

## Projecting trends in plant invasions in Europe under different scenarios of future land-use change

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## ABSTRACT

**Aim** Recent studies of plant invasions in habitat types across different climatic regions of Europe have made it possible to produce a European map of plant invasions. Parallel research led to the formulation of integrated scenarios of future socio-economic development, which were used to create spatially explicit scenarios of European land-use change for the 21st century. Here we integrate these two research lines and produce the first spatially explicit projections of plant invasions in Europe for the years 2020, 2050 and 2080.

**Location** The European Union (except Bulgaria and Romania), Norway and Switzerland.

**Methods** We used vegetation plots from southern, central and north-western Europe to quantify mean levels of invasion by neophytes (post-1500 alien plants) for forest, grassland, urban, arable and abandoned land. We projected these values on the land-use scenarios for 2020, 2050 and 2080, and constructed maps of future plant invasions under three socio-economic scenarios assuming: (1) deregulation and globalization, (2) continuation of current policies with standing regulations, and (3) a shift towards sustainable development.

**Results** Under all scenarios an increase in the level of invasion was projected for north-western and northern Europe, and under the first two scenarios a decrease for some agricultural areas of eastern Europe where abandonment of agricultural land is expected. A net increase in the level of invasion over Europe was projected under scenarios 2 and 3.

**Main conclusions** The polarization between more and less invaded regions is likely to increase if future policies are oriented on economic deregulation, which may result in serious future problems in some areas of Europe. However, an implementation of sustainability policies would not automatically restrict the spread of alien plants. Therefore invasions require specific policy approaches beyond the more general ones, which are currently on the policy agenda and were tested in the scenarios.

## **Keywords**

ALARM scenarios, alien plants, biological invasions, environmental change, habitat types, neophytes, non-native species, risk assessment.

## INTRODUCTION

Human-mediated spread of alien species is a significant component of global environmental change (Vitousek, 1994; Sala et al., 2000; Millennium Ecosystem Assessment, 2005) with serious impacts on biodiversity, economy and human health (Mack et al., 2000; Perrings et al., 2010; Vilà et al., 2010). Invasions are closely associated with other components of global change such as climate change, elevated atmospheric CO<sub>2</sub> concentrations, land eutrophication or land-use change (Vilà et al., 2006; Walther et al., 2009). However, the use of habitat types or landuse categories for invasion risk assessment has scarcely been explored in spite of the fact that species spread is largely determined by other components of global change beyond climate (Ibáñez et al., 2008). Recent studies of plant invasions performed at a regional scale but with fine spatial resolution (within areas  $< 1000 \text{ m}^2$ ) revealed that the proportion of the number of aliens to all plant species is mainly determined by habitat types and much less so by the direct effect of climate, although climate does play a role in fine-tuning the habitatrelated patterns (Chytrý et al., 2008a). This suggests that future regional trends in alien plant invasions will be mainly driven by land-use changes, which are associated with alterations of habitat types, disturbance regimes and rapid changes of species composition (Hobbs, 2000).

European studies focusing on the relationship between habitat types and the level of plant invasion (i.e. the number or proportion of species that are aliens; Lonsdale, 1999; Richardson & Pyšek, 2006; Chytrý *et al.*, 2008a) revealed that the same habitat types contain similar proportions of alien plant species in oceanic, subcontinental and Mediterranean regions (Chytrý *et al.*, 2008b). This remarkable consistency within habitats across regions made it possible to project data for the mean levels of plant invasion in a range of European habitats on land-cover maps and produce the first European map of the level of invasion by alien vascular plants (Chytrý *et al.*, 2009a). However, the development of effective strategies for the management of alien plant species requires additional information on possible future trends.

Recently developed scenarios of future land-use change for Europe (Reginster *et al.*, 2010) provide a suitable platform for projecting spatially explicit trends in future levels of plant invasion. These land-use scenarios were generated by models that used input parameters from three storylines, i.e. qualitative and partly semi-quantitative descriptions of possible futures, resulting from an analysis of socio-economic processes (Spangenberg, 2007; Spangenberg *et al.*, 2012). At the same time, these models were linked to other models based on the same storylines (i.e. having the same assumptions), which made it possible to assess the effect of future global trade and climate change on European land use.

In this paper, we link the two previously separated research lines, one on plant invasions in different habitats and the other on scenarios of future land-use changes. For the first time, we: (1) develop maps of possible future patterns of alien plant invasions across Europe for three socio-economic scenarios representing different emphases on economic growth, and (2) assess and compare the levels of invasions and their geographical pattern under these scenarios to find out how they are likely to translate into future problems with invasive alien plants in Europe.

#### MATERIALS AND METHODS

#### **ALARM** scenarios

In this study we use recently developed spatially explicit scenarios of future land use in Europe for the years 2020, 2050 and 2080 (Reginster *et al.*, 2010) to project possible future trends in the level of plant invasion across the continent. These scenarios were developed within the EU project ALARM ('Assessing largescale risks for biodiversity with tested methods'; Settele *et al.*, 2005) as a result of combined qualitative and semi-quantitative analyses of possible futures with model runs.

The first part of the scenario development was a formulation of storylines (or narratives; Alcamo, 2001). Three core storylines were developed within ALARM, describing three internally consistent alternative scenarios of future socio-economic development, which reflect different policy options currently being discussed in the European Union (Spangenberg *et al.*, 2012). As these scenarios involved a large number of assumptions, they were developed in two steps. First, the overall policy trajectories were defined and checked with current decision-makers to see if these were relevant from their point of view. Then the policies expected in different policy fields (based on, e.g., the EU Lisbon Strategy, the EU Sustainable Development Strategy and the Biodiversity Action Plan) were formulated and discussed again with decision-makers regarding their comprehensiveness, plausibility and coherence.

It is important to note that scenarios are not predictions, because the future cannot be predicted. Neither is it possible to calculate the probability of realization of alternative scenarios or to validate the scenarios before the future happens. Scenarios simply illustrate possible future situations by making assumptions and examining what would happen if they turn out to be correct (Alcamo, 2001; van der Sluijs, 2002).

The three core ALARM scenarios, described in the storylines (Spangenberg *et al.*, 2012), are the following:

1. GRAS: the 'growth applied strategy' scenario supposes that economic and political paradigms of deregulation and globalization will mainly determine future decision-making, whereas biodiversity and sustainability policies will have little effect on the decisions. Environmental policies will focus on damage repair and limited prevention. The European Spatial Development Perspective (ESDP) will not be applied, which will result in expansion of urban areas. Subsidies provided as a part of the Common Agricultural Policy (CAP) will be removed and arable land will only be maintained in areas where it is profitable. Current protected areas will be preserved, but the Natura 2000 network will not be enforced.

2. BAMBU: the 'business-as-might-be-usual' scenario is based on the assumption that current policy trajectories (including regulations) will be implemented by the EU member states. Environmental policy will include mitigation of climate change and adaptation measures. ESDP will be applied, and consequently peri-urbanization in rural areas will be limited. The CAP will be maintained, but overproduction will be avoided. Agriculture will be supported in areas where it is profitable and to some extent in other traditional rural areas ('disadvantaged areas' in EU parlance). The Natura 2000 network will be enforced.

**3.** SEDG: the 'sustainable European development goal' scenario combines what is considered necessary from a sustainability and biodiversity point of view, and desirable from a social and political perspective. It aims at a competitive economy, a healthy environment and international cooperation. Urban sprawl will be restricted, extensive agricultural management and organic farming will be supported, and agriculture will be maintained across the landscape by subsidising it in less productive areas. The Natura 2000 network will be extended and enforced.

#### Land-use projections

For each of the three ALARM scenarios (described in the storylines), each of the three target years (2020, 2050 and 2080) and for baseline data, which correspond to the situation in the year 2000, proportions of land-use categories were projected in grid cells of  $10' \times 10'$  (roughly 12 km × 18 km in central Europe) in the countries of the European Union plus Norway and Switzerland. Romania and Bulgaria were not considered because they joined the European Union after the completion of the modelling project. This modelling was performed using MOLUSC ('model of land-use scenarios'), an automated generator of land-use scenarios (Reginster et al., 2010). The model input parameters were set based on the interpretation of the three storylines. MOLUSC was linked with a global macroeconomic model (GINFORS; Stocker et al., 2012) and a global ecosystem model (LPJmL; Bondeau et al., 2007). In such a way, the landuse scenarios included the effects of global socio-economic factors, e.g. world population and international trade, on the future socio-economic situation in Europe (summarized in GINFORS), and the effects of climate change on European agriculture (summarized in LPJmL), all based on the same assumptions.

Nine land-use categories were distinguished in MOLUSC: forest, grassland, urban areas, arable land, permanent crops, liquid biofuel plantations (e.g. oil-seed rape or sunflower), non-woody biofuel plantations (e.g. *Sorghum* or *Miscanthus*), woody biofuel plantations (e.g. willow, poplar or eucalypt) and abandoned land. We merged permanent crops with arable land, because the level of invasion is similar in these two categories (Chytrý *et al.*, 2008b). The area of biofuel plantations is expected to increase across Europe (Tuck *et al.*, 2006; Spangenberg & Settele, 2009), but currently there are no data on the level of invasion by alien plants in those biofuel crops that have not been traditionally planted in Europe. However, as the agricultural management of non-woody and liquid biofuel crops will correspond to that of traditional crops (many of them also being potential biofuels, e.g. cereals, potato or sugar beet; Tuck *et al.*, 2006), and therefore the level of invasion will probably be similar to that of the traditional arable land, we also merged these two biofuel land-use categories with arable land. Finally, there are few data on the level of invasion in plantations of potential woody biofuel crops, but the data from deciduous tree plantations indicate that these levels are close to those recorded for arable land (Chytrý *et al.*, 2005). Therefore the category of woody biofuel plantations was also included in the category of arable land. Thus we used five broad land-use categories, distinct in terms of the level of invasion: forest, grassland, urban areas, arable land and abandoned (surplus) land.

# Data on the level of invasion and their projection on the land-use scenarios

By the term level of invasion we mean the number or proportion of plant species that are alien in a given habitat or at a site (Richardson & Pyšek, 2006; Chytrý et al., 2008a,b). This term is different from habitat invasibility, which is the susceptibility of the habitat to invasion imposed by abiotic and biotic constraints under the assumption of constant propagule pressure (Lonsdale, 1999). This implies that a habitat with low invasibility due to its inherent properties can be highly invaded if the propagule pressure at a given site is high, and vice versa. Our estimation of the levels of invasion for particular habitat types and land-use categories is based on the proportion of the number of neophytes, i.e. those aliens that arrived in the target area after AD 1500 (Pyšek et al., 2004), and relates to local scale (areas < 1000 m<sup>2</sup>; Chytrý et al., 2009a,b). We used proportions of total species numbers rather than absolute species numbers, because absolute numbers of alien and native species are positively correlated at large scales (Kühn et al., 2003; Pino et al., 2005; Stohlgren et al., 2005); thus the large-scale pattern of the absolute number of neophytes would be similar to the pattern of total or native species richness.

In a previous study (Chytrý *et al.*, 2008b) the fine-scale level of plant invasions in 33 European habitats was assessed using 52,480 vegetation plots from phytosociological or landscape monitoring surveys in Catalonia (north-east Spain), the Czech Republic and Great Britain (Schaminée *et al.*, 2009). These plots had been sampled since the 1970s and ranged in size from a few  $m^2$  to a few hundred  $m^2$ . Habitats were defined according to the European Nature Information System (EUNIS) classification (Davies *et al.*, 2004). This study revealed a striking consistency in the level of invasion of the same habitats among different regions, which justified extrapolation of the data from these three countries to other European regions where data were not available.

To obtain the mean value of the local level of plant invasion for each of the five land-use categories defined above, we transferred the EUNIS habitat types to those categories. As each land-use category corresponds to more than one habitat type, we estimated the proportional contribution of each EUNIS habitat type to each of the land-use categories in different European regions (Appendix S1 in Supporting Information). This estimation was based on the cross-tabulation of the EUNIS habitats and CORINE land-cover classes (Chytrý et al., 2009a), interpretation of the five land-use categories used here in terms of the CORINE land-cover classes (Bossard et al., 2000) and proportional representation of each CORINE land-cover class in each region. For the Mediterranean areas, we made separate interpretations for irrigated and non-irrigated arable land because of a much higher level of invasion in the former (Chytrý et al., 2009a). A special problem was the interpretation of the category of abandoned land, which can include very different vegetation types, ranging from recently abandoned arable land with weed vegetation to grasslands in the mid-successional stages and forests at sites abandoned for a long time. In the extra-Mediterranean areas we also considered the late successional stages such as broad-leaved forests, but in the Mediterranean areas, only herbaceous and shrubland vegetation types were assigned to this category because of the slower rate of succession in this summer-dry part of Europe (Escarré et al., 1983; Bonet & Pausas, 2004).

As in the previous study, which mapped current levels of plant invasion in Europe (Chytrý et al., 2009a), we extrapolated quantitative data on the level of invasion from Catalonia, the Czech Republic and Britain to wider areas of Europe within the limits of European biogeographical regions (European Topic Centre on Biological Diversity, 2006, http://dataservice.eea.europa.eu/ dataservice/metadetails.asp?id=839) as follows: (1) for the Mediterranean region we used the Catalonian data; (2) for the Continental and Pannonian regions, including embedded patches of the Alpine region, we used the Czech data; (3) for the British Isles we used the British data; (4) for the remaining part of the Atlantic region and for the Boreal region, including the embedded patches of the Alpine region, we used average values obtained from British and Czech data. We believe these mean values provide a reasonable approximation for the areas of Atlantic region on the European continent due to their transitional biogeographical position between oceanic and subcontinental climates, and also for the Boreal region, because Scottish and Czech mountains contain most of the habitat types typical of the Boreal region, such as coniferous forests, alpine grasslands and mires.

For each cell of  $10' \times 10'$  in each scenario, we plotted the weighted mean of the levels of invasion for land-use categories occurring in that cell, where weights were percentage areas of the cell occupied by the particular land-use categories. Weights for irrigated or non-irrigated arable land in the Mediterranean bioregion were adjusted according to the proportion of these two land-cover types in the CORINE land-cover map of Europe (Moss & Wyatt, 1994; Bossard *et al.*, 2000; version 8/2005 obtained from the European Environment Agency).

The level of invasion was visualized using four categories: < 1, 1-3, 3-5 and > 5% of alien (neophyte) species. Boundaries of the categories were set up arbitrarily to allow for optimum visualization. All GIS analyses and map visualizations were done in the ARCGIS 9.2 program (http://www.esri.com).

#### Statistical analysis

In statistical comparisons, individual grid cells were the units of observation. To allow for autocorrelation among the grid cells, all statistics were fitted as generalized least-square models with spatially correlated errors because these models appeared more parsimonious based on the Akaike information criterion (AIC; Burnham & Anderson, 2002) than models with spatially independent errors. Models with different assumptions about the correlated errors were compared, and the model with a rational quadratic description of spatial autocorrelation which had the lowest AIC value was chosen for description of the shape of spatial autocorrelation (Legendre & Legendre, 1998, pp. 728-731; Crawley, 2002, pp. 723-729). The resulting generalized least-square models thus do not violate the statistical assumption of independently and identically distributed errors and include corrections for pseudoreplications resulting from spatial autocorrelations (Rangel et al., 2006; Dormann et al., 2007).

The relationship between the occurrence of species that are included among the 100 worst invasive species in Europe in the DAISIE database (Lambdon *et al.*, 2008; DAISIE, 2009) and the mean level of invasion in grid cells was examined by linear regression. As the DAISIE database contains data on species occurrences in larger grid cells (50 km × 50 km) than used for the projections of land use and the level of invasion, mean levels of invasion for the  $10' \times 10'$  grid cells contained within each 50 km × 50 km grid cell were used for this analysis. Percentage of invasive species from the DAISIE database in the 50 km × 50 km grid cells was the response variable and the mean level of invasion in the same grid cells for the baseline data for 2000 the explanatory variable.

Temporal trends in the level of invasion were examined by analysis of covariance (ANCOVA). Mean levels of invasion in each grid cell for the three target years and positive or negative differences in each grid cell for the three target years relative to the 2000 baseline were the response variables, the three scenarios were factors, and the three target years were covariates. To test for nonlinear components in temporal trends, square powers of target years were added to the models. Differences among the temporal trends were tested by deletion tests on common slopes of temporal trends for all three target years in minimal adequate models, in which all parameters were significantly different from zero and from one another, and all non-significant parameters were removed (Crawley, 2002).

Scenarios were examined by linear mixed-effect models using the same response variables as those which were used in ANCOVAs. Scenarios were a fixed factor, and target years a random factor nested within scenarios (Crawley, 2002, pp. 723– 729). Significant differences among all scenarios were tested by ANOVA and significant differences between the individual scenarios by least square difference (LSD) tests (Sokal & Rohlf, 1995, pp. 240–260).

To normalize the data, the percentage of invasive species from the DAISIE database in each grid cell was angular transformed (Sokal & Rohlf, 1995, pp. 419–422), the mean level of invasion ln + 0.5 transformed (Yamamura, 1999) and positive and negative differences relative to the baseline  $x^{0.1}$  transformed, based on a Box–Cox series of transformations (Sokal & Rohlf, 1995, pp. 417–419). All models were checked by plotting normalized residuals against fitted values, by normal probability plots and by inspection of variograms for normalized residuals (Crawley, 2002, pp. 726–729). All calculations were done in s-plus 8.1.1 (TIBCO Software<sup>®</sup>).

## RESULTS

The highest levels of alien plant invasions among the five landuse categories (Table 1) were projected for arable land, followed

Table 1Mean percentage levels of invasion by alien plants fordifferent land-use categories in five European biogeographicalregions.

Land-use category	British Isles	Atlantic*	Boreal	Continental	Mediterranean
Forest	7.8	1.8	0.9	0.9	0.1
Grassland	1.3	1.5	1.7	1.4	1.2
Urban	5.4	5.0	5.0	4.8	4.8
Arable land†	13.0	8.6	8.7	5.1	2.8/14.2‡
Abandoned	4.9	3.0	2.8	2.6	2.4

\*Atlantic region on the European mainland, excluding the British Isles. †Arable land includes permanent crops and biofuel plantations.

‡The first value refers to non-irrigated and the second to irrigated arable land, because irrigation strongly affects the level of invasion in Mediterranean areas.

The level of invasion is defined as the percentage number of species that are aliens (neophytes) in vegetation plots.

by urban areas and abandoned land. In the Mediterranean areas irrigated arable land was projected as much more invaded than dry arable land. In the British Isles a high level of invasion was also projected for forests.

The map of the level of invasion for the baseline of 2000 (Fig. 1) projected the highest levels of invasion in lowland areas of western, central and eastern Europe and some agricultural areas of southern Europe. Low levels of invasion were mapped in the boreal and arctic zones, areas with extremely oceanic climate, mountain areas across the continent and Mediterranean areas that are not used for intensive agriculture. There was a strong positive relationship ( $F_{1, 2370} = 57.63$ , P < 0.0001) between the mean level of invasion in 50 km × 50 km grid cells (Fig. 1) and the percentage of the total number of the invasive plant species that are included among the 100 worst invasive species in Europe and occur in these cells.

Projected patterns of the level of invasion in 2020, 2050 and 2080 across Europe are not dramatically different from the baseline under any of the three scenarios (Figs 2–4). Still, there are clear trends in the level of invasion under different scenarios and for different time periods. Both changes in temporal trends for the three years (deletion test on mean levels of invasion, mean increases and decreases per grid cell, respectively:  $F_{4, 265383} = 10.48$ ,  $F_{2, 124468} = 249.56$ ,  $F_{2, 65586} = 37.83$ , all P < 0.0001) and among the scenarios (ANOVAs on mean levels of invasion, mean increases and decreases per grid cell, respectively:  $F_{2, 265383} = 33.40$ ,  $F_{2, 124468} = 790.0$ ,  $F_{2, 65586} = 7768.0$ , all P < 0.0001) are statistically significant.

Under the GRAS scenario (Fig. 2), both increases and decreases in the level of invasion were projected, the former



**Figure 1** Baseline map showing the level of invasion by alien plants in the year 2000. Average percentages of plant species that are alien (neophytes) in the plots (= level of invasion) were mapped for grid cells of  $10' \times 10'$ .



**Figure 2** Projected levels of plant invasion in 2020, 2050 and 2080 for the GRAS scenario (oriented on economic development and deregulation). Levels of invasion (left column) are percentages of vascular plant species that are aliens (neophytes). Increases and decreases are presented as positive or negative percentage changes in the level of invasion shown in the 2000 baseline map (Fig. 1).

being smaller but increasing continuously from the baseline to 2080 (Fig. 5b). The strongest increases were projected for Ireland, the Netherlands and some other areas of north-western and northern Europe where current levels of invasion are low or average. In contrast, decreases in the level of invasion were pro-

jected for the agricultural areas of eastern Europe, namely the Baltic countries, Poland and Hungary, the western part of central Europe and also some parts of south-western Europe, such as coastal areas and south-western France. The mean projected level of invasion per grid cell was significantly lower



**Figure 3** Projected levels of plant invasion in 2020, 2050 and 2080 for the BAMBU scenario (assuming implementation and enforcement of current policy decisions). Levels of invasion (left column) are percentages of vascular plant species that are aliens (neophytes). Increases and decreases are presented as positive or negative percentage changes in the level of invasion shown in the 2000 baseline map (Fig. 1).

under GRAS than under BAMBU and SEDG scenarios, which did not differ significantly, although their temporal trends differed (Fig. 5a).

Under the BAMBU scenario (Fig. 3), projected spatial patterns of increases and decreases in the level of invasion followed similar

trends as under GRAS. However, under BAMBU significantly smaller decreases and higher increases were projected than under GRAS by 2080 (Fig. 5b). This is likely to occur mainly in central and western Europe (Fig. 3) and results in a remarkable mean increase in the level of invasion by 2080 (Fig. 5a).



Figure 4 Projected levels of plant invasion in 2020, 2050 and 2080 for the SEDG scenario (oriented on sustainable development). Levels of invasion (left column) are percentages of vascular plant species that are aliens (neophytes). Increases and decreases are presented as positive or negative percentage changes in the level of invasion shown in the 2000 baseline map (Fig. 1).

Under the SEDG scenario (Fig. 4), both the projected increase and decrease in the mean level of invasion were the smallest (Fig. 5b). Generally the regions showing an increase and decrease were roughly the same as under the GRAS or BAMBU scenarios. Because of the small decreases in the levels of invasion, the SEDG scenario resulted in projections of significantly larger mean levels of invasion across Europe than the GRAS scenario.



Figure 5 Projected overall changes in the level of invasion by alien plants for all the grid cells in Europe by 2020, 2050 and 2080, under each of three ALARM scenarios: (a) mean levels of invasion (= number of alien species/number of all species, %) per grid cell; (b) mean positive (increases) or negative (decreases) changes in the levels of invasion per grid cell relative to the 2000 baseline. Vertical lines show standard errors, figures inside the bars are numbers of grid cells. Least square differences (LSD tests; P < 0.05) between projected changes for individual scenarios are indicated by small letters below the scenario acronyms: identical letters indicate no differences.

#### DISCUSSION

In this study, we first mapped the current levels of invasion for the baseline land-use data, which corresponded to the year 2000, and then we projected levels of invasion on the land-use scenarios for three target years: 2020, 2050 and 2080. Because of increased uncertainty towards the future (Rounsevell *et al.*, 2006), it was necessary to use coarser spatial resolution and coarser habitat classification than in the previous study that mapped the current level of plant invasions in Europe (Chytrý *et al.*, 2009a). However, a considerable similarity between the current baseline map (Fig. 1) and the more detailed map of the previous study indicated that the current input data were reliable.

At a coarse European scale, distribution of land-use categories is driven by climate (Thuiller *et al.*, 2004), but at finer scales it depends on socio-economic processes. Species invasions are driven by both climate (Walther *et al.*, 2009) and land use, but the effect of climate on the level of invasion of particular sites is much weaker than the effect of land use or habitats (Chytrý *et al.*, 2008a). The land-use scenarios used in this study involved projections of future climate change (Bondeau *et al.*, 2007), assuming that socio-economic processes cause climate change, but they are themselves changed in response to climate change. Land-use changes thus depend on both socioeconomics and climate, while plant invasions depend on all these three factors, being most closely linked to land-use change.

Under all the three scenarios of future socio-economic development examined in this study, the magnitude and pattern of the level of plant invasion within European regions is projected to change in the 21st century (Figs 2–4). Scenarios show that in north-western and northern Europe the levels of invasion may increase more than elsewhere, mainly due to the spread of alien plants to landscapes with biofuel crop plantations established in the places of former grasslands (Tuck *et al.*, 2006; Reginster *et al.*, 2010). In contrast, some areas such as eastern Europe and some parts of southern Europe may experience no increase, or even decrease, in the level of invasion. To a large extent, these projected changes in the level of invasion are due to the abandonment of arable land (Reginster & Rounsevell, 2010), because agricultural areas are particularly suitable for the spread of many alien species (Pyšek *et al.*, 2005; Chytrý *et al.*, 2008a,b).

Perhaps a surprising result of this study is that the largest overall decrease in the level of invasion is projected under the GRAS scenario (Fig. 5b). This scenario, assuming economic deregulation and globalization (Spangenberg et al., 2012), supposes that in the first half of the 21st century large areas of agricultural land will be abandoned, especially in eastern Europe, in some coastal areas, and some regions of southern Europe, most notably south-western France. In the second half of this century further abandonment is projected also in central and western Europe (Reginster & Rounsevell, 2010). Succession on abandoned fields may result in a decreased level of invasion across the landscapes, because the proportion of alien plant species is known to decrease during secondary succession due to the establishment of competitively strong native species in the mid and late successional stages (Rejmánek, 1989; Pino et al., 2006). In contrast, the establishment of biofuel plantations in areas of former grassland, as expected under the GRAS scenario, especially for north-western Europe, may result in increased levels of plant invasion there. Thus this scenario results in a strong geographical polarization between the areas with considerable increase of plant invasions and the areas where invasions can be less important than today (Fig. 2). However, areas with a projected decrease in the level of invasion are not likely to experience a parallel decrease in the distribution and impact of serious invaders that they already harbour. Established serious invaders (those with strong negative impacts on economy or biodiversity) are difficult to eradicate and unlikely to retreat due to changing land use without human intervention (Rejmánek & Pitcairn, 2002). As serious invaders are likely to arrive in 'increase' areas but not disappear from 'decrease' areas, invasions under the GRAS scenario may have more serious consequences than it appears just on the basis of levels of invasion.

The SEDG scenario (Fig. 4), which supposes sustainable development with a high priority for environmental issues and support for extensive agriculture even in areas where it is less profitable (Spangenberg et al., 2012), leads to higher overall levels of invasion in Europe. Under this scenario, the decrease in the level of invasion is very small and although the increase is smaller than under the GRAS or BAMBU scenarios, it results in a significantly larger net overall increase across Europe than under GRAS (Fig. 5). It should be noted that the current projections do not account for the increasing level of invasion within habitats, which is very likely to occur, given that more than six alien species capable of naturalization currently arrive in Europe every year (Lambdon et al., 2008; DAISIE, 2009). Thus the actual increase is likely to be even larger than projected here. Polarization between north-western and eastern Europe does occur under SEDG, but it is much less pronounced than under the GRAS or BAMBU scenarios.

The levels of invasion under the BAMBU scenario (Fig. 3), supposing implementation of current regulation policies, are similar to SEDG. However, due to an intermediate decrease in the level of invasion in some areas, coupled with large increases in other areas (Fig. 5b), this scenario results in the highest overall level of invasion across Europe by 2080 (Fig. 5a). Thus, if the regulation-oriented policy decisions already made, but not yet fully implemented, are implemented and enforced, the problem of invasive plant species may increase in importance especially in countries of north-western Europe which are already now most affected by invasions. For example, the United Kingdom and Belgium have the highest densities of naturalized neophytes of all European countries (Lambdon *et al.*, 2008). The risk of future invasions is highest in the British Isles, and Ireland in particular.

The measure used here to quantify future invasions is based on all alien species rather than invasive pest species, which are of interest to environmental managers. However, the strong positive relationship for the 2000 baseline data between the mean level of invasion in grid cells and the percentage of the total number of plant species that are included among the 100 worst invaders in Europe (DAISIE, 2009) clearly illustrates that a high level of invasion also means an increased probability of the occurrence of invasive pest species (Rejmánek & Randall, 2004). Areas for which high levels of invasion are projected are thus likely to receive not only more alien species but also more invasive species that cause environmental or economic damage (Vilà *et al.*, 2010).

## CONCLUSIONS

The three scenarios considered in this study provide internally consistent illustrations of plausible and possible futures. However, their probability cannot be quantified and their realization depends on whether or not their assumptions will be realized. Deviations from the linear development trajectories of these scenarios are possible (shock events: Spangenberg *et al.*, 2012). Nevertheless, these scenarios provide valuable insights into the relationships between possible future orientations of European policy and plant invasions.

An important lesson learned from this study is that none of the currently dominating policy options in itself will be able to stop or reduce the ongoing process of plant invasions, although minor reductions are possible in some regions. This conclusion is also valid for policies favouring sustainable development and environmental protection (the SEDG scenario). By supporting agriculture in less productive areas and associated invasionprone land use, these policies may even result in an increased rate of spread of alien plants in some regions. Therefore, invasions require specific policy approaches beyond the general ones which are currently on the policy agenda. A proactive development and implementation of effective strategies for prevention, eradication and control of invasive alien plants across Europe (Hulme, 2006; Hulme *et al.*, 2009a,b) continue to be of crucial importance, regardless of the future economic development.

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### REFERENCES

- Alcamo, J. (2001) *Scenarios as tools for international environmental assessments*. Office for the Official Publications of the European Communities, Luxembourg.
- Bondeau, A., Smith, P., Zaehle, S., Schaphoff, S., Lucht, W., Cramer, W., Gerten, D., Lotze-Campen, H., Müller, C., Reichstein, M. & Smith, B. (2007) Modelling the role of agriculture for the 20th century global terrestrial carbon balance. *Global Change Biology*, **13**, 679–706.
- Bonet, A. & Pausas, J.G. (2004) Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. *Plant Ecology*, **174**, 257–270.
- Bossard, M., Feranec, J. & Otahel, J. (2000) *CORINE land cover technical guide – addendum 2000.* Technical Report No. 40. European Environment Agency, Copenhagen.
- Burnham, K.P. & Anderson, D.R. (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York.
- Chytrý, M., Pyšek, P., Tichý, L., Knollová, I. & Danihelka, J. (2005) Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. *Preslia*, 77, 339–354.
- Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L. & Danihelka, J. (2008a) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology*, **89**, 1541– 1553.
- Chytrý, M., Maskell, L.C., Pino, J., Pyšek, P., Vilà, M., Font, X. & Smart, S.M. (2008b) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology*, **45**, 448–458.
- Chytrý, M., Pyšek, P., Wild, J., Pino, J., Maskell, L.C. & Vilà, M. (2009a) European map of alien plant invasions based on the quantitative assessment across habitats. *Diversity and Distributions*, **15**, 98–107.
- Chytrý, M., Wild, J., Pyšek, P., Tichý, L., Danihelka, J. & Knollová, I. (2009b) Maps of the level of invasion of the Czech Republic by alien plants. *Preslia*, **81**, 187–207.
- Crawley, M. (2002) Statistical computing. An introduction to data analysis using S-Plus. Wiley, Chichester.
- DAISIE (2009) *Handbook of alien species in Europe*. Springer, Berlin.

- Davies, C.E., Moss, D. & Hill, M.O. (2004) EUNIS habitat classification revised 2004. European Environment Agency, Copenhagen and European Topic Centre on Nature Protection and Biodiversity, Paris.
- Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.
- Escarré, J., Houssard, C., Debussche, M. & Lepart, J. (1983) Evolution de la végétation et du sol après abandon cultural en région méditerranéenne: étude de successions dans les Garrigues du Montpellierais (France). Acta Oecologica – Oecologia Plantarum, 4, 221–239.
- European Topic Centre on Biological Diversity (2006) The indicative map of European biogeographical regions: methodology and development. Muséum National d'Histoire Naturelle, Paris.
- Hobbs, R.J. (2000) Land-use changes and invasions. *Invasive species in a changing world* (ed. by H.A. Mooney and R.J. Hobbs), pp. 55–64. Island Press, Washington, DC.
- Hulme, P.E. (2006) Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology*, **43**, 835–847.
- Hulme, P.E., Nentwig, W., Pyšek, P. & Vilà, M. (2009a) Common market, shared problems: time for a coordinated response to biological invasions in Europe? *Neobiota*, 8, 3–19.
- Hulme, P.E., Pyšek, P., Nentwig, W. & Vilà, M. (2009b) Will threat of biological invasions unite the European Union? *Science*, **324**, 40–41.
- Ibáñez, I., Clark, J.S. & Dietze, M.C. (2008) Evaluating the sources of potential migrant species: implications under climate change. *Ecological Applications*, 18, 1664–1678.
- Kühn, I., Brandl, R., May, R. & Klotz, S. (2003) Plant distribution patterns in Germany: will aliens match natives? *Feddes Repertorium*, **114**, 559–573.
- Lambdon, P.W., Pyšek, P., Basnou, C. *et al.* (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia*, **80**, 101–149.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*, 2nd edn. Elsevier, Amsterdam.
- Lonsdale, M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M.
  & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, 10, 689–710.
- Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: synthesis.* Island Press, Washington, DC.
- Moss, D. & Wyatt, B.K. (1994) The CORINE Biotopes project: a database for conservation of nature and wildlife in the European Community. *Journal of Applied Geography*, **14**, 327–349.
- Perrings, C., Mooney, H. & Williamson, M. (eds) (2010) Bioinvasions and globalization. Ecology, economics, management, and policy. Oxford University Press, Oxford.

- Pino, J., Font, X., Carbó, J., Jové, M. & Pallarès, L. (2005) Largescale correlates of alien plant invasion in Catalonia (NE of Spain). *Biological Conservation*, **122**, 339–350.
- Pino, J., Seguí, J.M. & Alvarez, N. (2006) Invasibility of four plant communities in the Llobregat Delta (Catalonia, NE of Spain) in relation to their historical stability. *Hydrobiologia*, 570, 257–263.
- Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G., Williamson, M. & Kirschner, J. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, **53**, 131–143.
- Pyšek, P., Jarošík, V., Chytrý, M., Kropáč, Z., Tichý, L. & Wild, J. (2005) Alien plants in temperate weed communities: prehistoric and recent invaders occupy different habitats. *Ecology*, 86, 772–785.
- Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Bio*geography, 15, 321–327.
- Reginster, I., Rounsevell, M., Butler, A. & Dedoncker, N. (2010) Land use change scenarios for Europe. *Atlas of biodiversity risk* (ed. by J. Settele, L. Penev, T. Georgiev, R. Grabaum, V. Grobelnik, V. Hammen, S. Klotz, M. Kotarac and I. Kühn), pp. 100–105. Pensoft Publishers, Sofia and Moscow.
- Rejmánek, M. (1989) Invasibility of plant communities. *Biological invasions: a global perspective* (ed. by J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson), pp. 369–388. John Wiley and Sons, Chichester.
- Rejmánek, M. & Pitcairn, M.J. (2002) When is eradication of exotic pest plants a realistic goal? *Turning the tide: the eradication of invasive species* (ed. by C.R. Veitch and M.N. Clout), pp. 249–253. IUCN, Gland and Cambridge.
- Rejmánek, M. & Randall, R. (2004) The total number of naturalized species can be a reliable predictor of the number of alien pest species. *Diversity and Distributions*, **10**, 367–369.
- Richardson, D.M. & Pyšek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, **30**, 409–431.
- Rounsevell, M.D.A., Reginster, I., Araújo, M.B., Carter, T.R., Dendoncker, N., Ewert, F., House, J.I., Kankaanpää, S., Leemans, R., Metzger, M.J., Schmit, C., Smith, P. & Tuck, G. (2006) A coherent set of future land use change scenarios for Europe. *Agriculture, Ecosystems and Environment*, **114**, 57–68.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Biodiversity global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774.
- Schaminée, J.H.J., Hennekens, S.M., Chytrý, M. & Rodwell, J.S. (2009) Vegetation-plot data and databases in Europe: an overview. *Preslia*, 81, 173–185.

- Settele, J., Hammen, V., Hulme, P. *et al.* (2005) ALARM: assessing large-scale environmental risks for biodiversity with tested methods. *GAIA – Ecological Perspectives for Science and Society*, **14**, 69–72.
- van der Sluijs, J. (ed.) (2002) *Management of uncertainty in science for sustainability*. Utrecht University, Utrecht.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry. The principles and practice of statistics in biological research*, 3rd edn. Freeman, New York.
- Spangenberg, J.H. (2007) Integrated scenarios for assessing biodiversity risks. *Sustainable Development*, **15**, 343–356.
- Spangenberg, J.H. & Settele, J. (2009) Neither climate protection nor energy security: bio-fuels for biofools? *Uluslararasi İlişkiler – International Relations*, **20**, 89–108.
- Spangenberg, J.H., Bondeau, A., Carter, T.R., Fronzek, S., Jäger, J., Jylhä, K., Kühn, I., Omann, I., Paul, A., Reginster, I., Rounsevell, M., Stocker, A., Sykes, M.T. & Settele, J. (2012) Scenarios for investigating risks to biodiversity. *Global Ecology and Biogeography* 21, 5–18 (this issue).
- Stocker, A., Omann, I. & Jäger, J. (2012) The ecologicaleconomic modelling of the ALARM scenarios with GINFORS: results and analysis of selected European countries. *Global Ecology and Biogeography*, **21**, 36–49 (this issue).
- Stohlgren, T.J., Barnett, D., Flather, C., Kartesz, J. & Peterjohn, B. (2005) Plant species invasions along the latitudinal gradient in the United States. *Ecology*, **86**, 2298–2309.
- Thuiller, W., Araújo, M.G. & Lavorel, S. (2004) Do we need land-cover data to model species distributions in Europe? *Journal of Biogeography*, **31**, 353–361.
- Tuck, G., Glendining, M.J., Smith, P., House, J.I. & Wattenbach, M. (2006) The potential distribution of bioenergy crops in Europe under present and future climate. *Biomass and Bioenergy*, **30**, 183–197.
- Vilà, M., Corbin, J.D., Dukes, J.S., Pino, J. & Smith, S.D. (2006) Linking plant invasions to global environmental change. *Terrestrial ecosystems in a changing world* (ed. by J. Canadell, D. Pataki and L. Pitelka), pp. 93–102. Springer, Berlin.
- Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W.O., Roques, S., Roy, A., Hulme, D. & DAISIE partners (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European cross-taxa assessment. *Frontiers in Ecology and the Environment*, **8**, 135–144.
- Vitousek, P. (1994) Beyond global warming: ecology and global change. *Ecology*, **75**, 1861–1876.
- Walther, G.-R., Roques, A., Hulme, P.E. *et al.* (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution*, **24**, 686–693.
- Yamamura, K. (1999) Transformation using (x + 0.5) to stabilize the variance of populations. *Researches on Population Ecology*, **41**, 229–234.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Cross-tabulation of the EUNIS habitat types and the MOLUSC land-use categories used for projecting the level of invasion in different European biogeographical regions.

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