + sdist_sett_r  1  45.61749     10331   178.4879  83.78114
5       + sdist_water  1  11.62841     10330   166.8595  81.01264
> VarImportance
$A.negundo
      slope sdist_sett_r sdist_water maxtwarm mintcold   sat
GAM   0.161        0.361       0.000    0.625    0.000 0.000
GBM   0.270        0.124       0.041    0.483    0.011 0.007
GLM   0.110        0.344       0.065    0.764    0.000 0.148
MARS  0.327        0.138       0.056    0.673    0.589 0.410
RF    0.223        0.052       0.047    0.406    0.184 0.180
```

Ambrosia artemisiifolia L.

Maxent:

Jackknife of regularized training gain for A_artem

Jackknife of test gain for A_artem
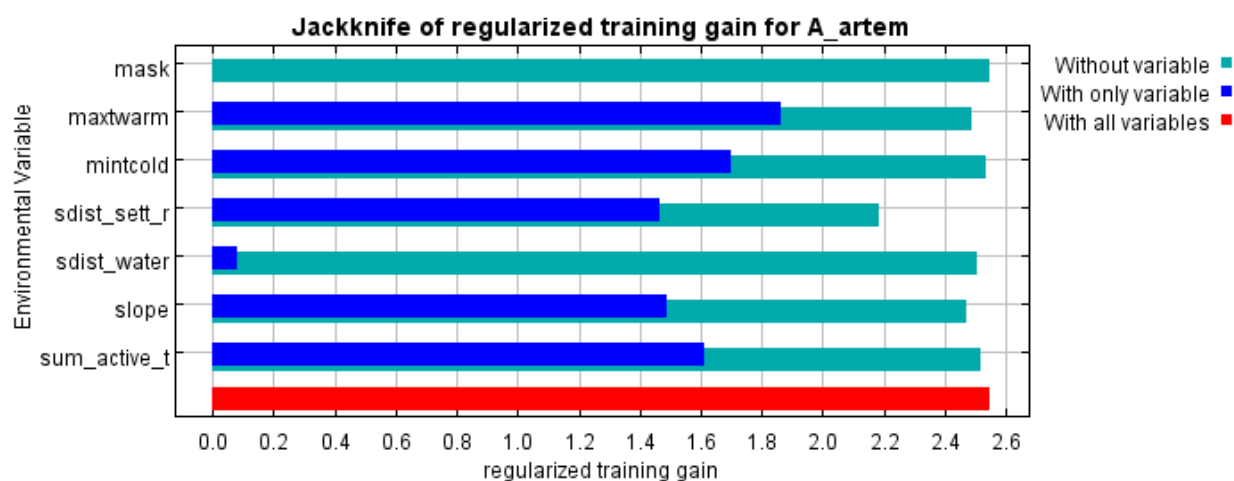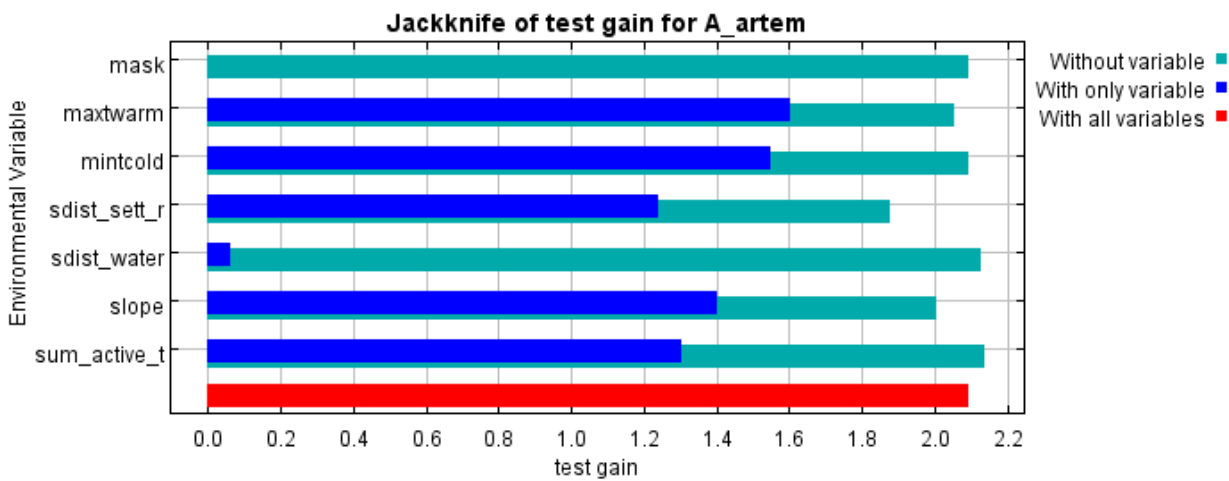
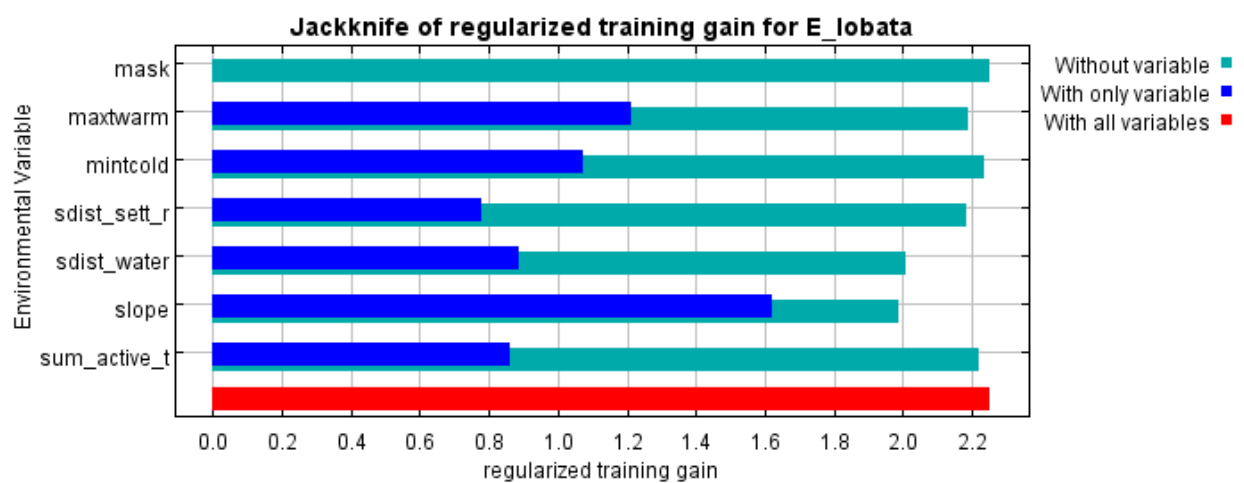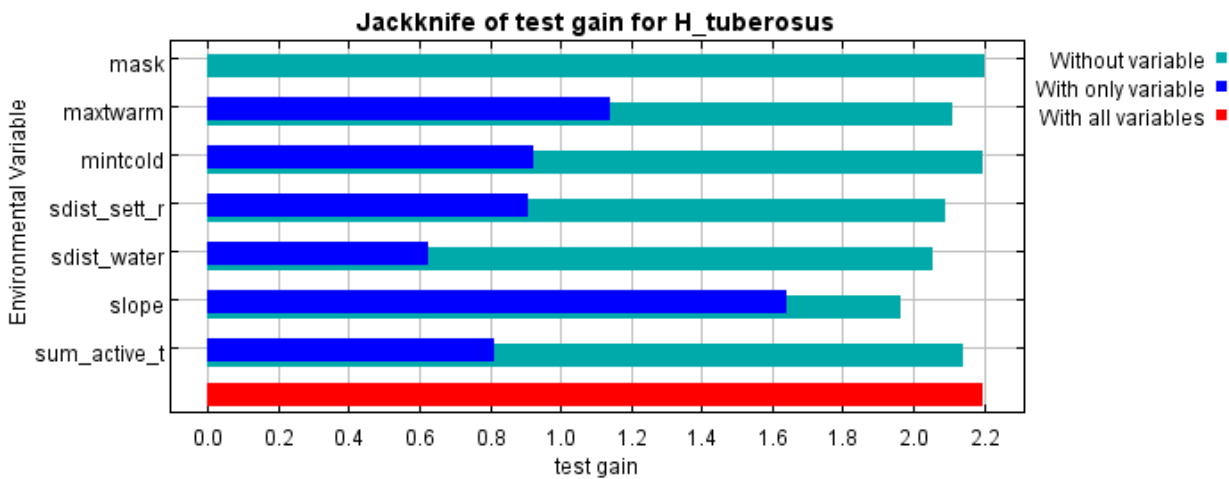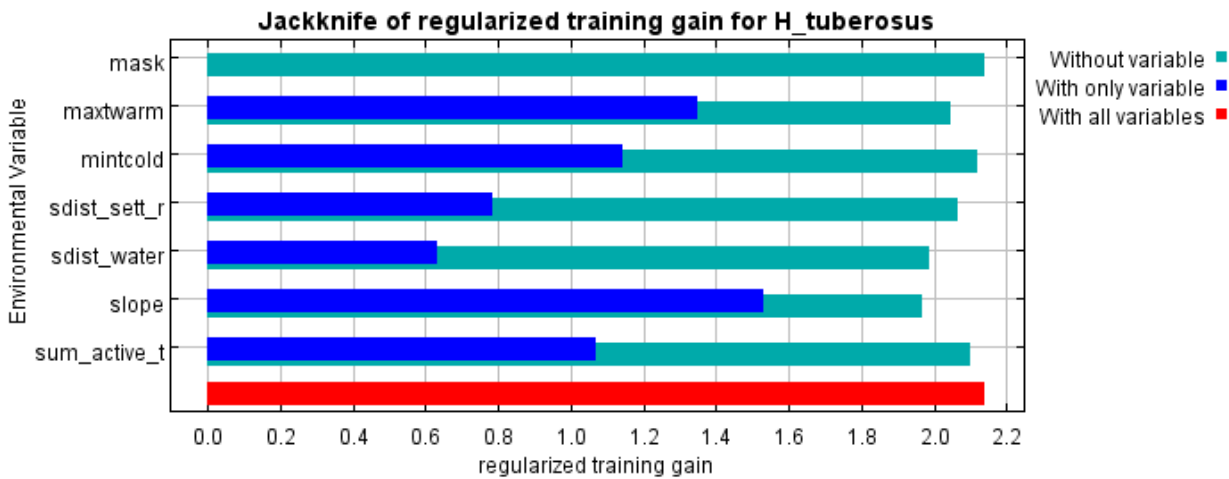| Variable	Percent contribution	Permutation importance
maxtwarm	33.9	19.7
sdist_sett_r	32.9	73.7
slope	14.2	3.8
sum_active_t	11.1	1.1
mintcold	7.2	0.5
sdist_water	0.8	1.1
mask	0	0

BIOMOD_GBM:
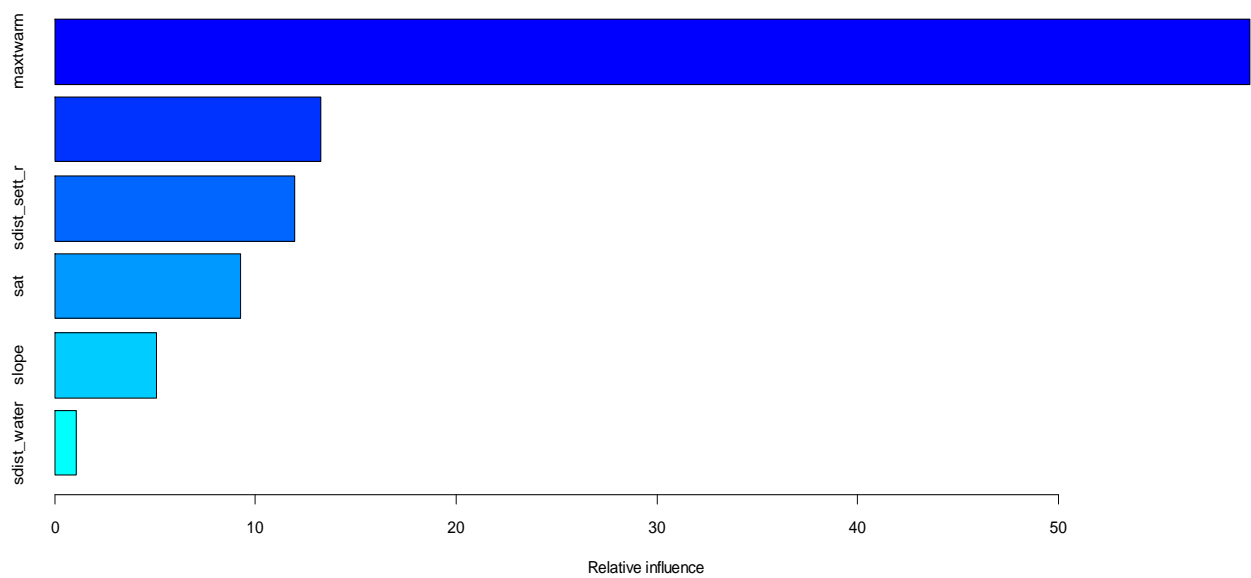
```
> VarImportance
$A.artem
      slope sdist_sett_r sdist_water maxtwarm mintcold    sat
GAM   0.000        0.545       0.000    0.739    0.000 0.000
GBM   0.081        0.397       0.003    0.329    0.055 0.077
GLM   0.079        0.483       0.016    0.665    0.000 0.000
MARS  0.275        0.236       0.000    0.577    0.236 0.544
RF    0.091        0.187       0.013    0.275    0.079 0.090
```

Echinocystis lobata (Michx.) Torr. & Grey

Maxent:
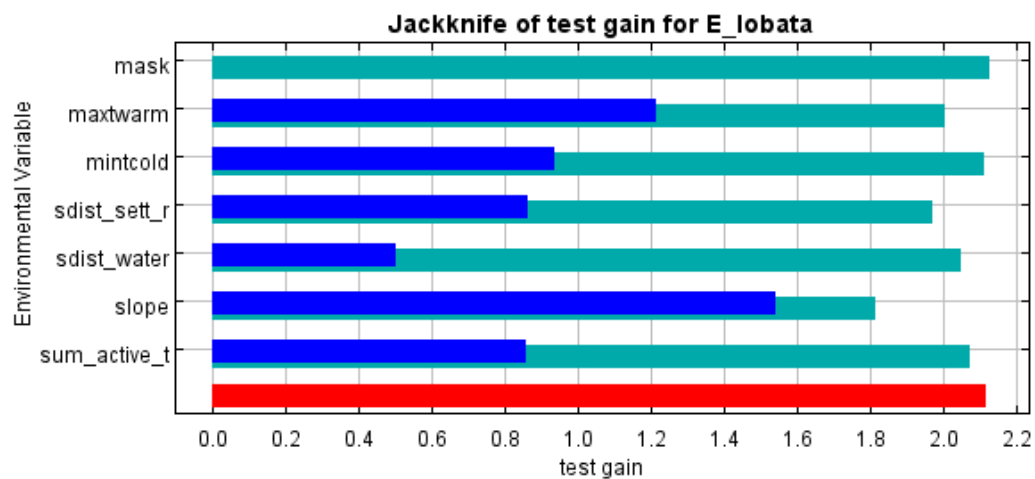
Jackknife of regularized training gain for E_lobata

Jackknife of test gain for E_lobata

Variable	Percent contribution	Permutation importance
slope	54.6	24.8
sdist_water	18.2	16.6
maxtwarm	14.9	31.9
sdist_sett_r	7.9	20.4
mintcold	2.5	1.5
sum_active_t	1.9	4.7
mask	0	0

BIOMOD_GBM:
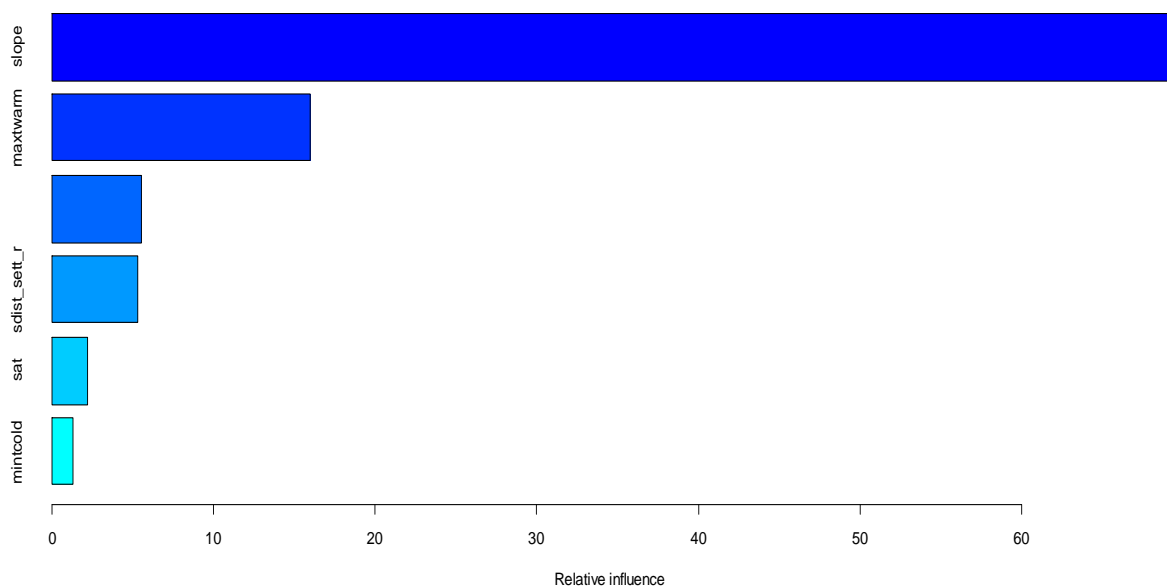

```
> VarImportance
$E.lobata
      slope sdist_sett_r sdist_water maxtwarm mintcold    sat
GAM   0.224        0.231       0.154    0.318    0.000 0.000
GBM   0.302        0.083       0.170    0.448    0.002 0.004
GLM   0.199        0.237       0.137    0.627    0.000 0.107
MARS  0.350        0.095       0.144    0.830    0.442 0.101
RF    0.259        0.072       0.102    0.331    0.128 0.077
```

Helianthus tuberosus **L.**

Maxent:

Jackknife of regularized training gain for H_tuberosus

Jackknife of test gain for H_tuberosus

Variable	Percent contribution	Permutation importance
slope	53.3	14.4
maxtwarm	22.2	44.4
sdist_water	11	11.7
sdist_sett_r	10.2	22.5
sum_active_t	1.8	5.7
mintcold	1.5	1.3
mask	0	0

BIOMOD_GLM:

```
> H.tuberosus_GLM_PA1$anova
Stepwise Model Path
Analysis of Deviance Table

Initial Model:
H.tuberosus ~ 1

Final Model:
H.tuberosus ~ poly(slope, 3) + poly(maxtwarm, 3) + poly(sdist_sett_r,
    3) + sdist_water + poly(sat, 3)


                       Step Df  Deviance Resid. Df Resid. Dev      AIC
1                                           10342   950.9979 477.4990
2         + poly(slope, 3)    3 541.49224     10339   409.5057 216.1858
3      + poly(maxtwarm, 3)    3 122.95501     10336   286.5507 153.4365
4 + poly(sdist_sett_r, 3)    3  52.53398     10333   234.0167 125.9662
5            + sdist_water    1  24.66858     10332   209.3481 115.0162
6           + poly(sat, 3)    3  19.20654     10329   190.1416 111.1969
> VarImportance
$H.tuberosus
     slope sdist_sett_r sdist_water maxtwarm mintcold   sat
GAM  0.111        0.189       0.107    0.746    0.000 0.141
GBM  0.217        0.152       0.071    0.412    0.003 0.007
GLM  0.106        0.205       0.114    0.744    0.000 0.205
MARS 0.204        0.022       0.041    0.925    0.100 0.309
RF   0.161        0.081       0.057    0.485    0.104 0.130
```

Heracleum sosnowskyi Manden

Maxent:

Appendix F: Variable Importance

Jackknife of test gain for H_sos
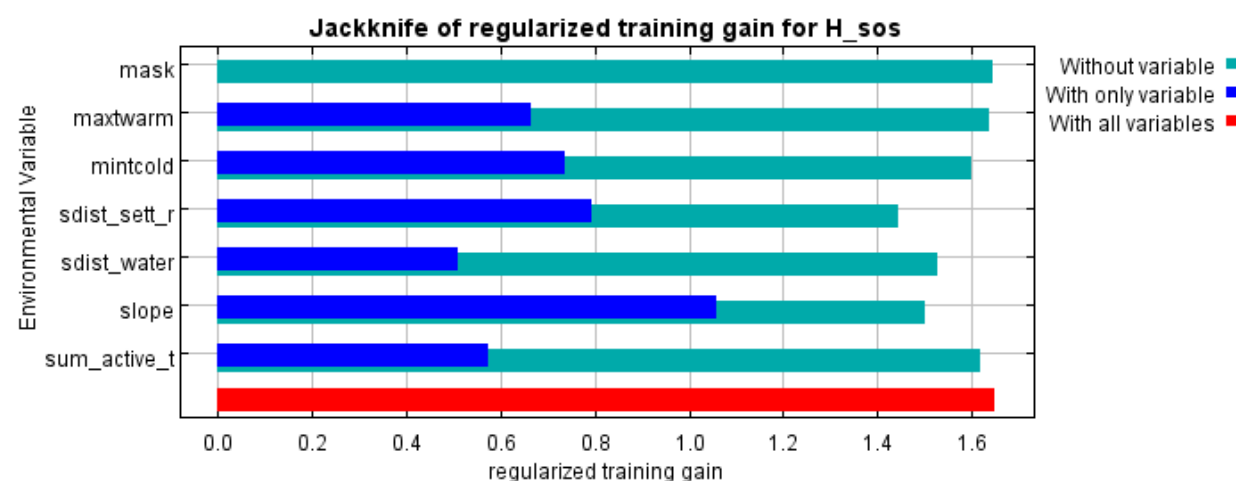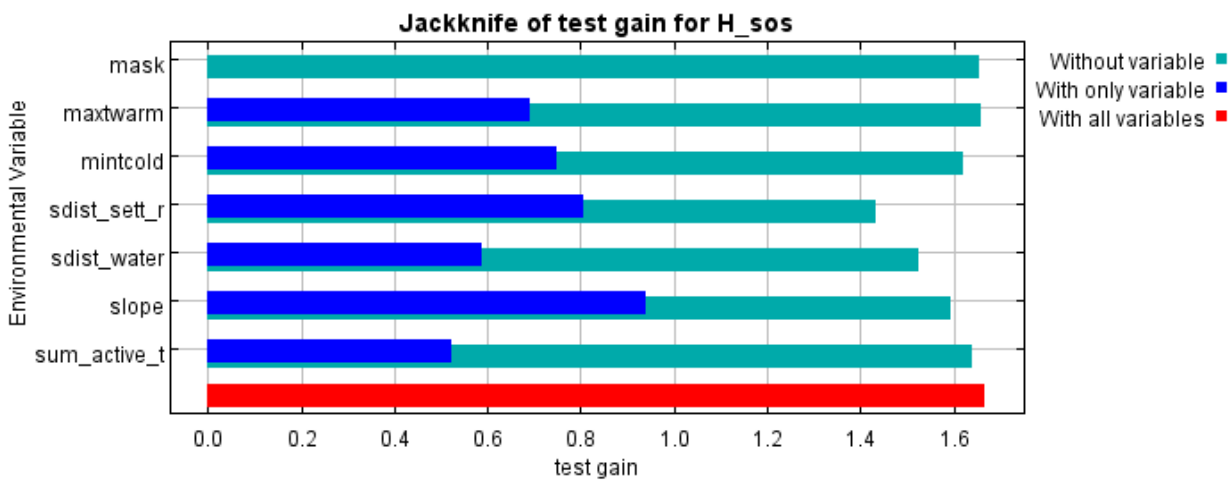
Variable	Percent contribution	Permutation importance
slope	41.1	15.4
sdist_sett_r	25.9	46.5
mintcold	15.3	18
sdist_water	13	12.5
sum_active_t	3.2	5.7
maxtwarm	1.6	2
mask	0	0

BIOMOD_GBM:
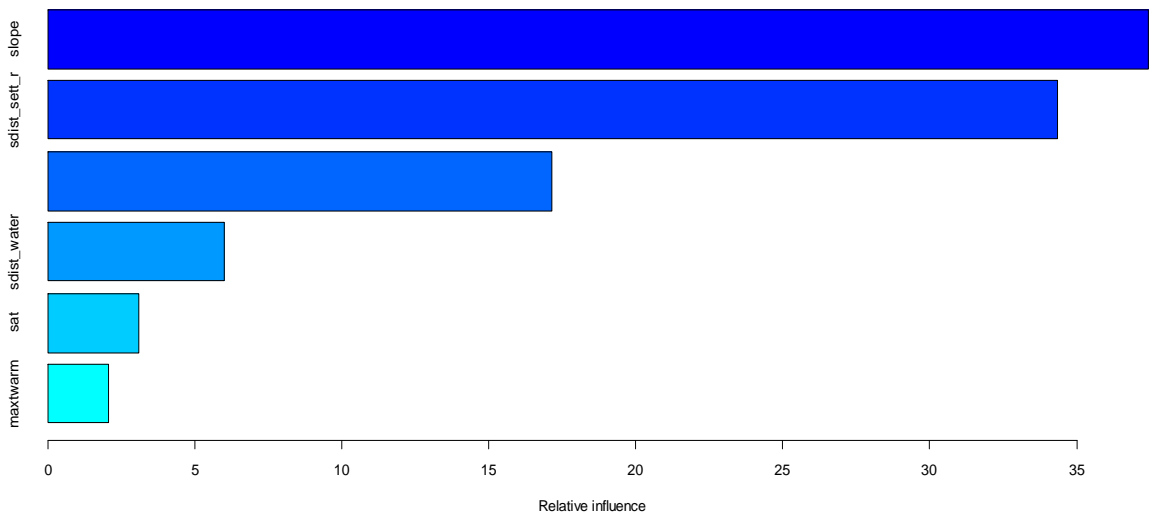
```
> VarImportance
$H.sos
      slope sdist_sett_r sdist_water maxtwarm mintcold   sat
GAM   0.074        0.381       0.059    0.000    0.296 0.041
GBM   0.120        0.400       0.055    0.004    0.236 0.011
GLM   0.072        0.409       0.064    0.030    0.525 0.012
MARS  0.525        0.115       0.118    0.000    0.433 0.422
RF    0.274        0.263       0.126    0.134    0.263 0.139
```

Impatiens glandulifera Royle

Maxent:
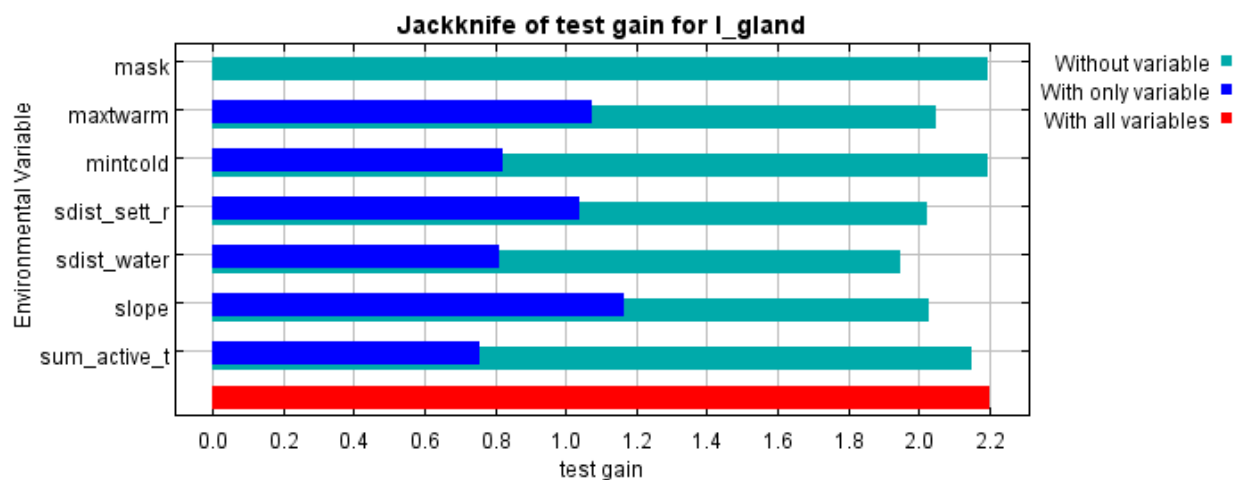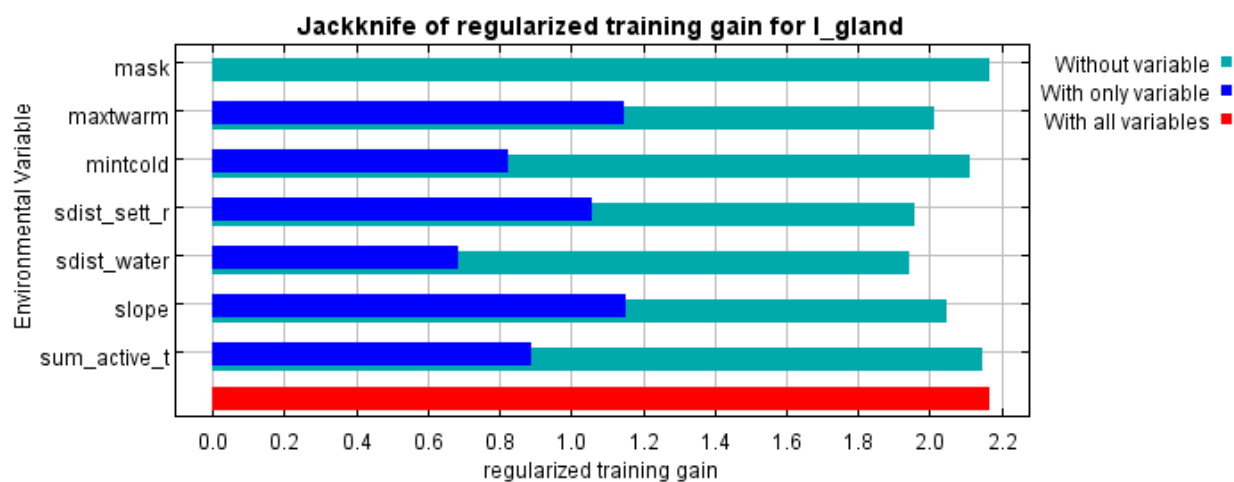
Variable	Percent contribution	Permutation importance
sdist_sett_r	31.5	39.9
maxtwarm	24.8	29.5
slope	23.3	6.6
sdist_water	16.8	18.9
sum_active_t	2	2.1
mintcold	1.6	3.1
mask	0	0

BIOMOD_GLM:

```
> I.gland_GLM_PA2$anova
                        Step Df  Deviance Resid. Df Resid. Dev      AIC
1                             NA        NA     10264   734.7360 369.36801
2        + poly(maxtwarm, 3)  3 360.00839     10261   374.7276 181.61008
3 + poly(sdist_sett_r, 2)  2 118.58744     10259   256.1402 124.49327
4             + sdist_water  1  57.40414     10258   198.7360  97.25451
5             + poly(sat, 2)  2  17.95005     10256   180.7860  94.70890
6           + poly(slope, 2)  2  10.71550     10254   170.0705  94.63299
> summary(I.gland_GLM_PA2)

Call:
glm(formula = I.gland ~ poly(maxtwarm, 3) + poly(sdist_sett_r,
    2) + sdist_water + poly(sat, 2) + poly(slope, 2) + mintcold,
    family = binomial, data = DataBIOMOD[calib.lines, ], weights = RunWeights[calib.lines])
> VarImportance
$I.gland
      slope sdist_sett_r sdist_water maxtwarm mintcold    sat
GAM   0.069        0.375       0.289    0.702    0.142 0.000
GBM   0.079        0.422       0.188    0.464    0.001 0.016
GLM   0.052        0.405       0.258    0.827    0.092 0.153
MARS 0.637        0.115       0.080    0.876    0.229 0.119
RF    0.202        0.225       0.101    0.467    0.164 0.212
```

Reynoutria spp. (*Reynoutria japonica* Houtt. and *Reynoutria x bohemica* Chrtek.& Chrtková)

Maxent:

Jackknife of regularized training gain for Reynoutria

Jackknife of test gain for Reynoutria
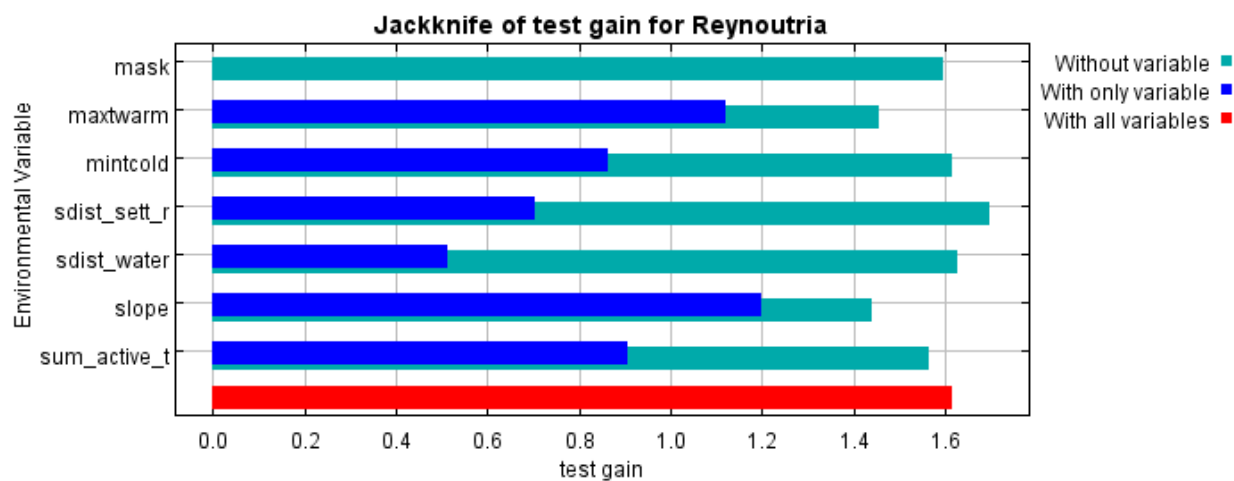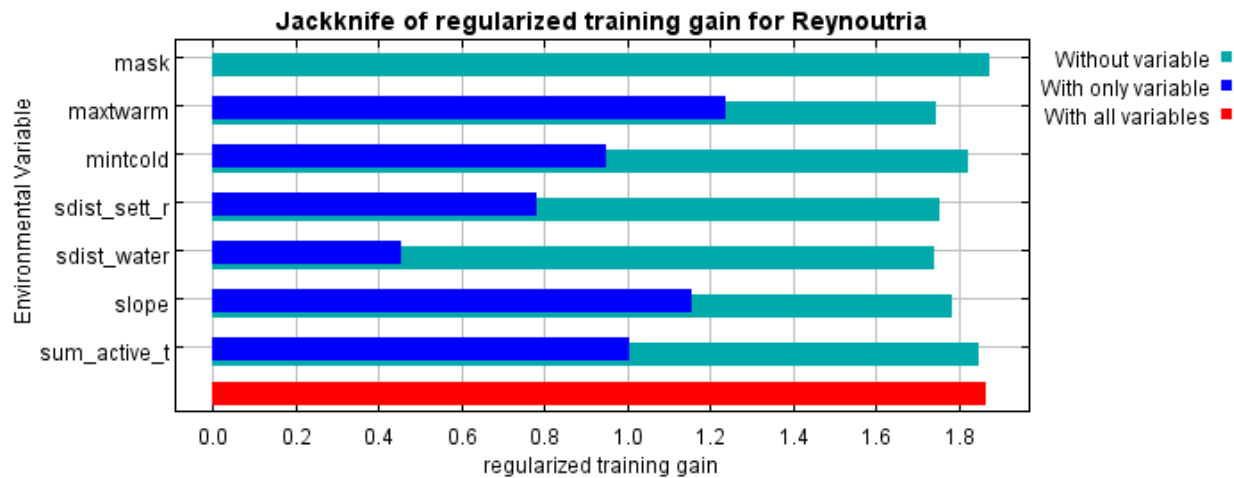
Variable	Percent contribution	Permutation importance
slope	37.4	8.7
maxtwarm	35.2	64
sdist_sett_r	12	13.4
sdist_water	8.9	6.6
mintcold	3.5	3.4
sum_active_t	3	3.8
mask	0	0

BIOMOD_GAM:

```
> Reynoutria_GAM_PA1$anova
Stepwise Model Path
Analysis of Deviance Table

Initial Model:
Reynoutria ~ 1

Final Model:
Reynoutria ~ s(slope, 4) + s(sdist_sett_r, 4) + s(sdist_water,
    4) + s(maxtwarm, 4) + s(mintcold, 4)

Scale: 0.1098299

      From To      Df Deviance Resid. Df Resid. Dev    AIC
[1,]    1  1                       10580    1610.87 854.23
[2,]    1  2 -4.0002  -902.72      10576     708.15 404.25
[3,]    1  4 -4.0000  -206.67      10572     501.48 316.84
[4,]    1  6 -3.9997   -56.74      10568     444.74 287.83
[5,]    1  3 -4.0000   -30.34      10564     414.41 271.02
[6,]    1  5 -3.9998   -40.38      10560     374.02 260.50
> VarImportance
$Reynoutria
      slope sdist_sett_r sdist_water maxtwarm mintcold    sat
GAM   0.056        0.225       0.078    0.886    0.081  0.054
GBM   0.089        0.224       0.044    0.520    0.004  0.004
GLM   0.052        0.261       0.073    0.859    0.067  0.119
MARS  0.270        0.037       0.014    1.043    0.127  0.395
RF    0.133        0.136       0.043    0.485    0.089  0.115
```

Robinia pseudoacacia L.

Maxent:
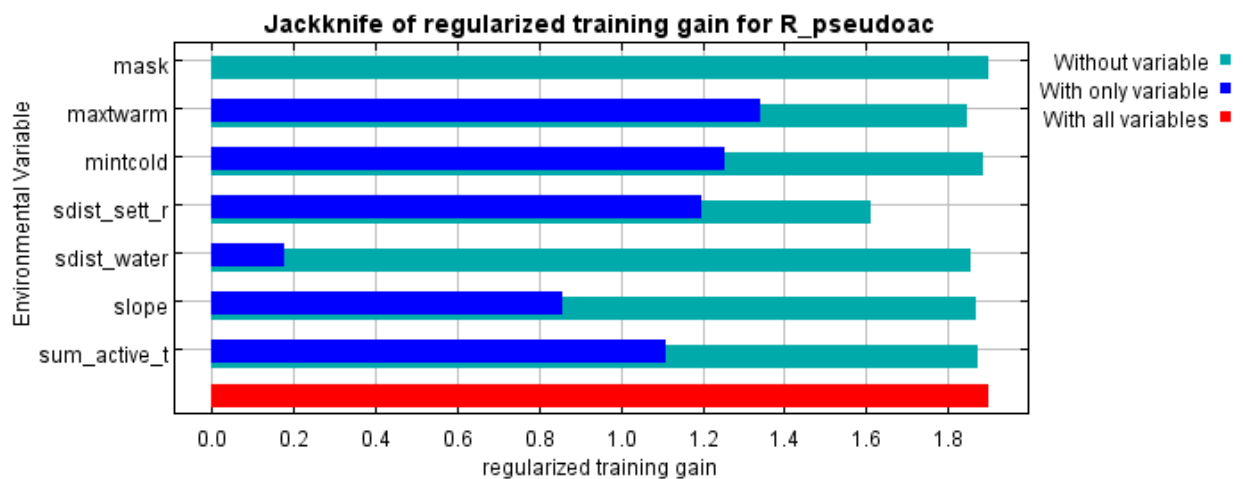
Jackknife of test gain for R_pseudoac
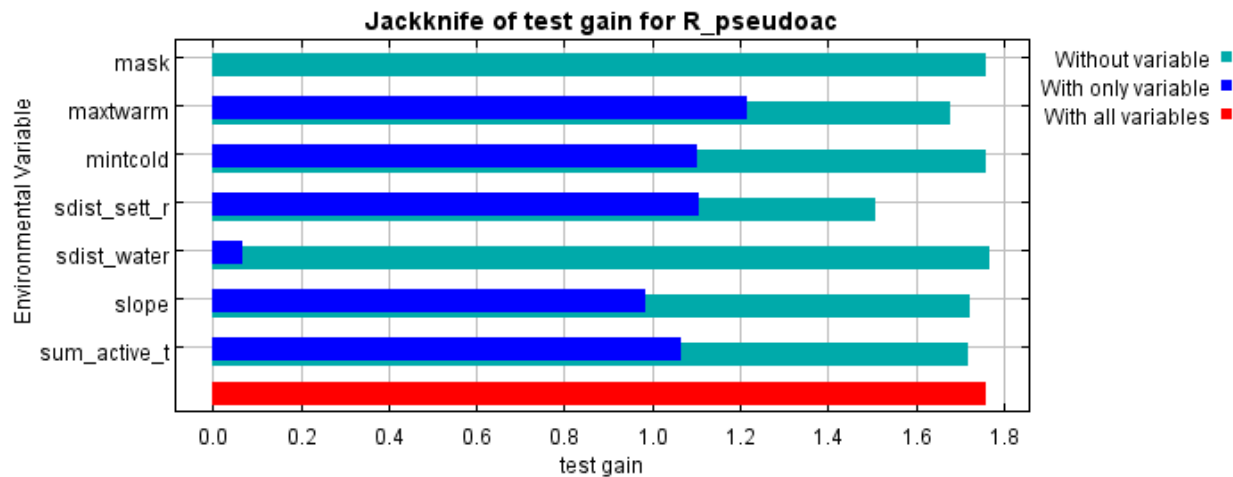
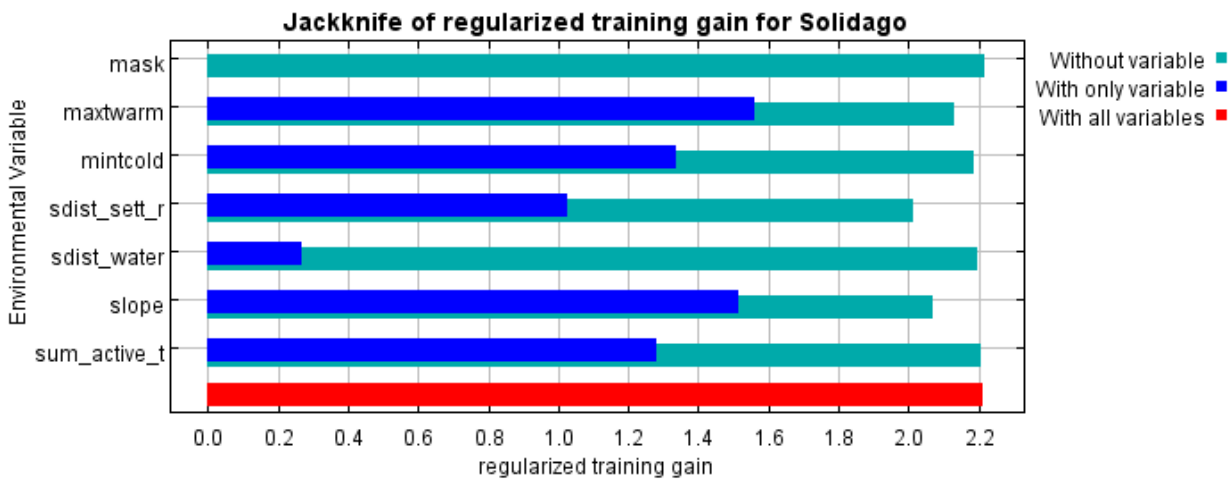| Variable	Percent contribution	Permutation importance
sdist_sett_r	43.2	47.8
maxtwarm	38.4	37.6
sum_active_t	8.1	4.4
mintcold	4.5	1.9
slope	4.2	5.2
sdist_water	1.7	3.1
mask	0	0

BIOMOD_GBM:

```
> summary(R.pseudoac_GBM_PA1)
                         var    rel.inf
maxtwarm            maxtwarm 51.194828
sdist_sett_r    sdist_sett_r 31.472221
sat                      sat  6.669064
mintcold            mintcold  4.864242
slope                  slope  3.824656
sdist_water      sdist_water  1.974991
```
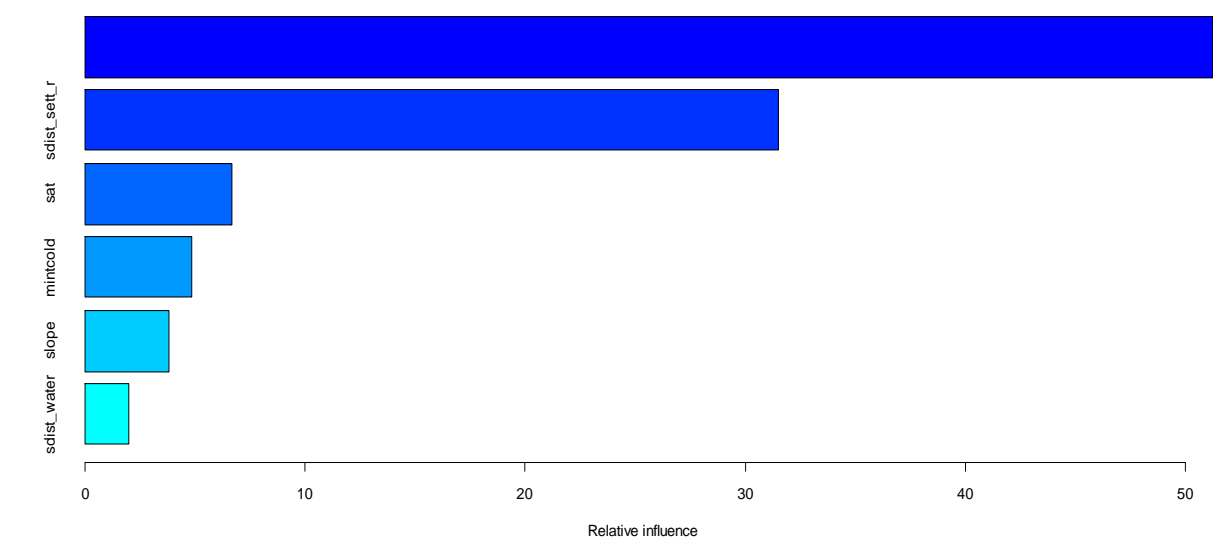
```
> VarImportance
$R.pseudoac
     slope sdist_sett_r sdist_water maxtwarm mintcold   sat
GAM  0.000        0.436       0.000    0.718    0.000 0.035
GBM  0.035        0.416       0.006    0.417    0.015 0.040
GLM  0.013        0.420       0.017    0.556    0.000 0.000
MARS 0.060        0.330       0.005    0.947    0.035 0.072
RF   0.068        0.250       0.041    0.393    0.113 0.120
```

Solidago spp. (*Solidago canadensis* L. and *Solidago gigantea* Aiton)

Maxent:

Appendix F: Variable Importance

Jackknife of test gain for Solidago
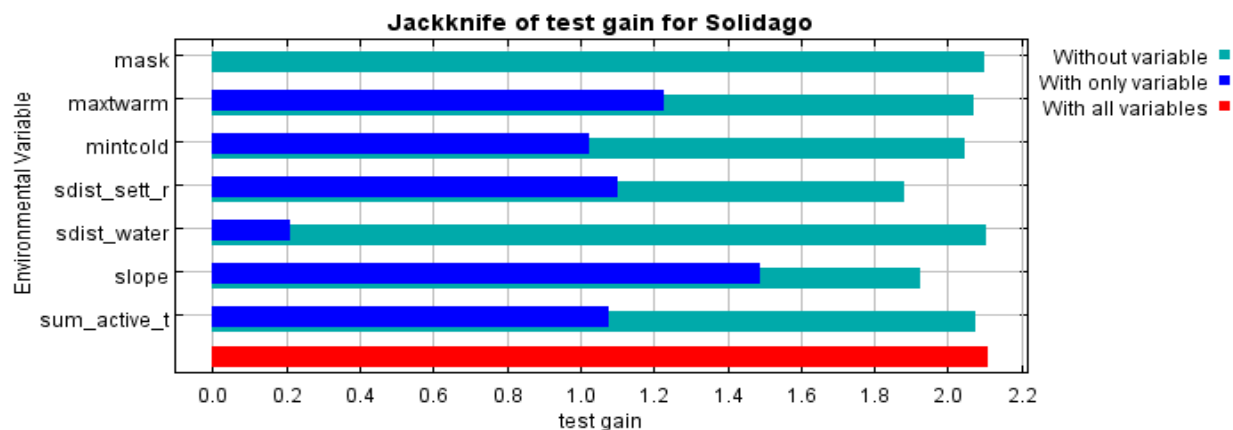
Variable	Percent contribution	Permutation importance
slope	38	16.9
maxtwarm	34.2	26
sdist_sett_r	21.5	52.2
mintcold	3	1.7
sdist_water	1.7	0.9
sum_active_t	1.6	2.3
mask	0	0

BIOMOD_GLM:

```
> Solidago_GLM_PA2$anova
Stepwise Model Path
Analysis of Deviance Table

Initial Model:
Solidago ~ 1

Final Model:
Solidago ~ poly(maxtwarm, 3) + poly(sdist_sett_r, 3) + slope +
    mintcold + sdist_water


                      Step Df   Deviance Resid. Df Resid. Dev      AIC
1                                        10329    914.9543 459.47714
2       + poly(maxtwarm, 3)   3 592.395059    10326    322.5592 168.56640
3 + poly(sdist_sett_r, 3)   3 139.947162    10323    182.6121  88.41225
4               + slope   1  21.364021    10322    161.2480  83.44058
5            + mintcold   1  15.190737    10321    146.0573  78.87650
6         + sdist_water   1   5.981819    10320    140.0755  77.10303
> VarImportance
$Solidago
      slope sdist_sett_r sdist_water maxtwarm mintcold    sat
GAM   0.185        0.484       0.000    0.773    0.131 0.000
GBM   0.150        0.345       0.005    0.647    0.009 0.008
GLM   0.129        0.475       0.026    0.812    0.177 0.000
MARS  0.203        0.077       0.000    0.854    0.049 0.221
RF    0.110        0.166       0.019    0.276    0.076 0.094
```
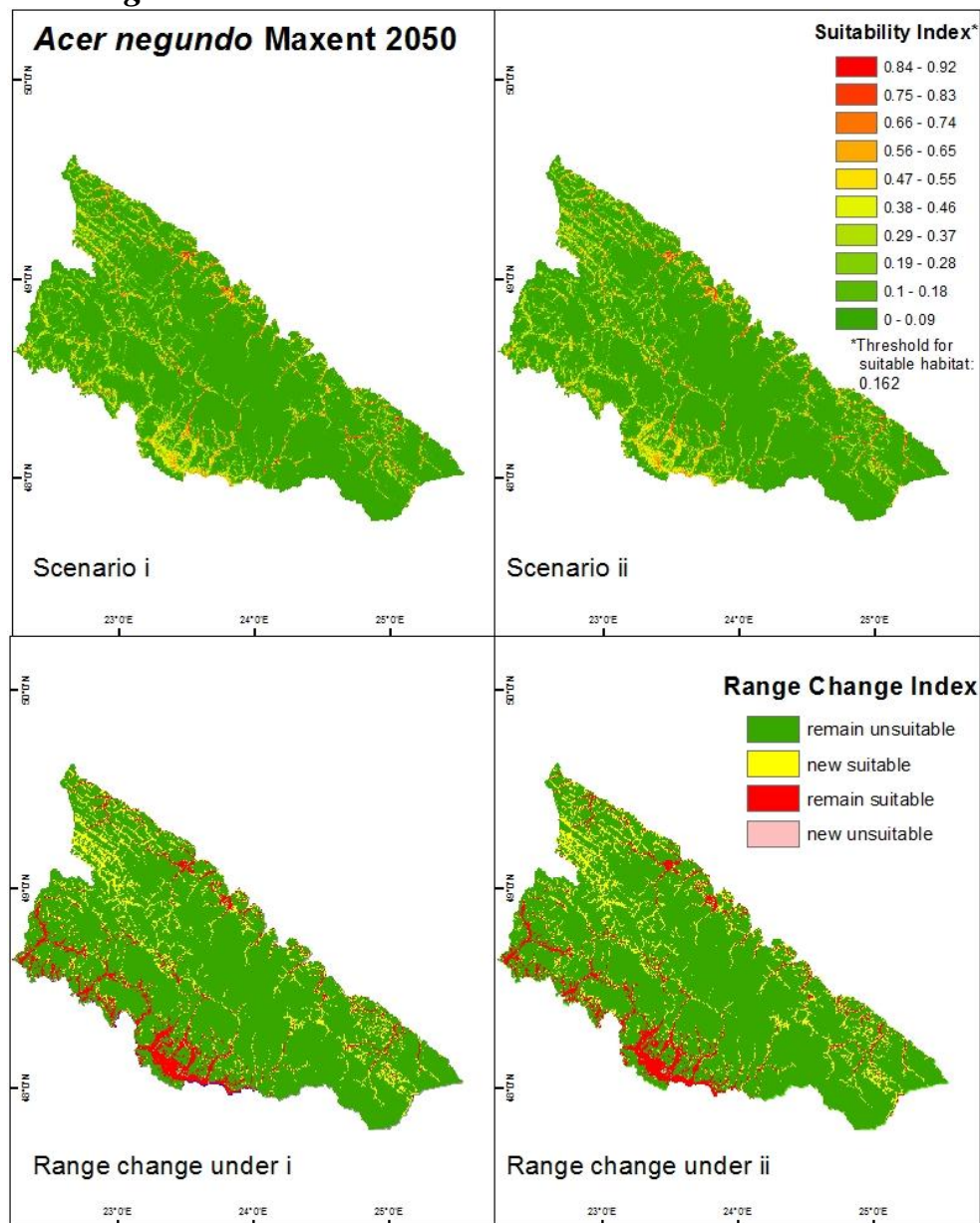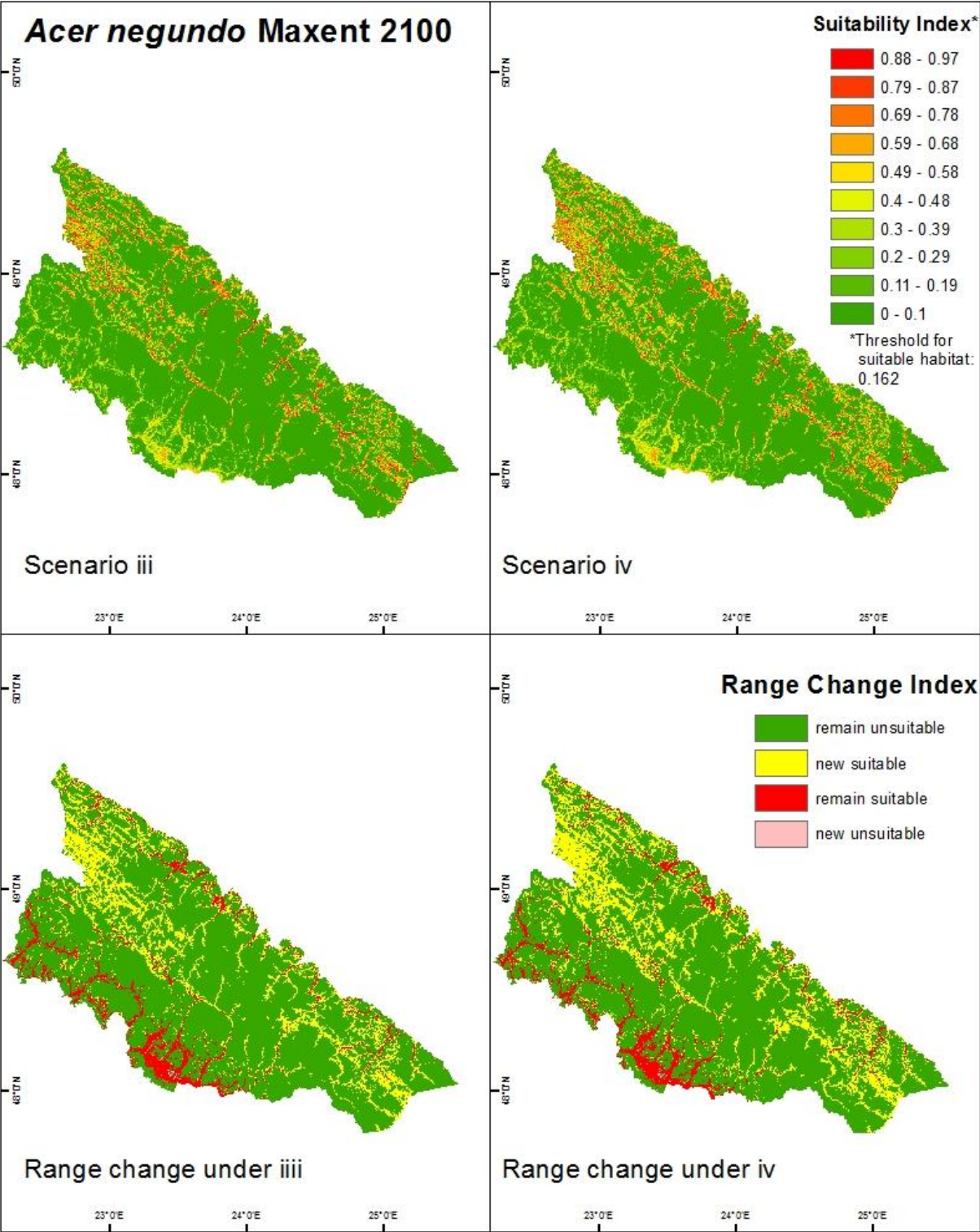
A54

References

Phillips, S.J. (2010). *A Brief Tutorial on Maxent.* AT&T Labs-Research: Princeton University, USA. Retrieved January 15, 2011 from http://www.cs.princeton.edu/~schapire/maxent/.

StatSoft, Inc. (2011). *Electronic Statistics Textbook*. StatSoft: Tulsa (OK), USA. Retrieved July 3, 2011 from http://www.statsoft.com/textbook/.

Thuiller, W., Lafourcade, B., Araujo, M.B. (2009). *ModOperating Manual for BIOMOD*. Université Joseph Fourier – Laboratoire d'Ecologie Alpine: Grenoble, France.

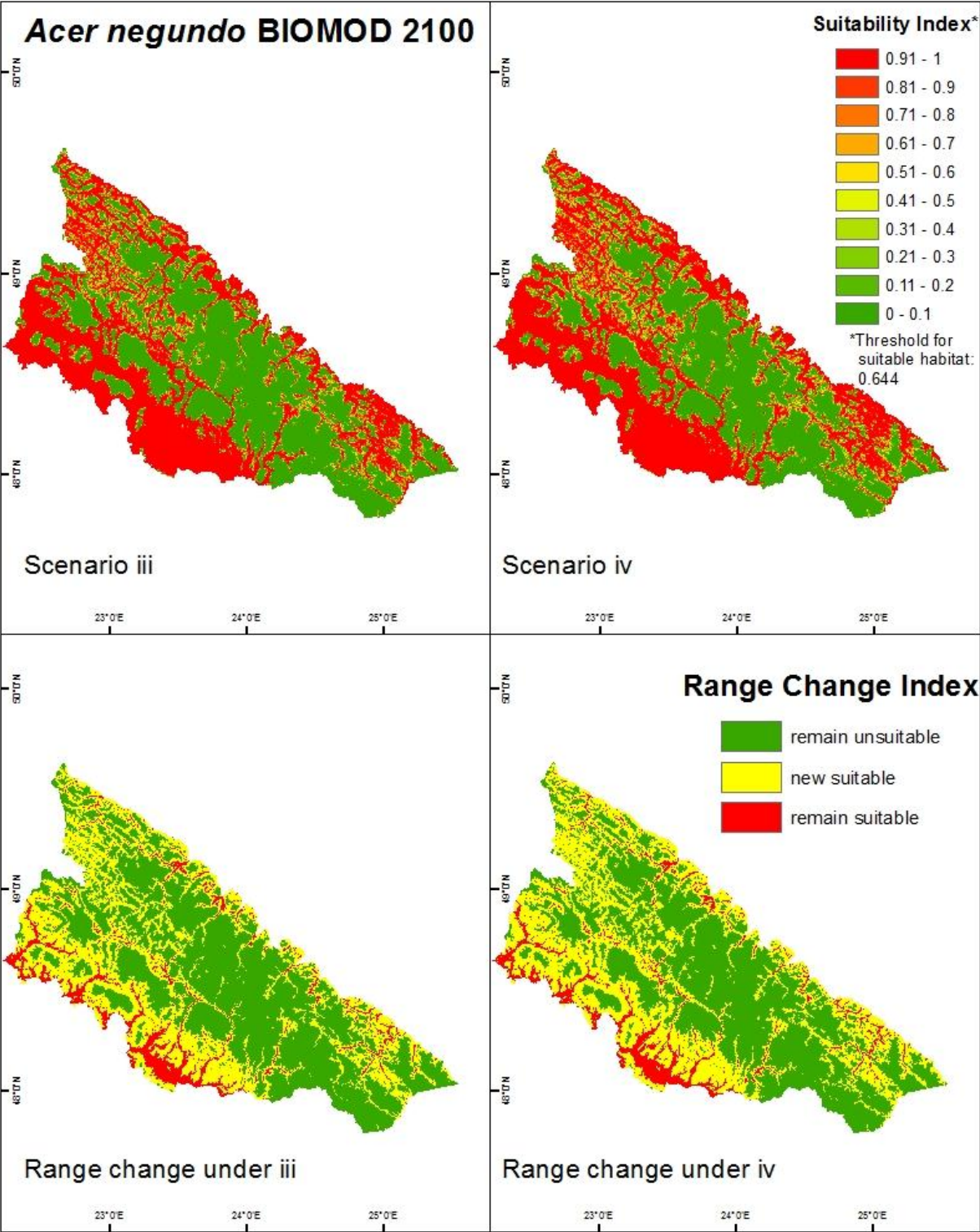## Appendix G: Projections for 2050 and 2100 Based on Four Change Scenarios

For each species, four sets of four maps are displayed, each set representing projections by Maxent or BIOMOD for 2050 and 2100. Within each set, the two upper maps display relative suitability of areas for establishment of species. The two lower maps display the range change between areas predicted as suitable under current conditions and under future scenarios (binary predictions are based on optimized threshold as indicated on the maps).
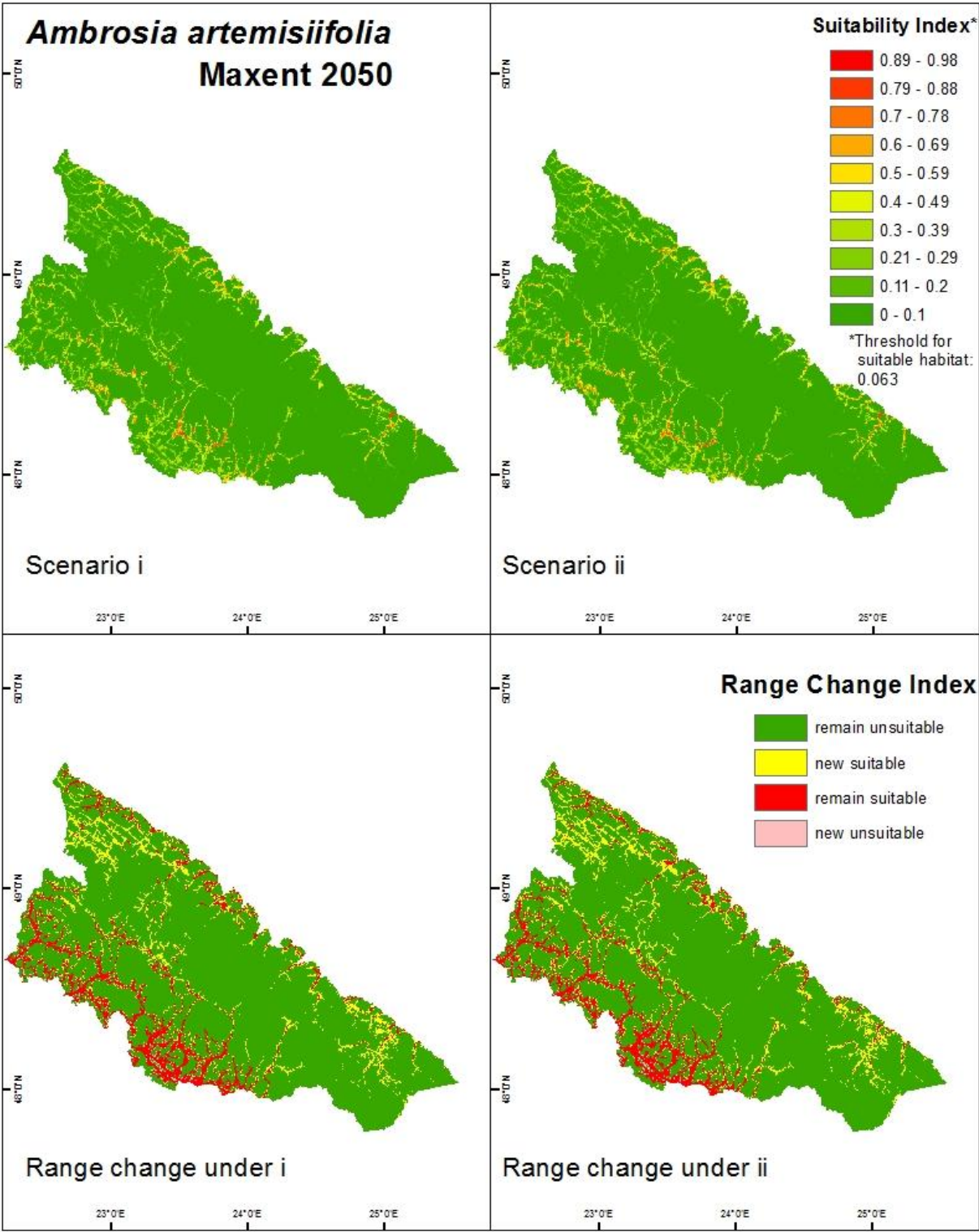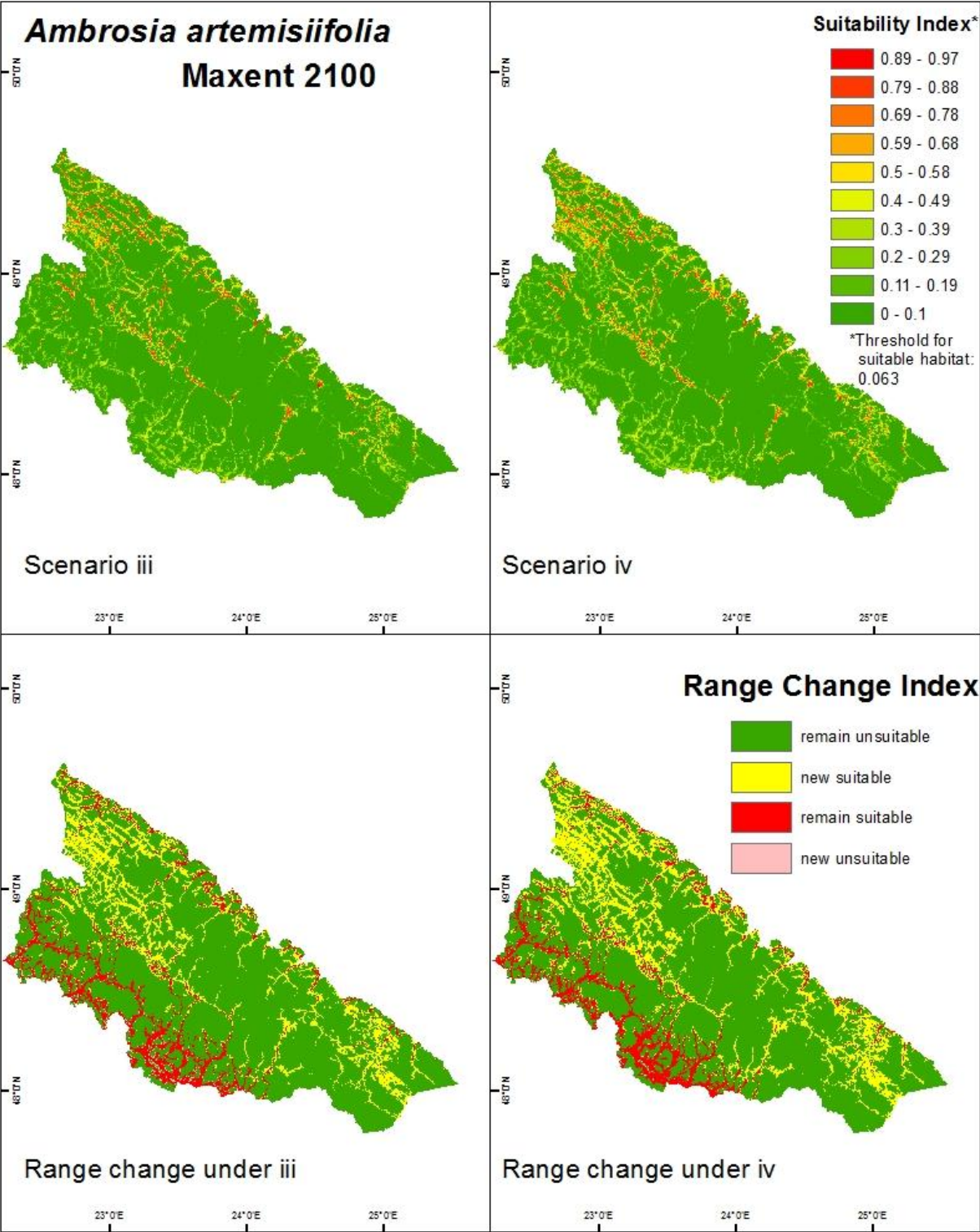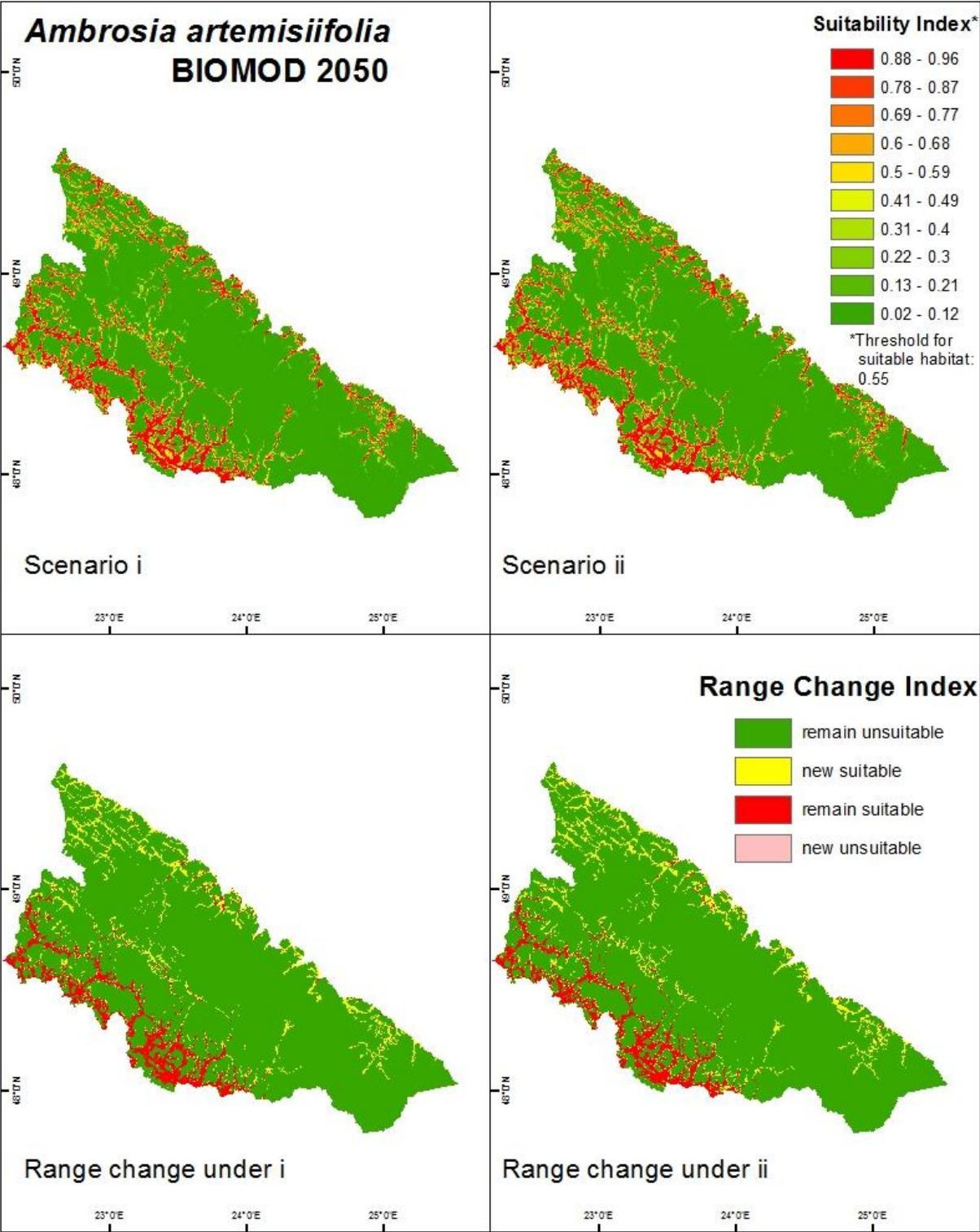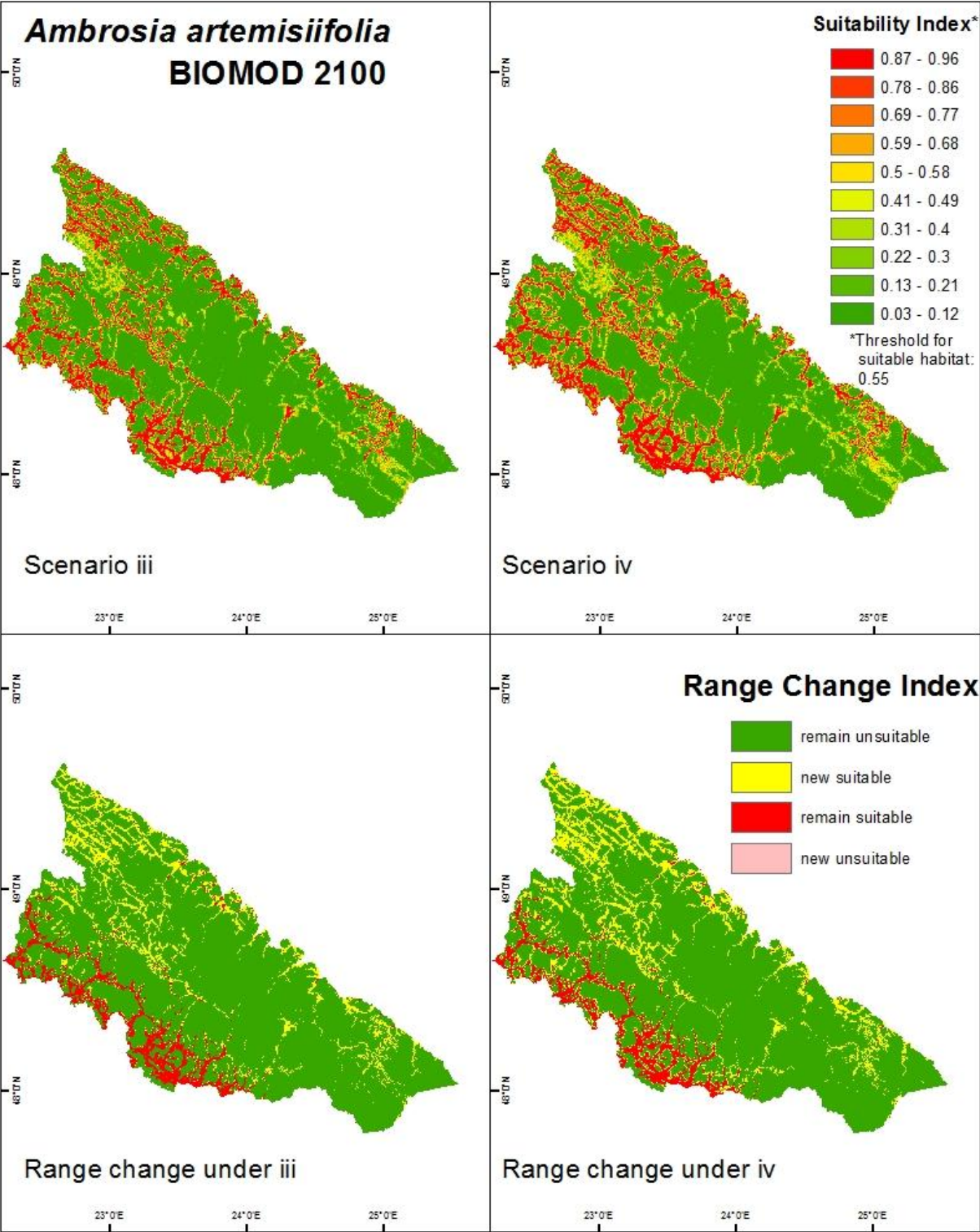
Acer negundo L.:

Acer negundo Maxent 2100

Suitability Index*

- 0.88 - 0.97
- 0.79 - 0.87
- 0.69 - 0.78
- 0.59 - 0.68
- 0.49 - 0.58
- 0.4 - 0.48
- 0.3 - 0.39
- 0.2 - 0.29
- 0.11 - 0.19
- 0 - 0.1

*Threshold for suitable habitat: 0.162

Scenario iii

Scenario iv

Range Change Index

- remain unsuitable
- new suitable
- remain suitable
- new unsuitable

Range change under iiii

Range change under iv

Acer negundo BIOMOD 2100

Scenario iii

Scenario iv

Suitability Index*

- 0.91 - 1
- 0.81 - 0.9
- 0.71 - 0.8
- 0.61 - 0.7
- 0.51 - 0.6
- 0.41 - 0.5
- 0.31 - 0.4
- 0.21 - 0.3
- 0.11 - 0.2
- 0 - 0.1

*Threshold for suitable habitat: 0.644

Range change under iii

Range change under iv

Range Change Index

- remain unsuitable
- new suitable
- remain suitable

Ambrosia artemisiifolia **L.:**

Ambrosia artemisiifolia BIOMOD 2100

Scenario iii

Scenario iv

Range change under iii

Range change under iv

Suitability Index*

- 0.87 - 0.96
- 0.78 - 0.86
- 0.69 - 0.77
- 0.59 - 0.68
- 0.5 - 0.58
- 0.41 - 0.49
- 0.31 - 0.4
- 0.22 - 0.3
- 0.13 - 0.21
- 0.03 - 0.12

*Threshold for suitable habitat: 0.55
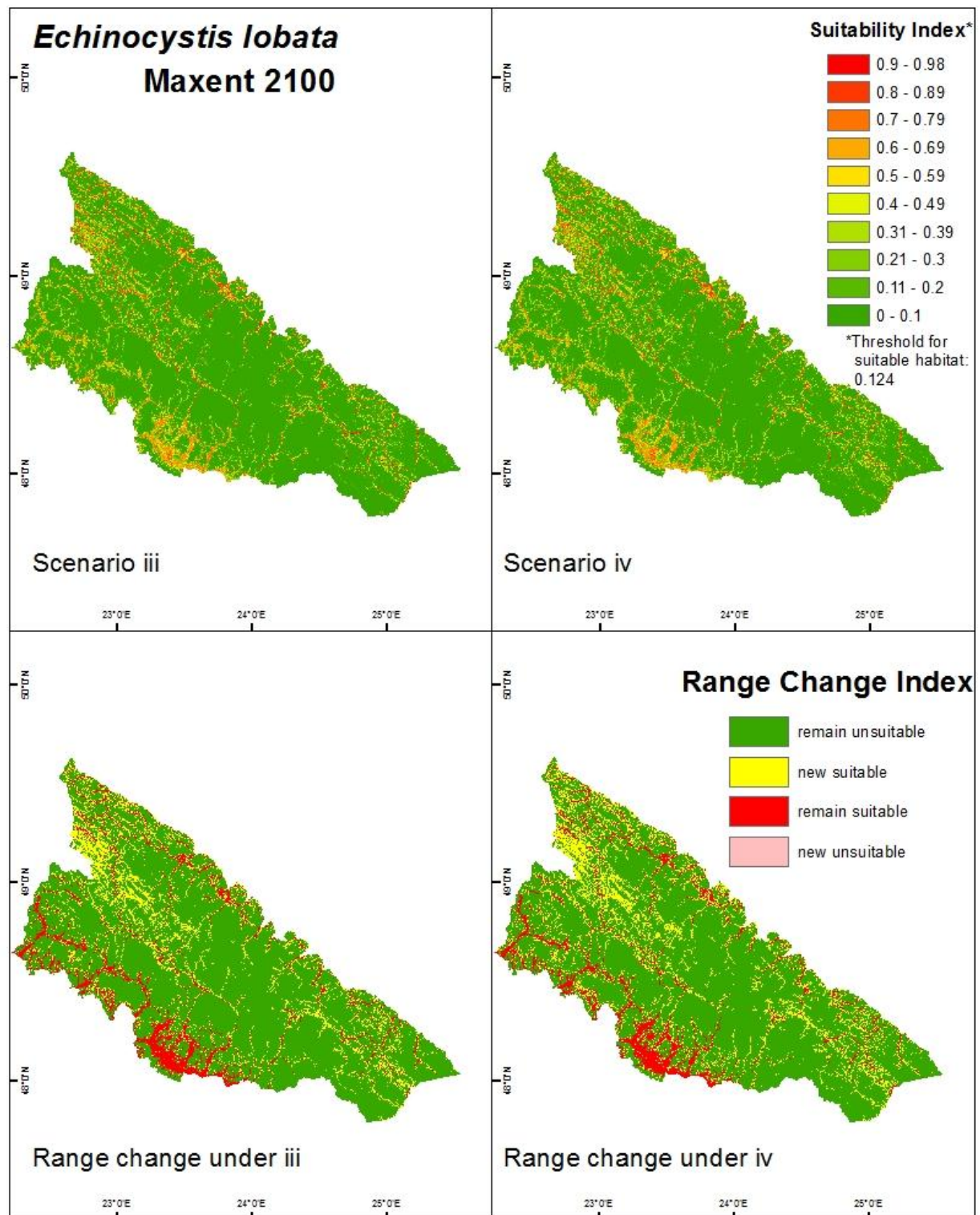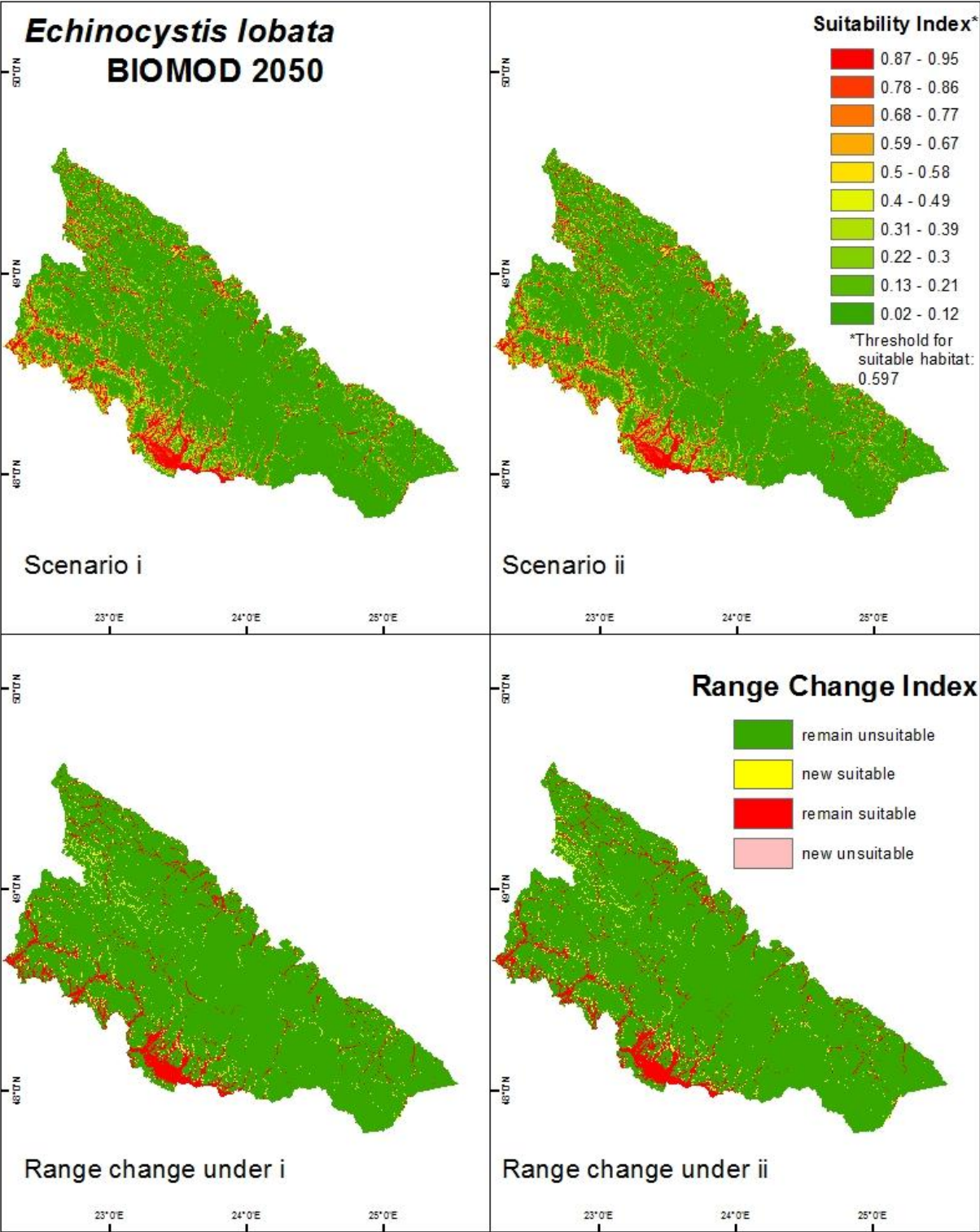
Range Change Index
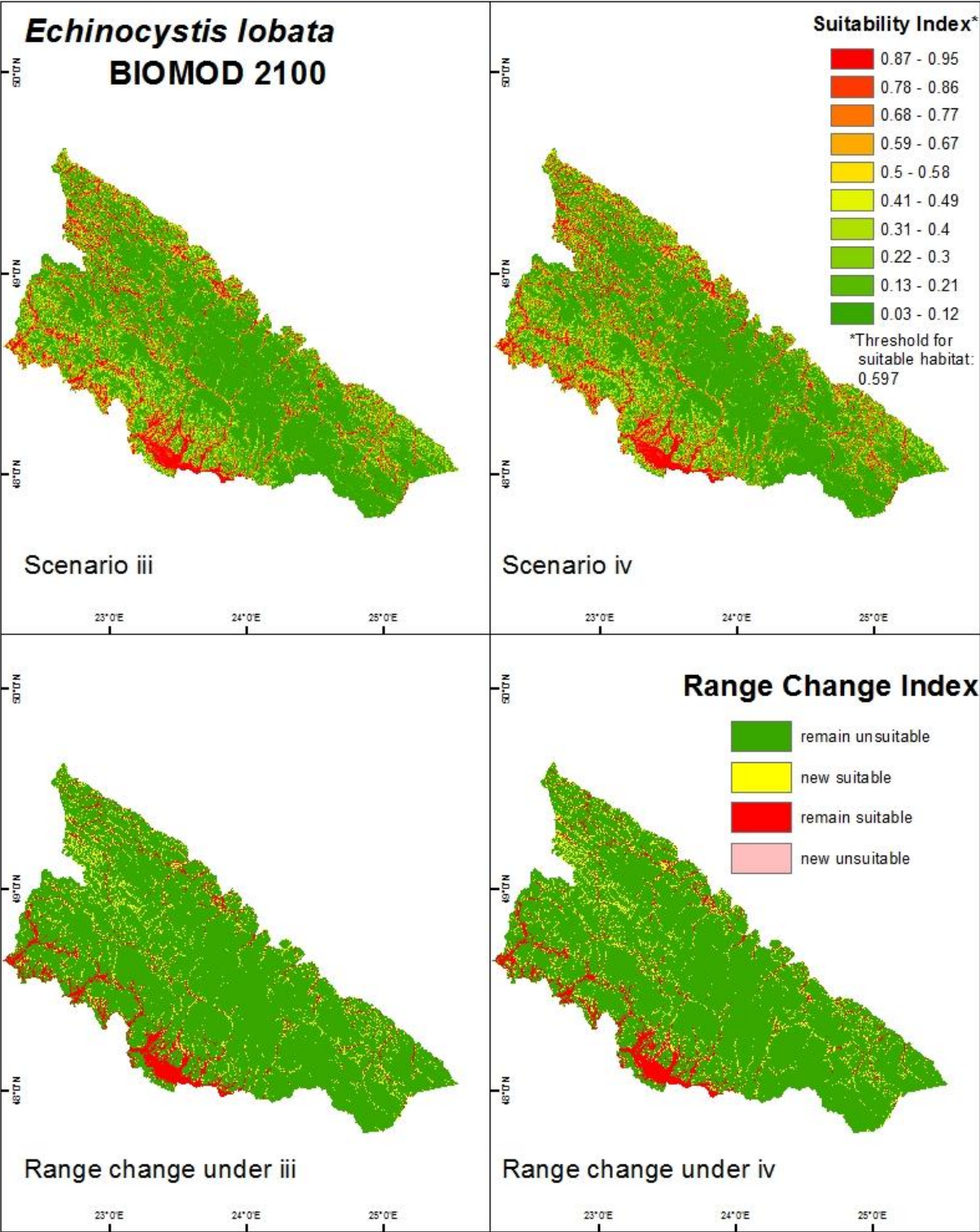
- remain unsuitable
- new suitable
- remain suitable
- new unsuitable

Echinocystis lobata (Michx.) Torr. & Grey:

Helianthus tuberosus **L.:**

Helianthus tuberosus Maxent 2100

Suitability Index*

■	0.86 - 0.95
■	0.77 - 0.85
■	0.67 - 0.76
■	0.58 - 0.66
■	0.48 - 0.57
■	0.39 - 0.47
■	0.29 - 0.38
■	0.2 - 0.28
■	0.1 - 0.19
■	0 - 0.09

*Threshold for suitable habitat: 0.111

Scenario iii

Scenario iv

Range Change Index

■	remain unsuitable
■	new suitable
■	remain suitable
■	new unsuitable

Range change under iii

Range change under iv

Helianthus tuberosus
BIOMOD 2050

Scenario i

Scenario ii

Suitability Index*

- 0.91 - 1
- 0.81 - 0.9
- 0.71 - 0.8
- 0.61 - 0.7
- 0.51 - 0.6
- 0.41 - 0.5
- 0.31 - 0.4
- 0.21 - 0.3
- 0.11 - 0.2
- 0 - 0.1

*Threshold for suitable habitat: 0.62

Range change under i

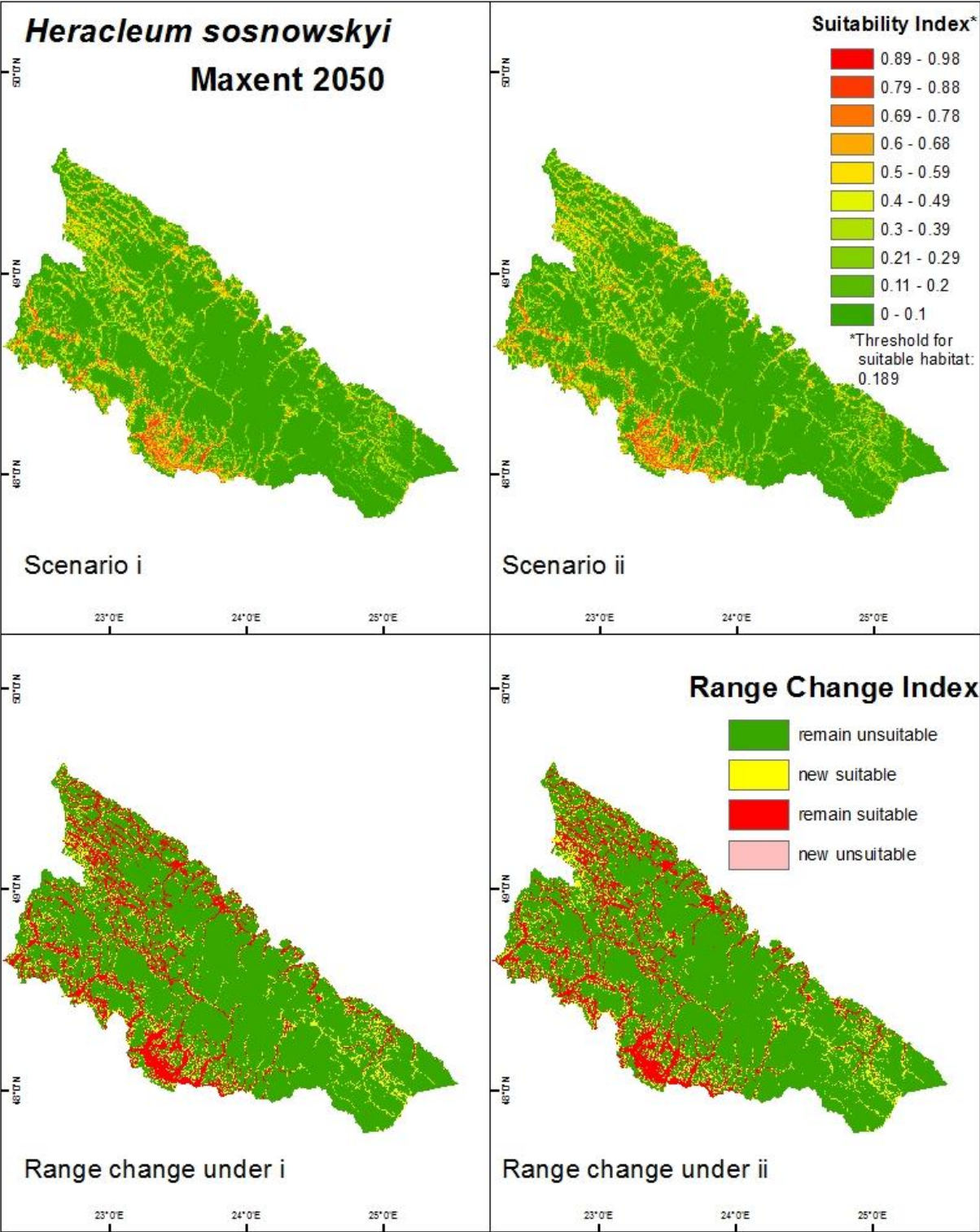Range change under ii
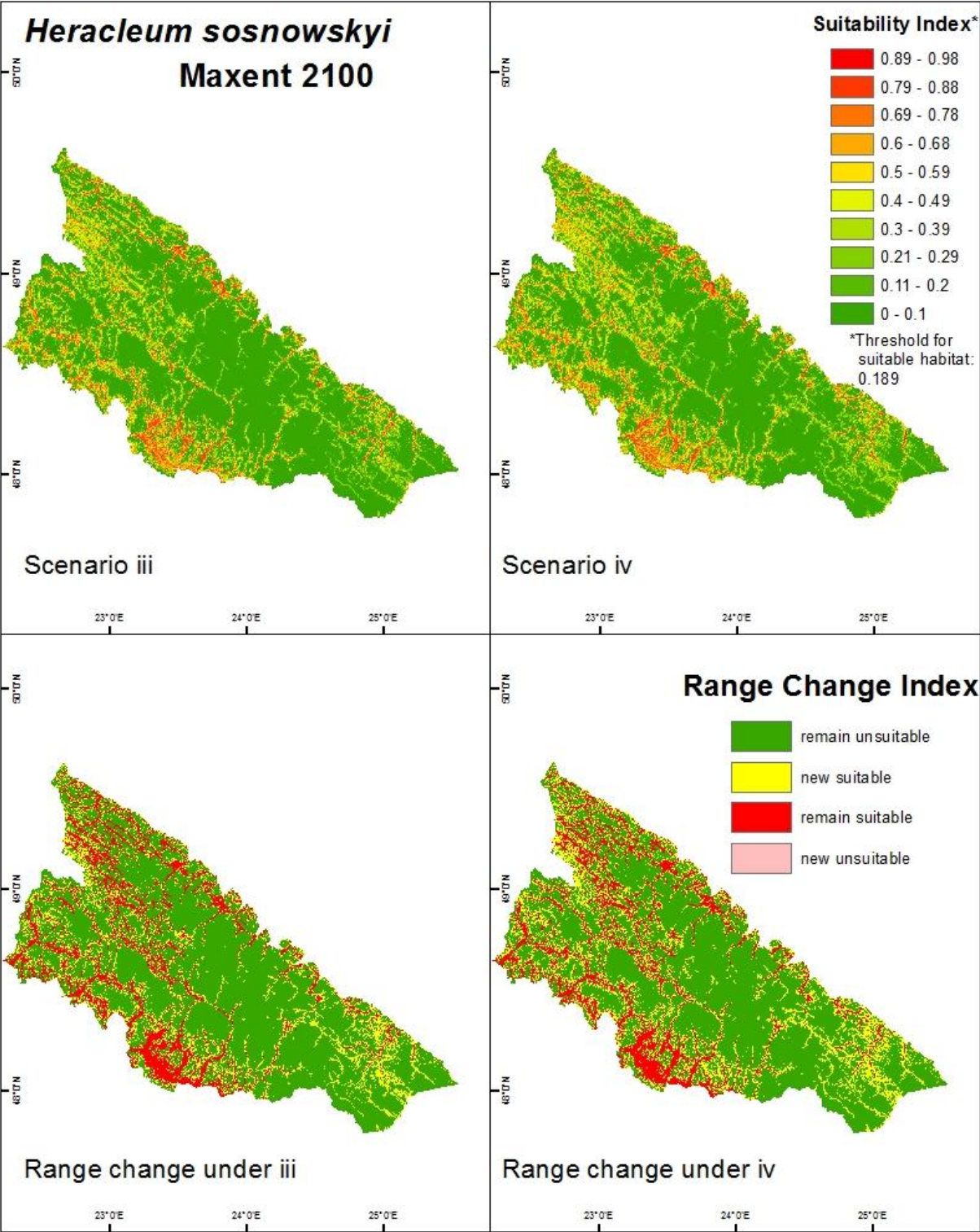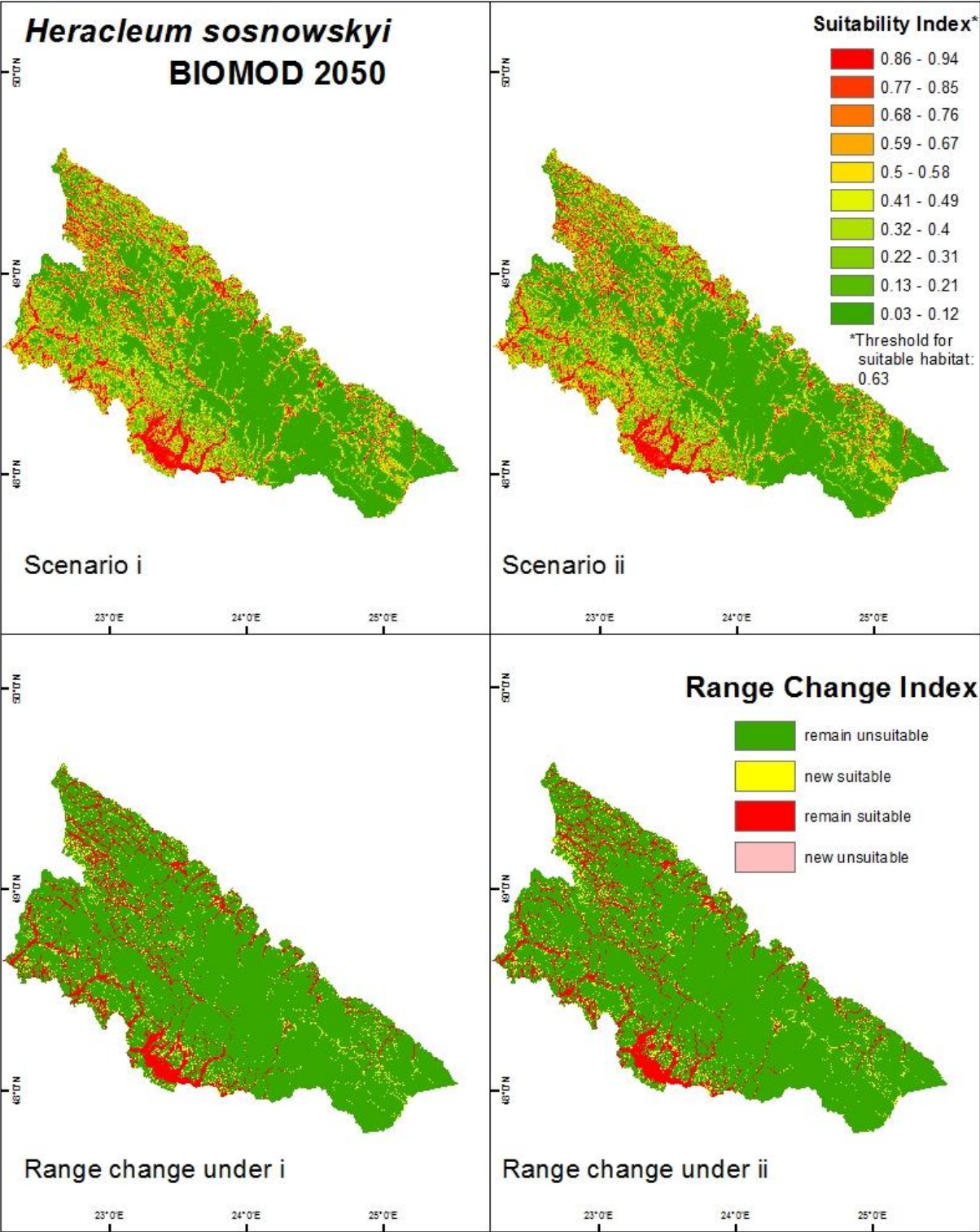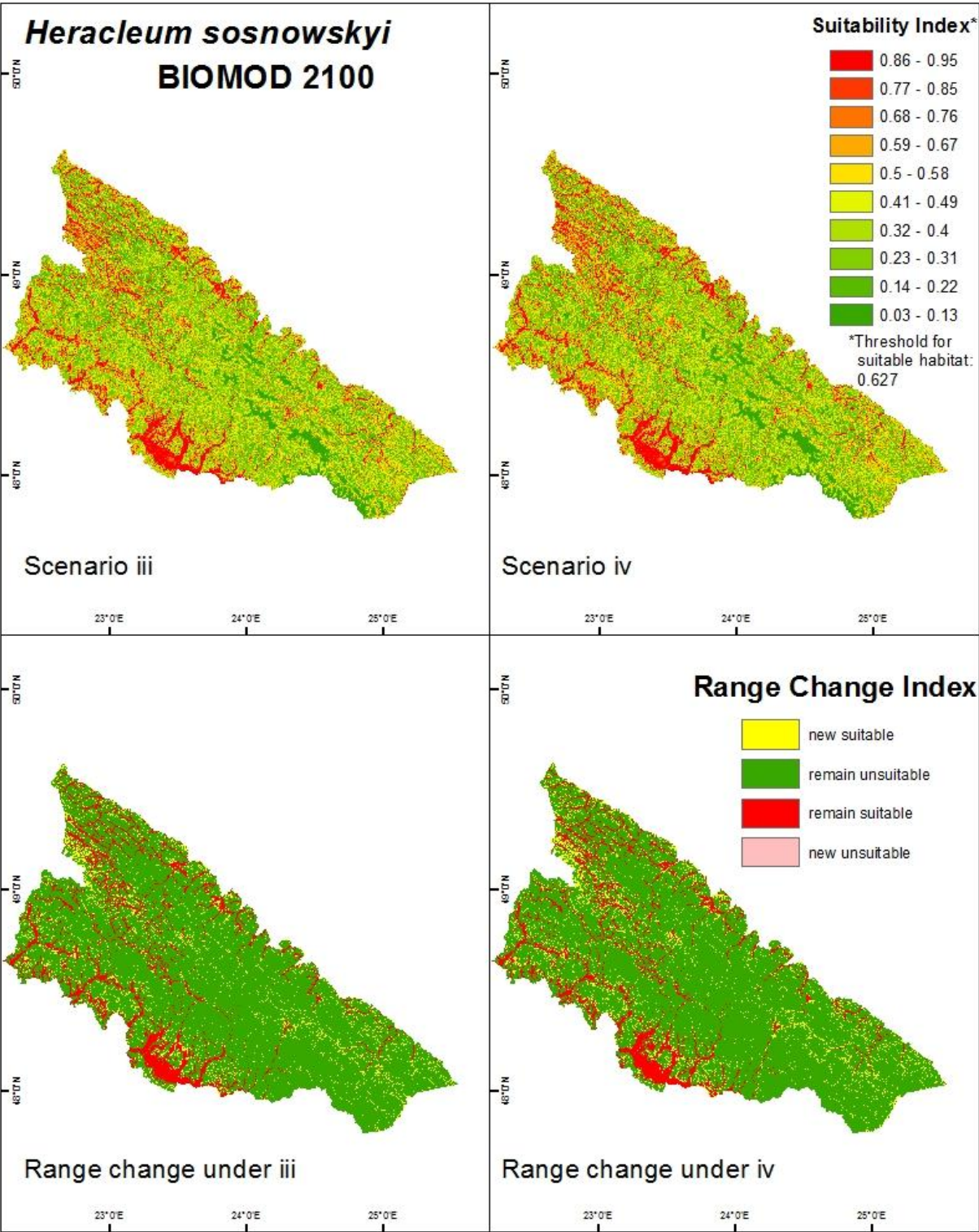
Range Change Index

- remain unsuitable
- new suitable
- remain suitable

Heracleum sosnowskyi **Manden:**

Heracleum sosnowskyi BIOMOD 2050

Scenario i

Scenario ii

Suitability Index*

- 0.86 - 0.94
- 0.77 - 0.85
- 0.68 - 0.76
- 0.59 - 0.67
- 0.5 - 0.58
- 0.41 - 0.49
- 0.32 - 0.4
- 0.22 - 0.31
- 0.13 - 0.21
- 0.03 - 0.12

*Threshold for suitable habitat: 0.63

Range change under i

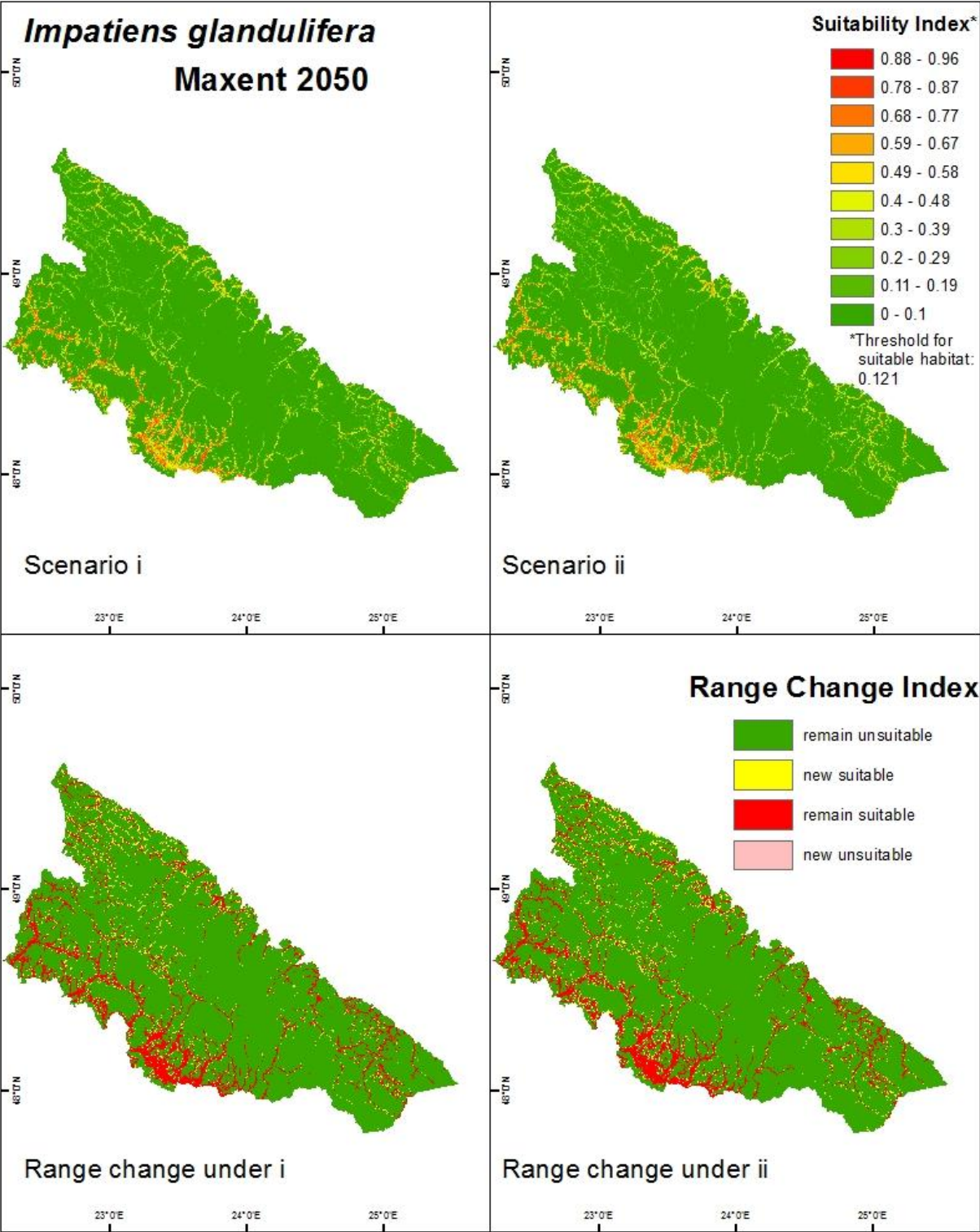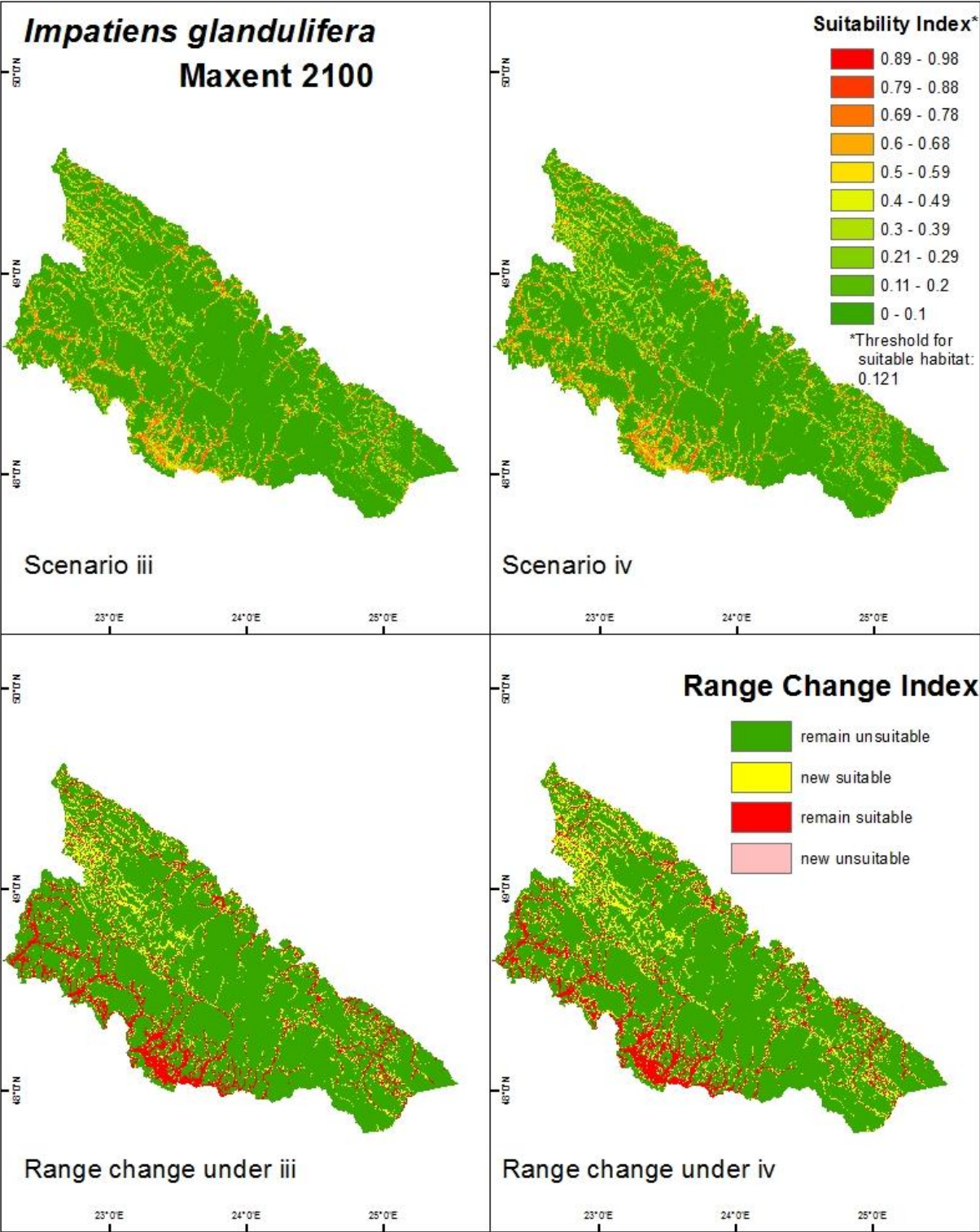Range change under ii
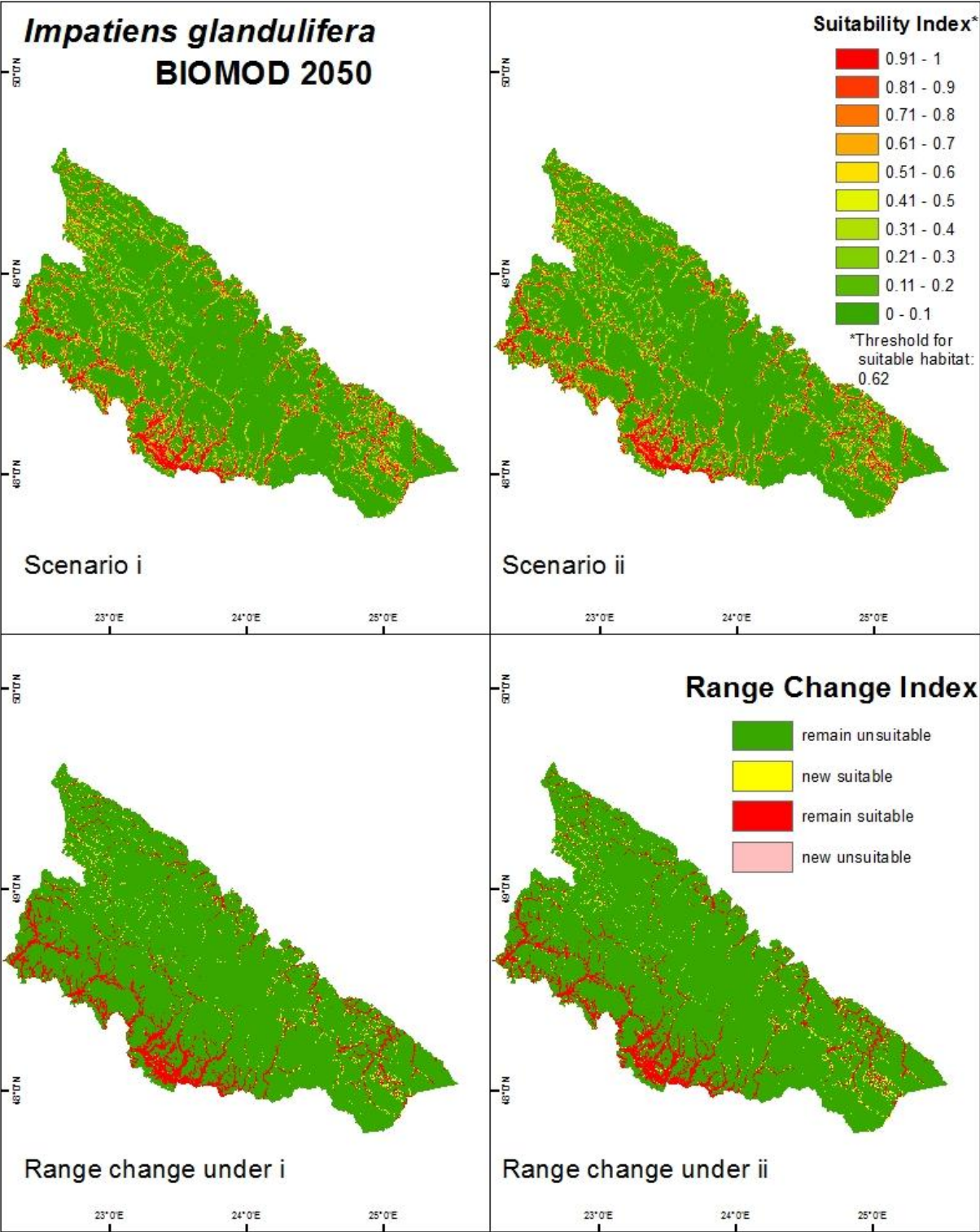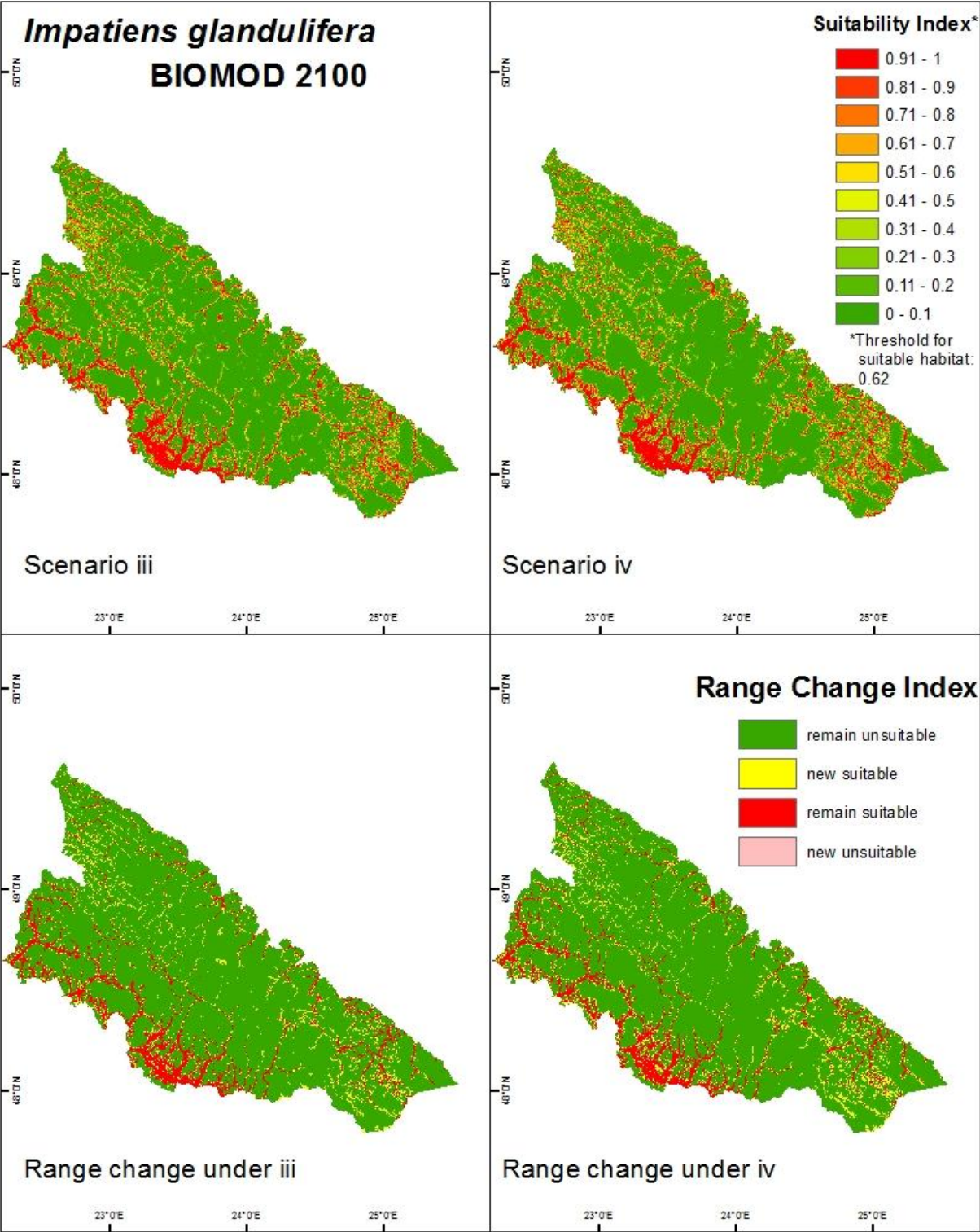
Range Change Index

- remain unsuitable
- new suitable
- remain suitable
- new unsuitable

Impatiens glandulifera **Royle:**

Impatiens glandulifera BIOMOD 2050

Scenario i

Scenario ii

Suitability Index*

- 0.91 - 1
- 0.81 - 0.9
- 0.71 - 0.8
- 0.61 - 0.7
- 0.51 - 0.6
- 0.41 - 0.5
- 0.31 - 0.4
- 0.21 - 0.3
- 0.11 - 0.2
- 0 - 0.1

*Threshold for suitable habitat: 0.62

Range change under i

Range change under ii

Range Change Index

- remain unsuitable
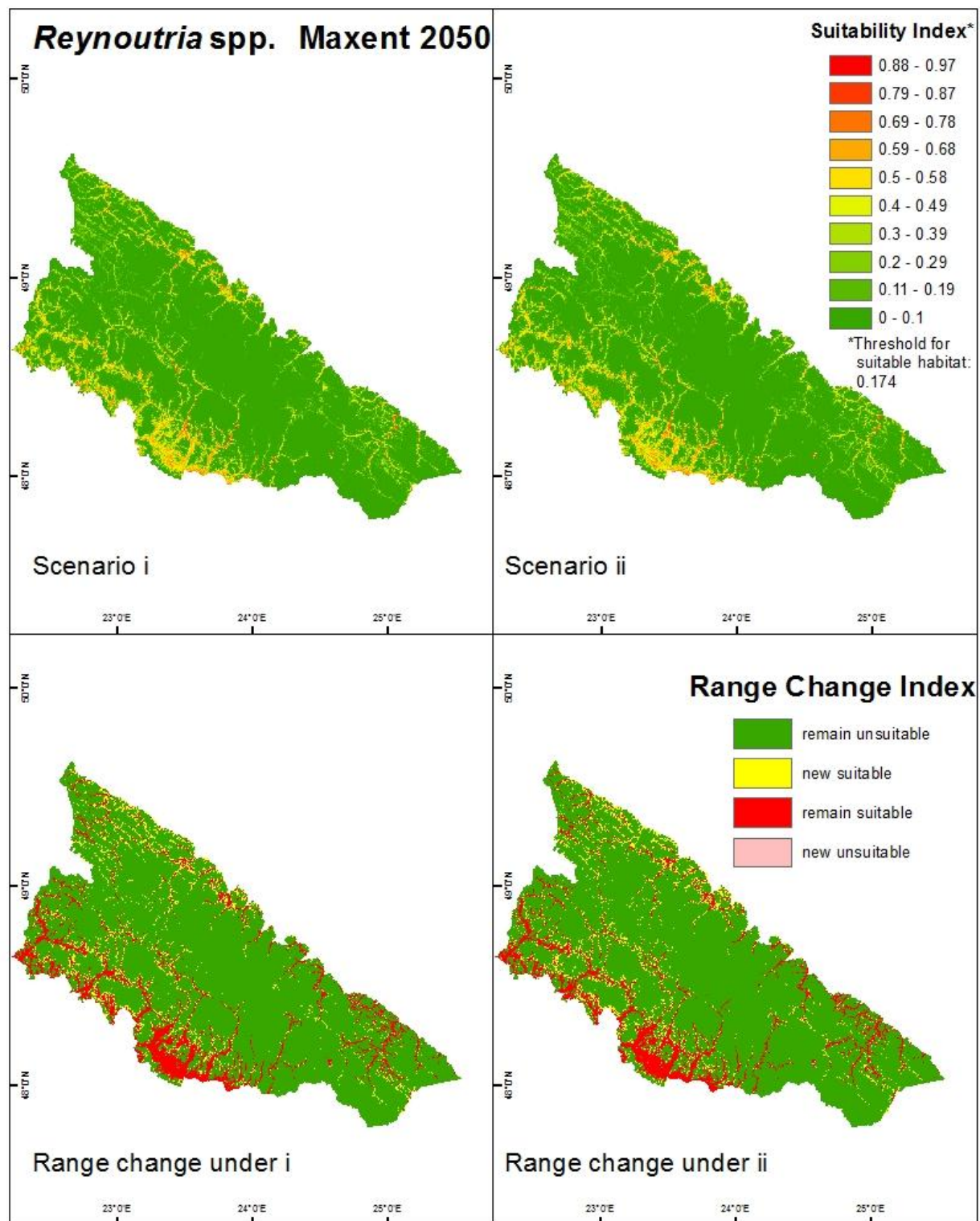- new suitable
- remain suitable
- new unsuitable

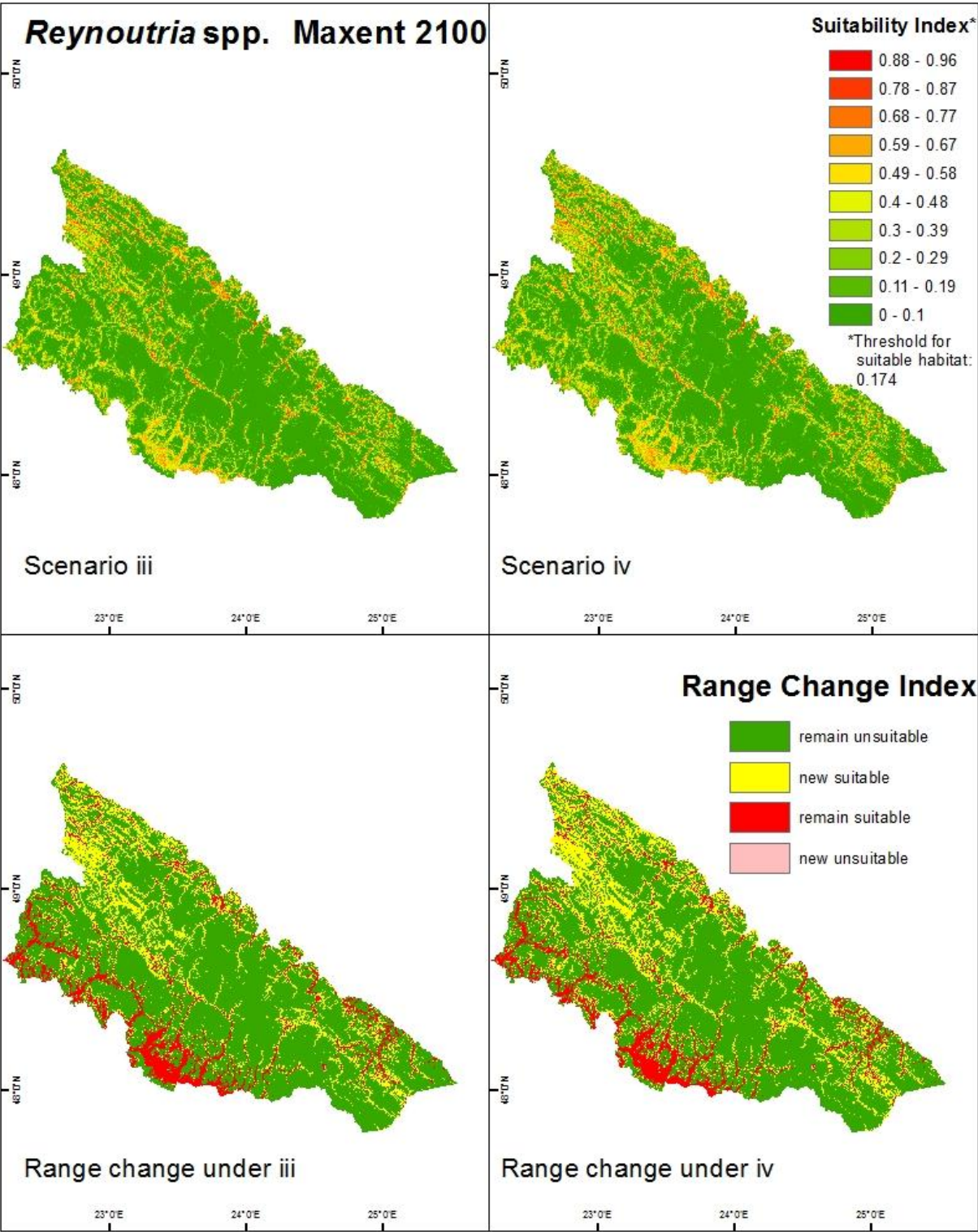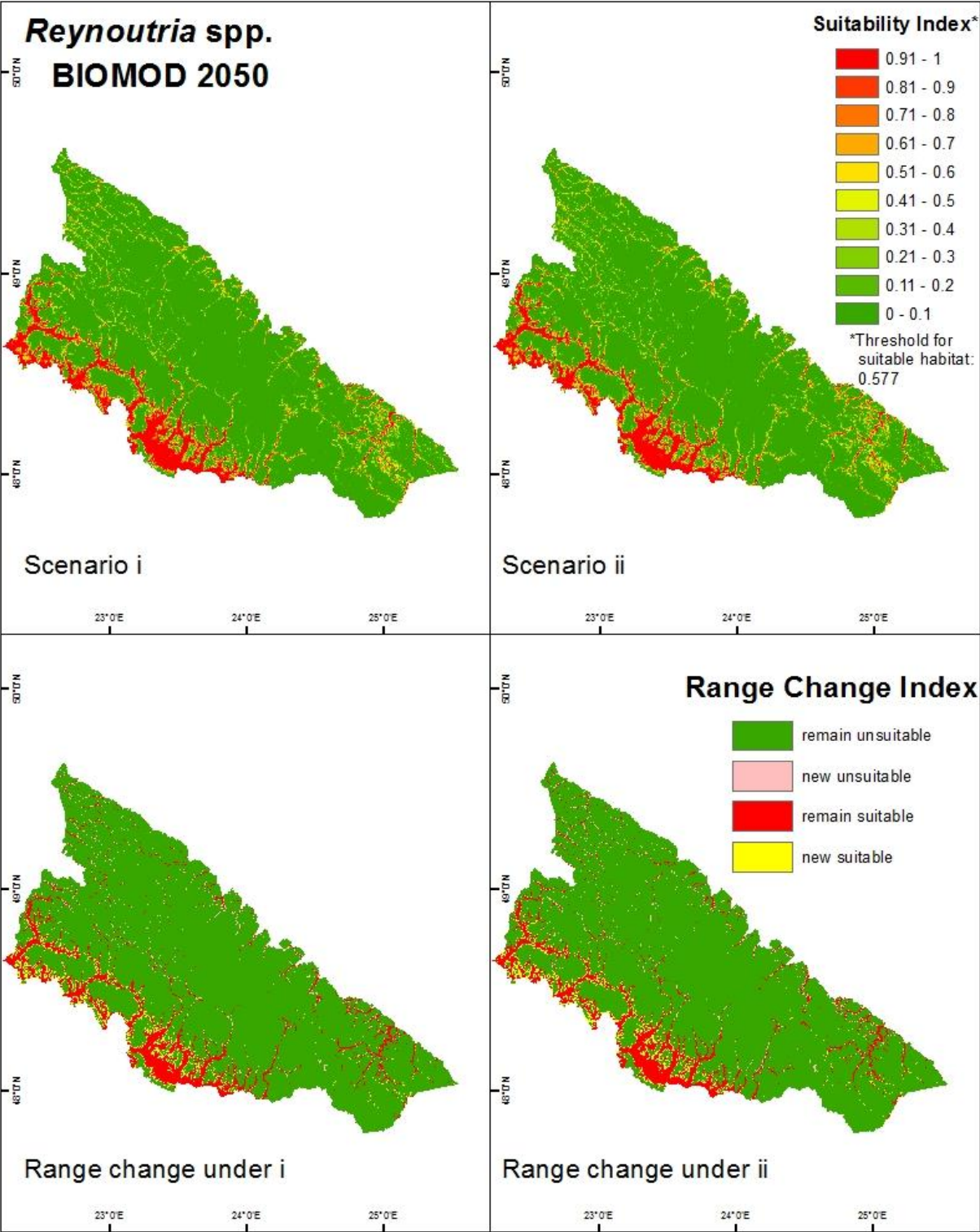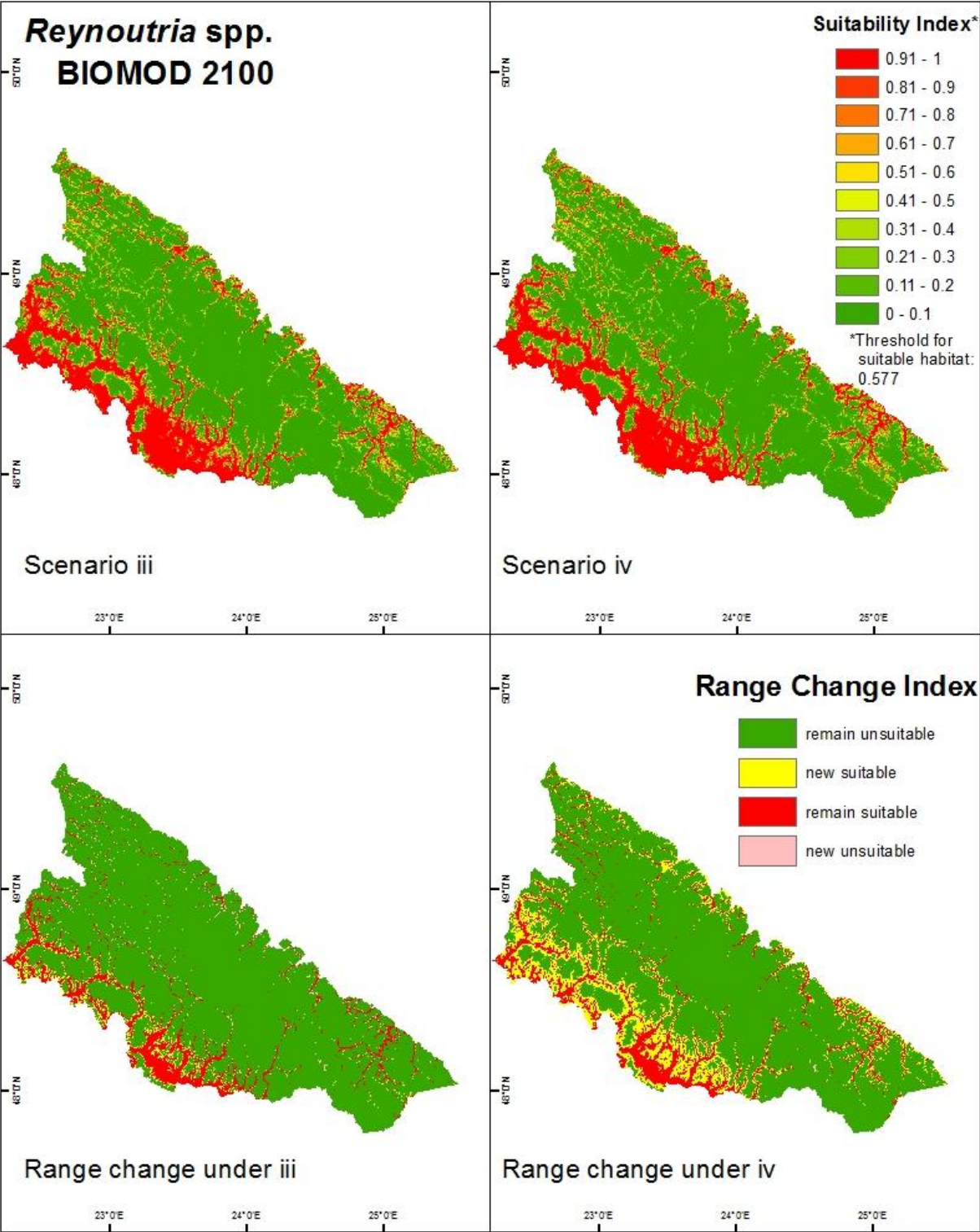## *Reynoutria* spp. - *Reynoutria japonica* Houtt. and *Reynoutria x bohemica* Chrtek.& Chrtková:

Reynoutria spp. BIOMOD 2050

Scenario i

Scenario ii

Suitability Index*
- 0.91 - 1
- 0.81 - 0.9
- 0.71 - 0.8
- 0.61 - 0.7
- 0.51 - 0.6
- 0.41 - 0.5
- 0.31 - 0.4
- 0.21 - 0.3
- 0.11 - 0.2
- 0 - 0.1

*Threshold for suitable habitat: 0.577

Range Change Index
- remain unsuitable
- new unsuitable
- remain suitable
- new suitable

Range change under i

Range change under ii

Robinia pseudoacacia **L.:**

Robinia pseudoacacia
Maxent 2100

Scenario iii

Scenario iv

Suitability Index*

- 0.91 - 1
- 0.81 - 0.9
- 0.71 - 0.8
- 0.61 - 0.7
- 0.51 - 0.6
- 0.41 - 0.5
- 0.31 - 0.4
- 0.21 - 0.3
- 0.11 - 0.2
- 0 - 0.1

*Threshold for suitable habitat: 0.156

Range change under iii

Range change under iv

Range Change Index

- remain unsuitable
- new suitable
- remain suitable
- new unsuitable

Robinia pseudoacacia BIOMOD 2100

Scenario iii

Scenario iv

Range change under iii

Range change under iv

Suitability Index*

	0.86 - 0.94
	0.77 - 0.85
	0.68 - 0.76
	0.59 - 0.67
	0.5 - 0.58
	0.41 - 0.49
	0.32 - 0.4
	0.23 - 0.31
	0.13 - 0.22
	0.03 - 0.12

*Threshold for suitable habitat: 0.585

Range Change Index

new suitable
remain unsuitable
remain suitable
new unsuitable

Solidago **spp. -** *Solidago canadensis* **L. and** *Solidago gigantea* **Aiton:**