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ECOSYSTEMS


# Using Life Strategies to Explore the Vulnerability of Ecosystem Services to Invasion by Alien Plants

Joana R. Vicente,[1,2]* Ana T. Pinto,[1] Miguel B. Araújo,[3,4,5] Peter H. Verburg,[6] Angela Lomba,[1,7] Christophe F. Randin,[8] Antoine Guisan,[7] and João P. Honrado[1,2]

*[1]Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO), Faculdade de Ciências da Universidade do Porto, Vairão, Portugal; [2]Departamento de Biologia, Faculdade de Ciências da Universidade do Porto, Rua do Campo Alegre, s/n, Edifício FC4, 4169-007 Porto, Portugal; [3]Department of Biodiversity and Evolutionary Biology, National Museum of Natural Sciences, CSIC, C/José Gutiérrez Abascal, 2, 28006 Madrid, Spain; [4]Cátedra Rui Nabeiro-Biodiversidade, Universidade de Évora, CIBIO, Largo dos Colegiais, 7000 Évora, Portugal; [5]Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, 2100 Copenhagen, Denmark; [6]Institute for Environmental Studies (IVM), VU University Amsterdam, De Boelelaan 1085-1087, 1081 HV Amsterdam, The Netherlands; [7]Département d'Ecologie et d'Evolution (DEE), Université de Lausanne , Bâtiment de Biologie, 1015 Lausanne, Switzerland; [8]Institute of Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland*

## Abstract

Invasive plants can have different effects on ecosystem functioning and on the provision of ecosystem services, with the direction and magnitude of such effects depending on the service and ecosystem being considered, but also on the life strategies of the invaders. Strategies can influence invasiveness, but also key processes of host ecosystems. To address the combined effects of these various factors, we developed a methodological framework to identify areas of possible conflict between ecosystem services and alien invasive plants, considering interactions between landscape invasibility and species invasiveness. Our framework combines multi-model inference, efficient techniques to map ecosystem services, and life strategies. The latter provides a functional link between invasion, functional changes, and potential provision of services by invaded ecosystems. The framework was applied to a region in Portugal, for which we could successfully predict current patterns of plant invasion, of ecosystem service provision, and of potential conflict between alien species richness and the potential provision of selected services. Potential conflicts were identified for all combinations of plant strategy and ecosystem service, with an emphasis on carbon sequestration, water regulation, and wood production. Lower levels of conflict were obtained between invasive plant strategies and the habitat for biodiversity supporting service. The value of the proposed framework for landscape management and planning is discussed with emphasis on anticipation of conflicts, mitigation of negative impacts, and facilitation of positive effects of plant invasions on ecosystems and their services.

**Key words:** ecosystem services; life strategies; CSR Grime; alien invasive plants; multi-model inference; ecosystem services mapping; spatial conflict.

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*Corresponding author; e-mail:* jsvicente@fc.up.pt

## Introduction

Alien invasive species are among the most important agents of change in ecosystems (Pyke and others 2008; Pejchar and Mooney 2009). The introduction of non-native species and the expansion of species that become invasive mainly as a result of human action have profound consequences for the invaded ecosystems (Crowl and others 2008; Ehrenfeld 2010; Dukes 2011) and thereby for the provision of valuable ecosystem services (Le Maitre and others 2004; Charles and Dukes 2007; Crowl and others 2008). Impacts of invasive plant species on ecosystem services have been reported for hydrological cycles, chiefly by changing the rate or timing of evapotranspiration or runoff (Levine and others 2003; Pejchar and Mooney 2009), but also for nutrient cycling or productivity (Dukes and Mooney 2004). Such impacts on ecosystem functioning and services are more likely to occur when invaders differ from native species in traits such as transpiration rate, leaf area index, photosynthetic tissue biomass, rooting depth, and phenology (Levine and others 2003). As a consequence, plant invasions may not only impact biodiversity and the stability of native ecosystems (Liao and others 2008), but also ecosystem functioning and the provision of services (Ehrenfeld 2003).

Although virtually all ecosystem services can be negatively impacted by invasive species, positive effects may also occur (Charles and Dukes 2007). Recent meta-analyses (Liao and others 2008; Vilà and others 2011) indicate that various invasive plants increase ecosystem productivity (by up to 57%) and promote inputs of carbon and nitrogen into ecosystems, by enhancing both their aboveground (up to 133% C and 85% N) and belowground (up to 5% C and 112% N) pools. This means that invasion by alien species can have differential effects on distinct ecosystem services, and that some alien species may even have positive impacts, for example, where such species provide essential cover/binding, or act as nurse plants for native species (Thuiller and others 2007).

Depending on their effects on ecosystem structure and function, drivers of ecosystem change can affect a single ecosystem service, with only trivial effects on other services of interest, or they can have significant effects on multiple services (Bennett and others 2009; Civantos and others 2012). In the case of plant invasions, the occurrence of positive or negative effects will always depend on the service and ecosystem being considered, but will also be influenced by the life strategies of invading organisms (Levine and others 2003; Godoy and others 2009; Pejchar and Mooney 2009; Ehrenfeld 2010). Plant life strategies have been shown to determine several aspects of ecosystem functioning (Levine and others 2003, Ehrenfeld 2010). For example, Grime's (1977) CSR classification of life strategies has been used to assess patterns and drivers of invasion at the regional scale (Vicente and others 2010). Also, differences in morphological, chemical, and physiological traits (such as higher values of resource-acquisition traits, larger size, and/or higher growth rates) are well documented for many plant invaders as a mechanism for change of ecological processes in receiving ecosystems (particularly NPP, litter decomposition, above- and belowground stocks of nutrients, and water use; Ehrenfeld 2010).

Here, we provide a spatially explicit connection between patterns of invasion, life strategies of invaders, and ecosystem services. We analyze potential conflicts between alien invasive plants and ecosystem services at the landscape level in a case-study region in Portugal, using plant life strategies as the functional link between alien species diversity and ecosystem functions and services. Specifically, we analyze interactions between landscape invasibility (that is, features that promote invasion by alien plants; Vicente and others 2010) and species invasiveness (through life forms or strategies; Goodwin and others 1999; Grotkopp and others 2002; Ricciardi and Cohen 2007) in connection to their potential effects on selected ecosystem services. Three questions are considered: (1) how will alien plant species affect different types of ecosystem services at the regional scale, namely the capacity of ecosystems to provide supporting, regulating and provisioning services? (2) how is landscape invasibility affected by species invasiveness, and how is the relation expressed in the spatial patterns of invasion? and (3) where are most vulnerable regions located, based on landscape susceptibility to invasion and on the potential impacts on ecosystem services? To address these questions, interactions between landscape invasibility and species invasiveness are considered. In particular, alien species richness (species with documented invasive behavior in Portugal; total and per plant life strategy) are modeled and projected onto geography to address potential conflicts with the provision of selected ecosystem services. Finally, the added value of the proposed framework in the context of landscape management and planning is discussed with emphasis on conflicts, mitigation of negative impacts, and facilitation of positive effects of plant invasions on ecosystems and their services.

## Methods

### Test Area and Sampling Strategy for Invasive Plants

The framework was tested in an area in the northwest of Portugal (8°52′ to 8°02′W; 41°24′ to 42°9′N; Figure 1). It covers 3,462 km$^2$ at the transition between the Atlantic and Mediterranean biogeographic regions. Elevation ranges from sea level to 1,540 m in the eastern mountains, with valleys of major rivers running from east to west. Annual mean temperature ranges from approximately 9 to 15°C, and mean total annual precipitation varies between about 1,200 mm in lowlands to 3,000 mm in the eastern mountain summits. The region is particularly susceptible to invasion by alien plants, with climate/elevation and geology/soils acting as key determinants of native biodiversity, land use, and plant invasion (Vicente and others 2010, 2011).

The region was stratified to support the sampling of alien invasive plants, based on mean annual temperature (climate), bedrock type (geology), and percentage of forest cover (land cover/use); these factors are expected to reflect the major environmental gradients within the geographic region (for more details see Appendix 1 in Supplementary material). We then used a balanced random-stratified sampling design (as recommended by Hirzel and Guisan 2002 and Araújo and Guisan 2006) to randomly select four plots of 1 km$^2$ in each stratum, except for one stratum that was represented by only three cells (in this latter case, all three cells were sampled). The 91 selected 1 km × 1 km grid cells (hereafter referred as ''cells'') were surveyed between April and May of 2008, and the occurrence of alien plant species was recorded using a fixed sampling effort of one hour per cell, while visiting all habitat types on a targeted, non-systematic approach. The number of land -cover classes per surveyed cell ranged from two to five, for a total of nine classes in the ensemble of 91 grid cells. The sampling effort was distributed according to the relative cover of habitat types in each landscape mosaic (that is, grid cell).

### Analytical Framework: Research Questions and Hypotheses

To address our research questions on the patterns of alien plant invaders and their conflicts with selected ecosystem services, our analytical framework consisted of three main steps (Figure 2).

#### *Step 1*

In the first step, a multi-model inference (MMI) approach (Burnham and Anderson 2002) was implemented to calibrate models for species richness distribution (Figure 2; see also Vicente and others 2011). The approach was applied to the whole set of species and also to the three sets of species grouped into C–S–R plant strategy classes (Grime 1977; see ''Response Variables, Predictors, Model Calibration, and Model Selection'' section

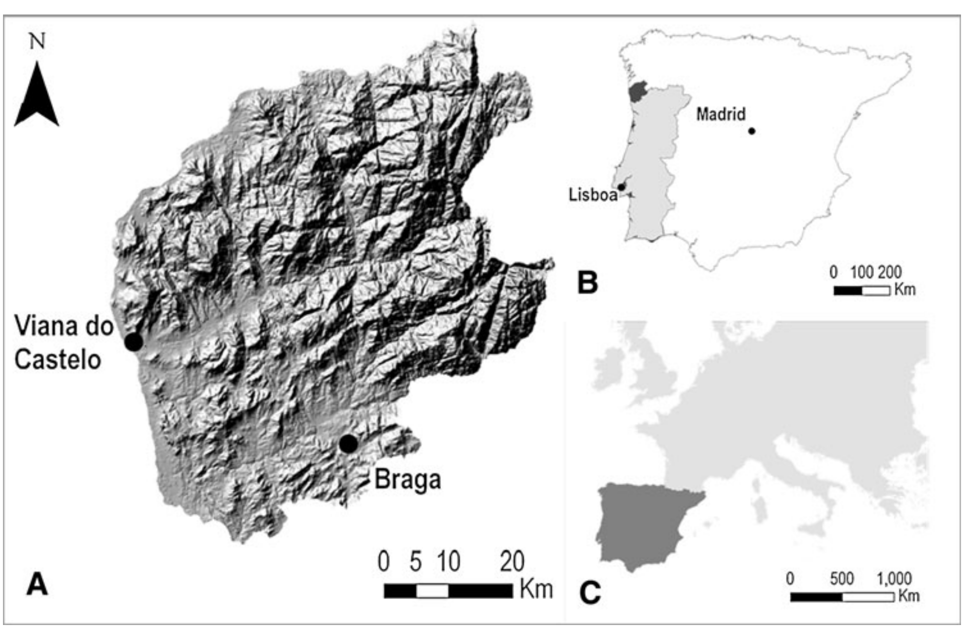


**Figure 1.** Digital elevation model for the test area (**A**) and its location in the Iberian Peninsula (**B**) and in Europe (**C**)

for more detail). Then, we classified the spatial predictions for species richness distributions into four equal classes (Table 4).

*Step 2*

This second step consisted of the mapping of ecosystem services for the study region, based on literature review, specific datasets, and expert knowledge to select the relevant factors/proxies to map ecosystem services. Land-cover maps were used to map the targeted ecosystem services at the landscape level, and outcomes from such mappings were also classified into four equal classes.

*Step 3*

Finally, in the third step, spatial projections from the species richness distribution models were overlaid with spatial mappings for ecosystem services and, as a result, areas of potential conflict were identified.

Spatial conflicts were identified for all the combinations of invasive species pools and focal ecosystem services. For exploration, we identified a reduced set of key conflicts between alien invasive species richness and ecosystem services. The reduced set of conflicts was inferred from plant life strategies combined with an assessment of how they affect invasiveness and the potential impacts of alien plant strategies on ecosystem services. As described in detail further below, we used Grime's (1977) classical C–S–R plant strategy scheme to group alien invasive plants into Ruderals (or R-strategists, that is, fast-growing annuals and perennials of nutrient-rich, frequently disturbed environments), Competitors (or C-strategists, that is, fast-growing perennials of nutrient-rich, stable environments) and Stress-tolerants (or S-strategists, that is, slow-growing perennials of nutrient-poor, stable environments). As mentioned above, because the goal of the manuscript is to develop a robust and efficient methodological framework that allows the identification of areas of possible conflict between ecosystem services and alien invasive plants, we did not try to illustrate all the possible relationships between life strategies and the focal ecosystem services. Instead, we inferred key plausible conflicts spanning across all invader species richness variables and all focal ecosystem services considered.

Specifically, for each of the targeted ecosystem services (Table 1), and based on the characteristics of plant life strategies, we predicted that: (i) species with a ruderal strategy (totally or partially; see ''Response Variables, Predictors, Model Calibration,

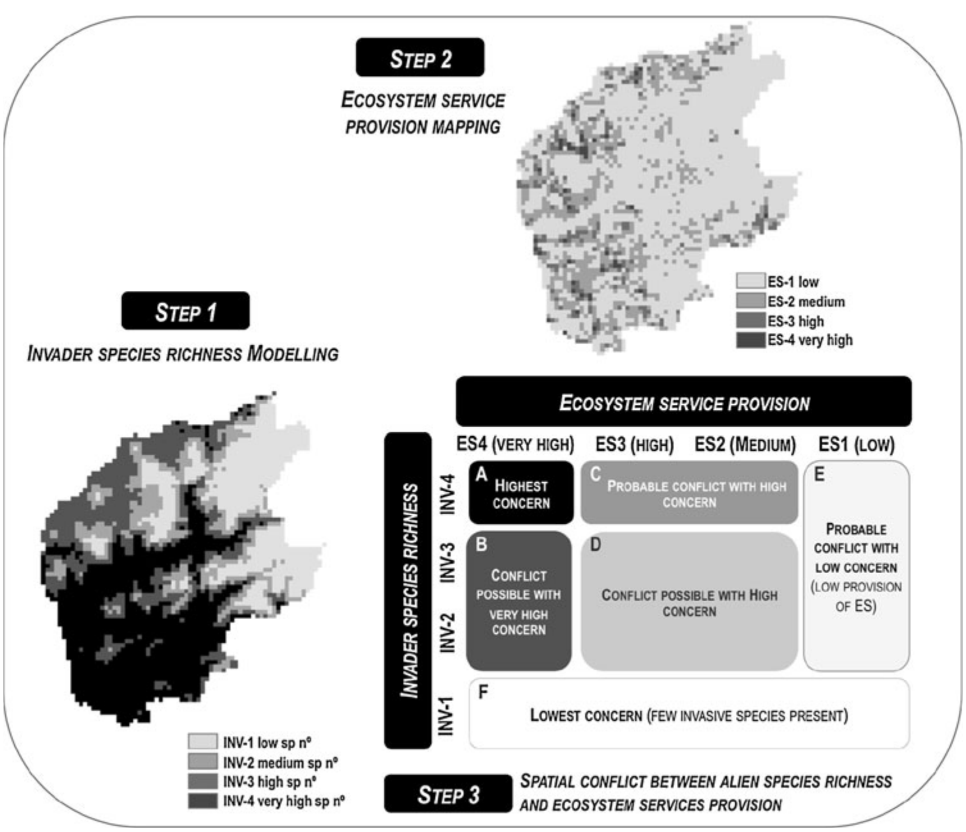


**Figure 2.** Analytical framework implemented to estimate the spatial conflicts between alien invasive species richness and the provision of a given ecosystem service

and Model Selection'' section), with long-distance dispersal, high propagule pressure, and ability to profit from disturbance, will mostly impact important areas for wood production by forests (a provisioning service) and for biodiversity (a supporting service); (ii) due to their high growth rates and ability to capture resources, species with a competitor strategy will mostly impact important areas for carbon sequestration and water regulation (two regulating services) and for biodiversity (a supporting service); and (iii) species exhibiting a stress-tolerant strategy will mostly impact important areas for wood production by forests (a provisioning service). Conflicts with total alien species richness were also tested for the two regulating services. From an ecosystem service perspective, these predictions establish that, among the set of life strategies being analyzed (Table 1): (i) wood provisioning from forests will mostly be impacted by ruderal and stress-tolerant species; (ii) water and carbon regulating services will mostly be impacted by competitor species; and finally (iii) biodiversity supporting services will mostly be in conflict with ruderal and competitor species.

## Response Variables, Predictors, Model Calibration, and Model Selection

The values for the several response variables related to alien plant species richness were obtained from the data collected in the 91 grid cells surveyed during the field campaigns. Alien invasive species were classified according to the C–S–R plant strategy classification of Grime (1977) by relating each species to one of the seven strategies (primary and intermediate; for more details see Appendix 2 in Supplementary material and Vicente and others 2010). Four response variables were considered for model fitting: total species richness (SR—86 species), competitor species richness ($SR_C$—52 species), stress-tolerant species richness ($SR_S$—51 species), and ruderal species richness ($SR_R$—68 species). Species belonging to one of the three primary strategies (C, R, and S) were used directly to calculate the corresponding species richness in each cell. Species belonging to intermediate strategies were used to compute the frequency of both corresponding primary strategies (for example, a species classified as CS was used to estimate the richness of both C-strategists and S-strategists because it exhibits traits related to both strategies; Vicente and others 2010).

From the factors that have been previously r eported in the scientific literature as potential determinants of ecosystem and landscape invasibility, and from previous research on alien plant invasions in the test region (Vicente and others 2010, 2011), 15 predictors were selected to explain alien species richness (Table 2). To prevent multicollinearity, only predictors with a Spearman correlation less than 0.7 and Generalized Variance Inflation Factor (VIF) less than 5 (Neter and others 1983) were considered. In the case of correlated pairs of predictors, we chose the one with the most direct ecological impact on plant species distributions (Guisan and Zimmermann 2000; Baselga and Araújo 2009).

We used averaged models for each of the four response variables (total, competitors, stress-tolerants, and ruderals). We fitted a set of competing models within a MMI framework (Burnham and Anderson 2002; for more details see Appendix 3 in in Supplementary material), and applied the corrected Akaike information criterion for small sample sizes ($AIC_c$; Shono 2000). To overcome dependence on sample size and allow comparability among models, we calculated the $AIC_c$ difference ($\Delta i = AIC_{c\ \mathrm{initial}} - AIC_{c\ \mathrm{minimum}}$; Burnham and Anderson 2002). From the Akaike differences ($\Delta i$), we derived Akaike weights ($w_i$), interpreted as the probability that a candidate model will be the best approximating and most parsimonious model given the data and set of models (for more details see Appendix 4 in Supplementary material). Finally, we averaged all competing models weighted by their $w_i$ and used the averaged model for spatial prediction. All models were fitted using Generalized Linear Models (GLMs) in R (version 2.4.1 2006) and associated packages available from CRAN (http://cran.r-project.org). In each model, one of the four species richness variables was used as the response variable in GLMs with Poisson variance and log link function (Vincent and Haworth 1983). Second order polynomials were allowed for each predictor in the GLMs, with the linear term being forced in the model each time the quadratic term was retained (adapted from Burnham and Anderson 2002). For validation purposes, we calculated the Pearson correlation value between observed and predicted values (performing a 10-folder cross validation; for more details see Appendix 5 in Supplementary material).

Spatial predictions from the best models were finally classified into four classes of species richness, to facilitate analyses of potential conflict with ecosystem service provision.

## Spatial Mapping of Ecosystem Services

Ecosystem service mapping was based on methods available in the literature, on specific datasets (for example, remote sensing products for ecosystem

**Table 1.** Ecosystem Services Considered in This Study, Their Possible Link to Alien Invasive Plants, Main Hypothesized Conflicts, and Key References

| Ecosystem services (ES) | Link with alien invasive plant species | Hypothesized conflicts between invasive plants and ES | References |
|---|---|---|---|
| Water cycle services (regulating ES) | Invasive alien plants can alter the flow of water for both drinking and irrigation, if they have at least one of the following characteristics in comparison to native species: (i) deeper roots; (ii) higher evapotranspiration rates; or (iii) greater biomass. The features mentioned allow many alien species to use more water than native species of invaded communities. Competitor invaders, due to their high growth rates and lack of water retention traits, are expected to be particularly important in this regard | Total species richness<br>Competitor species richness<br>(Negative effects on ES) | Dye and Jarmain (2004), Gerlach (2004), Gorgens and Van Wilgen (2004), Pejchar and Mooney (2009), Shafroth and others (2005), Ehrenfeld (2010) |
| Carbon sequestration (regulating ES) | Many invasive plants enhance productivity of invaded ecosystems, thereby promoting an increased carbon sequestration. Total biomass production can increase by up to 56.8% following invasions. Competitor and ruderal species, with their high growth rates and local abundances, are particularly important in this regard. There is a potential trade-off with increased fire proneness of invaded ecosystems, but we hypothesize that overall the final contribution for this ES will be positive | Total species richness<br>Competitor species richness<br>Ruderal species richness<br>(Positive effects on ES) | Liao and others (2008), Ehrenfeld (2010), Vilà and others (2011) |
| Provision of habitat for biodiversity (supporting ES) | Invasive alien species are defined as non-native species that threaten ecosystems, habitats or species. Negative impacts on biodiversity are substantial and widely documented, and derived from the fact that higher levels of abundance for some invaders have a negative impact on native biodiversity. Competitor and ruderal species, with their high growth rates and local abundances, are particularly important in this regard | Competitor species richness<br>Ruderal species richness<br>(Negative effects on ES) | Pejchar and Mooney (2009), Vilà and others (2011) |
| Forest wood production (provisioning ES) | Invasive species have negative impact on wood production because they compete with cropped tree species for resources, promoting the decrease of their biomass production. Ruderal species, with their high growth rates and local abundances, and stress-tolerant species, well suited to survive in shaded understory environments, are particularly important in this regard | Ruderal species richness<br>Stress-tolerant species richness<br>(Negative effects on ES) | Charles and Dukes (2007) |

**Table 2.** Predictors Used in the Models, Grouped into Environmental Types that Reflect Their Ecological Meaning, and the Corresponding Literature References

| Environmental type | Predictors | References |
|---|---|---|
| Climate | TMN (minimum temperature of the coldest month)<br>SPRE (summer precipitation) | Arévalo and others (2005), Pino and others (2005), Godoy and others (2009) |
| Land cover (landscape composition) | pNFo (% cover of natural forest)<br>pUrb (% cover of urban areas)<br>pAFo (% cover of forest stands)<br>SWIlu (local diversity of land cover types) | Pino and others (2005), Chytrý and others (2008) |
| Landscape structure and function | MSI (mean shape index—average perimeter-to-area ratio for all patches reflecting complexity)<br>dHNe (density of local hydrographic network)<br>GPP (mean gross annual primary productivity) | Le Maitre and others (2004), Williams and others (2005) |
| Fire disturbance | NFir (total number of fire occurrences) | Keeley and others (2005) |
| Geology and soils | pGra (percentage of granite)<br>SWIso (local diversity of soil types)<br>pFlu (percentage of fluvisols) | Rose and Hermanutz (2004), Dufour and others (2006) |
| Topography | SWIsl (local variation of slope) | Holmes and others (2005) |
| Hydrography | disH (distance to main rivers) | Pauchard and Shea (2006) |

productivity), and, when necessary, on expert knowledge (mainly from conservation biologists, hydrologists, and forest ecologists) to select the relevant factors/proxies to map the services. The mapping was done for regulating services (climate regulation through carbon sequestration, and water cycle services), supporting services (habitat for biodiversity), and provisioning services (wood production). The spatial datasets used to produce the final ecosystem service maps were selected based on the relevant literature and on expert judgment of the role of different determinants of each ecosystem service. Mapping of ecosystem services for spatial representation relied on a four-class scale ranking of each thematic map according to the relative significance for the regional provision of that service (from 4 = highest relative importance, to 1 = lowest relative importance). For each ecosystem service, the spatial combination of several sources of environmental information was performed and, as an outcome, a map with the mapping of each targeted ecosystem service was produced. Equal weighting was given to all maps. Cultural services were not considered in this study because they could not be consistently mapped.

The regulation of the water cycle by ecosystems is responsible for the provision of water for various uses, among other services (Brauman and others 2007). The mapping of water regulation was based on the spatial combination of four environmental maps: annual precipitation (representing water input; higher values will have a positive impact on the ecosystem service), topographic complexity (an important determinant of infiltration; higher values will have a negative impact on the ecosystem service), forest percentage cover (representing runoff prevention by permanent soil cover with complex vegetation; higher values will have a positive impact on the ecosystem service), and river network density (superficial water regulation; higher values will have a positive effect on the ecosystem service). After the spatial combination of the four maps (assigning an equal weight to all of them), the resulting spatial output was also classified into four equal classes.

Climate regulation through carbon sequestration was quantified indirectly using mean annual Gross Primary Productivity (GPP), which reflects the photosynthetic accumulation of carbon by plants and represents how much carbon dioxide ($CO_2$) is taken in by vegetation during photosynthesis (Gebremichael and Barros 2006). GPP has been used as a proxy indicator of biomass production and carbon sequestration (for example, Wu and others 2009; Peng and Gitelson 2012), and here we implemented the MODIS GPP algorithm (available at http://modis.gsfc.nasa.gov), which relies on the light use efficiency of plants as the mechanism controlling GPP and uses three different inputs: biome type information (MODIS land cover products), fraction of the photosynthetically active radiation (FPAR; MODIS products), and daily meteorological data from the NASA's Data Assimilation Office (DAO) products (Gebremichael and Barros 2006). The final GPP map was classified into four equal classes.

The nature conservation regime was selected as a proxy for the habitat of the biodiversity supporting service, based on the rationale that higher levels of biodiversity tend to occur in protected areas and more resources are invested in areas with higher protection status, thus enhancing the potential for the provision of the service. To map the conservation value of biodiversity, maps of two conservation area networks were considered: EU's Natura 2000, and the National Network of Protected Areas. Grid cells covered by one of the conservation networks were classified into four classes, from 1 (no protection, that is, protected areas absent) to 4 (highest protection). In the case of the national network, protection classes were those defined in the respective management plans, elaborated by the national agency for nature conservation (http://portal.icnb.pt/). In the case of the Natura 2000 map, the following classes were defined: 1—No protection, 2—Special Protection Area (SPA; EU Birds Directive), 3—Special Area of Conservation (SAC; EU Habitats Directive), and 4—Simultaneously SPA and SAC. For each grid cell (1 km$^2$), the protection value was weighted by the percentage of the cell occupied by each protection class (for a similar approach see Alagador and others 2011 and Araújo and others 2011). Finally, the two maps were combined, and a synthesis map ranging from a conservation value of 1 (no protection) to 16 (highest concern) was produced. The final map of conservation value was re-classified for consistency into four equal classes as previously described.

For provisioning services, the amount of wood produced in forest areas was determined based on tree growth models, assuming a sustainable harvesting model according to a theoretical regional vegetation model, and also considering the expected growth rates and management models for the several tree species. To calculate timber production for forests in the study area, the mean volume per tree (m$^3$) was estimated according to stand composition and the silvicultural models corresponding to each forest type. We used as input information the standard yield tables recommended by the European Forest Institute (Duarte and others 1991) and the growth models Globulus 2.0 (Tomé and others 2001) and Pbravov2.0 (Páscoa 2001). These models are tools to support forest management, in which the main objective is the profit associated to wood production. The corresponding forest management tables express the evolution of stand dendrometric variables (dominant height, basal area, mean diameter, volume) according to tree age classes and to stand productivity classes. Also, the National Forest Inventory database (available at http://www.afn.min-agricultura.pt/) was used to establish the baseline for stand composition, structure and age. Because broadleaved deciduous stands in the study region are traditionally exploited for domestic uses rather than for industrial timber production, a silvicultural growth model could not be applied directly. To overcome this, we used the National Forest Inventory data (AFN 2010) and the National Forest Authority data on wood production (DGSFA 1969). A mean value per hectare was obtained for each of the forest types and then used to estimate the value of each patch according to its surface area. Forest wood production was evaluated though the estimation of biomass production and resulting financial income. Reference values for timber prices were available from SICOP (http://cryptomeria.afn.min-agricultura.pt/enquadramento.asp). Three forest classes were considered: eucalypt stands, pine/conifer stands, and broadleaf deciduous stands (including native oaks and other species). Current management in the region is oriented toward timber production (pines and other conifers), cellulose pulp production for paper (eucalypts), and small-scale, localized wood/timber production (deciduous broadleaf forests). Values were aggregated to a 1-km$^2$ cell grid by summing up the value of the corresponding forest areas. It is known that trees growth declines with altitude (Coomes and Allen 2007). Therefore, we applied a gradient considering that higher elevation forest patches are less productive than lower elevation forest patches, which have higher productions. Elevation classes of 300 m range were considered, with a maximum weight of 1.0 assigned to areas below 100 m elevation, whereas areas above 1,300 m received the lowest weight (0.5). The resulting map was finally weighted by a 1 km$^2$ grid spatial layer representing the average elevation in the cell, expressing the reduced potential provision of services based on biomass production as we move up along the elevation gradient. The final output was then classified in four equal classes.

## Conflicts Between Alien Richness and Ecosystem Services

Areas of spatial conflict between distribution models and ecosystem services were calculated by overlapping mapped ecosystem service classes (four value classes) with invasion maps (four species richness classes). The 16 possible combinations were aggregated into six general conflict types that jointly express a gradient of concern (for negative effects on ecosystem services) or value (for positive effects on ecosystem services) of the conflicts between ES and alien invaders (see Figure 2). The six general conflict types can be defined as: A—''Highest concern'', where both invader species richness and ecosystem service provision are predicted to have the maximum values; B—''Conflict possible with very high concern'', where invader species richness is predicted to have high or medium values and ecosystem service provision is predicted to have very high value; C—''Probable conflict with high concern'', where invader species richness is predicted to have very high values and ecosystem service provision is predicted to have high or medium value; D—''Conflict possible with high concern'', where invader species richness is predicted to have high or medium values and ecosystem service provision is predicted to have high or medium value; E—''Probable conflict with low concern'', where invader species richness is predicted to have very high, high or medium values and ecosystem service provision is predicted to have low value; and finally F—''Lowest concern'', where invader species richness is predicted to have low values.

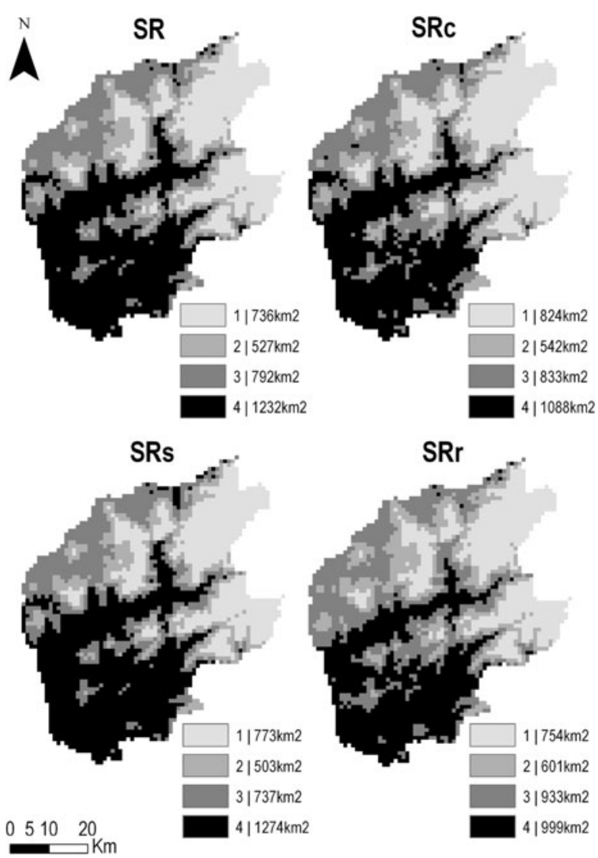


**Figure 3.** Regional patterns of alien plant species richness in the test area, for total species richness (SR) and for each of the three CSR life strategies ($SR_C$, $SR_S$, and $SR_R$) ranging from low species number (1) to very high species number (4)

# Results

## Patterns of Alien Invasion

Overall, the regional patterns of alien plant species richness were predicted to be similar across the three life strategies (Figure 3). For all three strategies, the best model was related to regional climate conditions, followed by the model expressing the prevalence of benign environmental conditions (Table 3; see also Appendix 3 in Supplementary material). Roughly 25% of the test area (mostly in higher elevation areas) was predicted to be invaded by few or no alien plants. However approximately 60% of the region (corresponding to the lowland warmer areas of main river valleys and along the coast) was predicted to be invaded by a high or very high number of alien plant species (Figure 3).

## Patterns of ES Provision

The range and distribution of values for potential provision of the four ecosystem services considered in this study are summarized in Table 4. The values for carbon sequestration and wood production services are expressed for each pixel as grams of carbon assimilated by ecosystems in each $m^2$ per year area and by the monetary value (in Euros) of wood products from forests, respectively. Application of the specific methodologies for spatial mapping of the water regulation and biodiversity services in the test area showed that: (i) water regulation is higher in areas that combine very high values of forest cover and hydrographic density, high values of annual precipitation and low values of topographic complexity; and (ii) the areas that potentially provide the highest biodiversity/habitat protection service are largely covered by high/very high conservation-value areas of National Park, Special Areas of Conservation (SAC) and Special Protection Areas (SPA) (Table 4).

The four ecosystem services measured have rather distinct patterns regarding potential provision in the region (Figure 4). For the water-related services, areas of highest potential provision are located along the lower valleys of the main rivers and scattered in mountain areas. Higher values for carbon sequestration were observed in forest landscapes at lower elevations. Biodiversity protection is higher in the eastern mountains (maximum protection areas of the Peneda-Gerês National Park) and ranging from medium to high in other Natura 2000 areas. Wood production is predominantly low to medium in the

**Table 3.** The Two Most Supported Models Selected for Each Response Variable, Predictors Included in the Competing Models, and Corresponding Values of wi

| | Competing models | Predictors | SR (wi) | $SR_C$ (wi) | $SR_S$ (wi) | $SR_R$ (wi) |
|---|---|---|---|---|---|---|
| Most supported model | Climatic model | TMN<br>SPRE | 0.855 | 0.867 | 0.864 | 0.878 |
| Second most supported model | Benign environmental conditions | TMN<br>SPRE<br>GPP | 0.145 | 0.133 | 0.136 | 0.122 |

*For more details see Appendix 4 in Supplementary material.*

**Table 4.** Ecosystem Service Value and Species Richness Classes and Corresponding Description or Ranges in the Original Ecosystem Service Maps

| ES value/species richness class | Range of species number | Carbon sequestration (g C/$m^2$/year) | Wood production (€) | Water regulation (dominant features of prevailing type of landscapes) | Biodiversity/habitat protection (dominant combinations of protection regimes) |
|---|---|---|---|---|---|
| 4 (very high) | SR 15–20<br>$SR_C$ 9–13<br>$SR_S$ 9–12<br>$SR_R$ 12–16 | 400–498 | 314,643–419,522 | Combination of very high values of forest cover and hydrographic density; high values of annual precipitation; low values of topographic complexity | Combination of high/very high value areas of National Park, Special Area of Conservation (SAC) and Special Protection Area (SPA) |
| 3 (high) | SR 10–15<br>$SR_C$ 6–9<br>$SR_S$ 6–9<br>$SR_R$ 8–12 | 302–400 | 209,761–314,643 | Combination of very high values of hydrographic density; medium values of forest cover, annual precipitation, and topographic complexity | Combination of medium value areas of National Park, SAC and SPA |
| 2 (medium) | SR 5–10<br>$SR_C$ 3–6<br>$SR_S$ 3–6<br>$SR_R$ 4–8 | 204–302 | 104,880–209,761 | Combination of high values of hydrographic density and topographic complexity; medium values of annual precipitation; low values of forest cover | Prevalence of SAC with low representation of SPA |
| 1 (low) | SR 0–5<br>$SR_C$ 0–3<br>$SR_S$ 0–3<br>$SR_R$ 0–4 | 106–204 | 0–104,880 | Combination of low values of precipitation, forest cover and hydrographic density, and very high values of topographic complexity | No protection value areas |

region, with scattered areas of high to very high potential provision toward the west, which reflects the fragmented distribution of forest areas across the test area.

## Conflicts Between Alien Invasions and ES

Patterns of conflict between alien invasive plants and the targeted ecosystem services were found to be different in the test region (Figure 5a). The most relevant spatial conflicts, that is, those of high to very high to highest concern/value, were predicted for services related to water (concern), carbon sequestration (value) and wood production (concern; Figure 5a). Conflicts between alien species richness and biodiversity protection were predicted to be low for most of the region, and no areas of very high concern were identified because the (mountain) areas with the greatest conservation

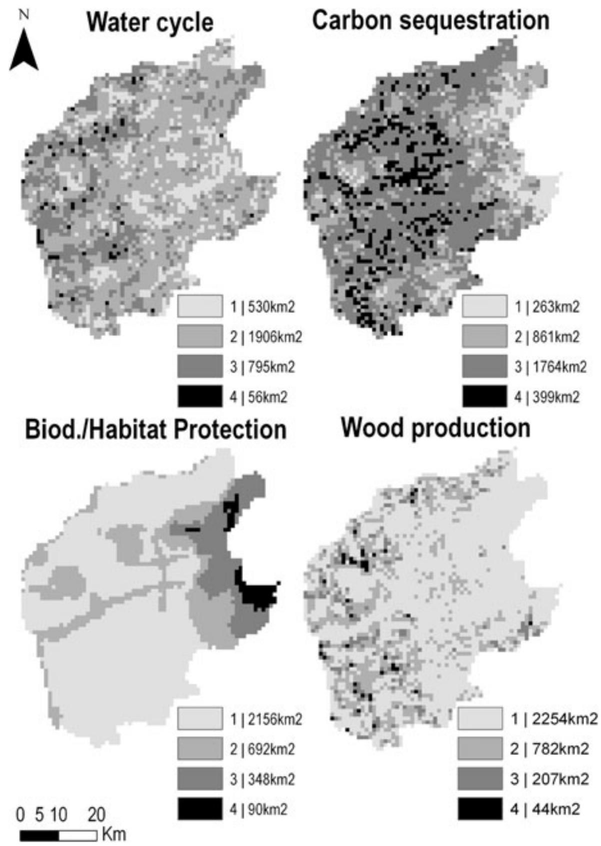


**Figure 4.** Regional patterns for the potential provision of the four targeted ecosystem services, ranging from low provision (*1*) to very high relative provision (*4*).

status were predicted as being invaded by few or no alien plants (see Figure 3). Overall, differences between plant life strategies in terms of conflicts with any of the considered ecosystem services were found to be smaller than those observed between ecosystem services (Figure 5a; for more details see Appendix 6 in Supplementary material).

Spatial patterns of conflict in the test region were also found to be quite different for the possible combinations of alien species richness (both for the total pool and for the species as divided across the three CSR life strategies) and ecosystem services. Such patterns are illustrated in Figure 5b for combinations of species richness classes and ecosystem service, selected according to the predicted major relationships expressed earlier (see Table 1; for details on all combinations see Appendix 6 in Supplementary material). High levels of spatial conflict of alien invasive plants with water-related services (C-strategists; concern) and carbon sequestration (whole species pool; value) were predicted across most of the test region, with scattered areas of conflict with highest concern/value (Figure 5b). Conversely, lower levels of conflict were predicted for biodiversity protection (R-strategists) and wood production (S-strategists), with the highest concern occurring in lowland areas within Natura 2000 (biodiversity protection) and in forest areas at mid-elevation areas in the western area (wood production).

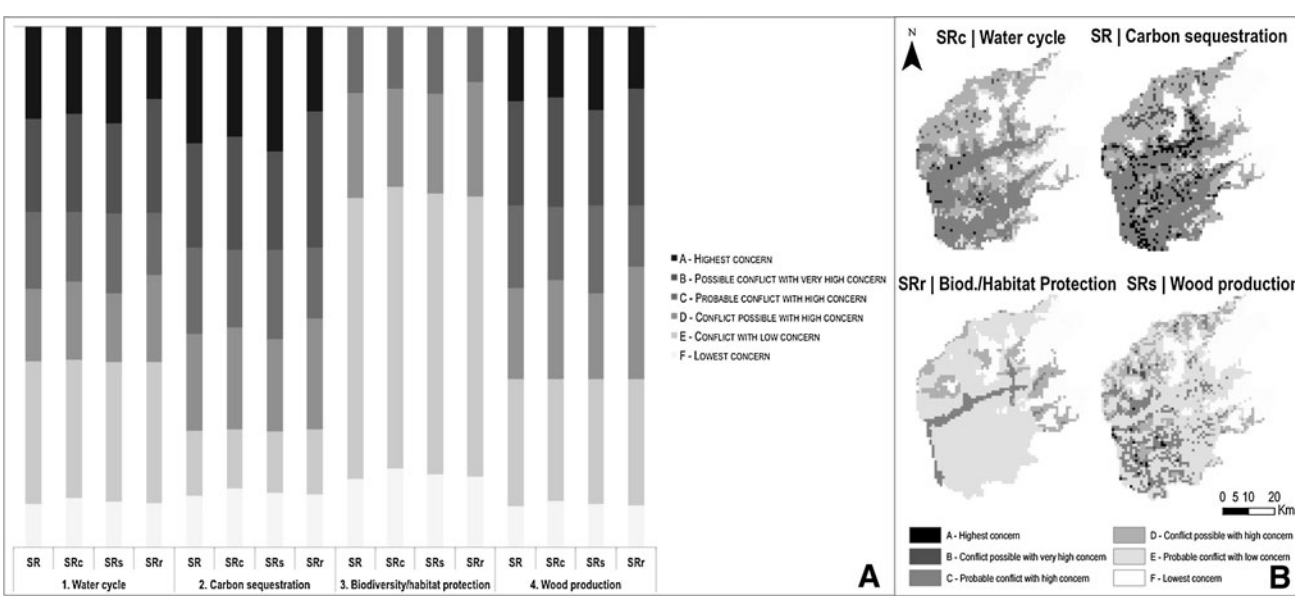


**Figure 5.** Conflicts between ecosystem services and alien invasive plants in the test region: **A** Patterns of conflict between ecosystem services and alien invasive plants (total and by plant strategy), organized according to distinct levels of concern; **B** Examples of spatial patterns of conflict between ecosystem services and alien invasive plants (all species or individual CSR life strategies).

# Discussion

## Life Strategies in the Assessment of Regional Patterns of Alien Invasive Plants

We described and tested a framework to efficiently assess spatial conflicts between alien invasive plants and ecosystem services. A MMI approach was implemented to calibrate models and predict patterns of alien species richness, for both the total species pool and the three CSR (Grime 1977) sets of species. This approach enabled the direct comparison of the relative importance of several environmental factors on alien species richness patterns, while providing spatial predictions for analyses of conflicts with the provision of ecosystem services.

Different responses of distinct plant functional types have previously been described when analyzing patterns of species richness against common sets of environmental drivers (for example, Steinmann and others 2009; Vicente and others 2010). Functional traits for individual species appear to act as filters for community assembly, due to their influence on the recruitment of species from the regional pool. Moreover, distinct life strategies of alien species have been related to different responses to environmental gradients (Vicente and others 2010), and those responses are then expressed on the different levels of susceptibility of heterogeneous landscapes to invasion by alien species.

Previous research highlighted climate as the prevailing environmental gradient underlying the distribution patterns for individual species as well as for species richness of alien plants (Vicente and others 2010, 2011). Our results are consistent with previous findings as climate was found to be a strong primary gradient (namely frost and low temperatures) on alien invasion (Walther 2002; Walther and others 2007). Here, all the best supported models for alien species richness (total and CSR plant strategies) were found to be mainly related to climate, providing further support to the hypothesis of climate acting as the prevailing driver of invasibility in mountainous regions (for example, Pino and others 2005; Godoy and others 2009). The observed pattern is unexpected as most of the alien species recorded in the region are neophytes, and many areas with potentially suitable environmental conditions for alien species in the tested pool may still not have been colonized due to dispersal limitations and/or a short time since introduction in the region (Alpert and others 2000; Steinitz and others 2006; Säumel and Kowarik 2010; Marco and others 2011). Furthermore, extreme climatic conditions (namely low winter temperatures in mountains) seem to exert an inhibitory effect on alien species richness, as most of the alien plant species that are invasive in the region are frost-sensitive, due to their sub-tropical and/or lowland origins. For such reasons, most of mountain landscapes in the region are currently devoid of alien invaders. Even so, they may become prone to invasion if impacts of climate change result in decreasing frost days in the future, particularly in the case of simultaneous landscape composition changes (for example, driven by land use change) toward facilitating invasions. In the specific case of our test region, and as most mountains are often covered by conservation areas (for example, the Peneda-Gerês National Park), our results have relevant implications for landscape management and conservation planning, as they have the potential to be used as a tool toward the prevention of new invasions in areas with the greatest conservation value and the highest potential provision of valuable ecosystem services in the regional context.

The application of species life strategies, in complement to total species richness, was found to be an added value for refining the detection and prediction of spatial patterns for species richness, enabling the inclusion of functional characteristics of the alien invader species and, eventually, responses from other biodiversity components to the environment (Honrado and others 2010; Lomba and others 2010; Vicente and others 2010). For such reasons, the application of different approaches for the control and eradication of alien invasions should be planned according to the target areas and alien species groups.

## Mapping and Spatial Patterns of Ecosystem Services

We mapped ecosystem services based on relatively simple standard methods that fit the knowledge and data available on ecosystem service provision in the region. The most accurate information on the determinants of the provision of the targeted ecosystem services was gathered and combined. The final index was then mapped following a four-scale ranking. Some services were derived by proxies, such as water regulation service for which spatial information from water catchments (annual precipitation, forest cover, density of river network, and topographic complexity) was combined. More complex approaches have been proposed for these ES, but these are difficult to implement because they involve hydrological modeling, are very time consuming, require specific datasets, and field sampling is often mandatory (for example, Shafroth and others 2005). In the specific case of carbon sequestration, it can be measured from annual GPP (Gebremichael and Barros 2006), and such a procedure was adopted in our research. Conversely, the biodiversity/habitat supporting service is more difficult to map in the absence of detailed biodiversity and habitat maps. To overcome the limitations in the mapping of such important services, we proposed a simple methodology that considers all conservation areas in the study area and combines them according to their protection status and importance. Finally, forest wood production was obtained using simple but accurate algorithms present in the literature (Duarte and others 1991; Páscoa 2001; Tomé and others 2001).

The several methodologies developed here expressed the distinct spatial patterns for the ecosystem services across the test region. Whereas water regulation, wood production, and carbon sequestration were mainly identified at lower altitudes, mountain areas present the highest potential for the biodiversity protection service (compare Figure 4). This heterogeneity of potential provision patterns in the maps corresponded with our expectations as a result of the different structural and functional features of ecosystems that determine the provision of such contrasting services (MA 2005). Therefore, the final maps of ecosystem service provision were considered suitable for analyzing conflicts with alien invasive plants.

## Assessment of Conflicts Between Invasive Plants and Ecosystem Services Through Life Strategies

Functional traits have been highlighted as major pathways for individual species impacts on ecosystems (Ehrenfeld 2010). Further, differences in prevalent traits for plant invaders have been reported as mechanisms enhancing species impacts on ecosystem services (particularly carbon sequestration, litter decomposition, stocks of nutrients, and water use; Ehrenfeld 2010). Even so, when analyzing the broad scope of research devoted to ecosystem services, both the mapping and identification of spatial conflicts mostly rely on individual species (for example, Dye and Jarmain 2004; Charles and Dukes 2007; Pejchar and Mooney 2009), total species richness (Gorgens and Van Wilgen 2004; Liao and others 2008), or communities (Vilà and others 2011). However, considering the close connection between species traits and ecosystem processes (Dukes and Mooney 2004; Pejchar and Mooney 2009), the application of life strategies for the assessment of potential conflicts between multiple invasive species and the provision of ecosystem services appears to be essential, because in heavily invaded regions multiple invaders will likely exhibit distinct traits and life strategies and will therefore have distinct potential impacts on different ecosystem services (Levine and others 2003; Godoy and others 2009).

Due to the ecological relevance of services provided by ecosystems, approaches toward their mapping have been focal areas of research (MA 2005; Meyerson and others 2005). However, in the case of some services, their spatial mapping is not a straightforward procedure, and some gaps and dependencies concerning information have been identified (for example, land cover maps have been considered essential to map food production through agricultural land use, or wood production from forestry; Metzger and others 2006; Nelson and others 2009). To overcome such constraints, we propose an approach for the spatial mapping of the targeted ecosystem services in the region, selected according to the potential conflict with alien plant invasions and especially with specific alien plant strategies. Conflicts between ecosystem services and total alien invasive species richness were found to exhibit differential patterns, with conflicts predicted for all service-species pool combinations but particularly those concerning conflicts with water regulation, carbon sequestration and wood production (compare Figure 5). Our predicted impacts of certain life strategies on the focal ecosystem services (see Table 1) were only partially confirmed by the spatial conflict analyses, namely those related with the conflicts of competitor invaders with regulation services and with the conflicts of wood production and stress-tolerant invaders (see Figure 5a). This confirms the complexity of possible relationships between species traits, ecosystem processes and the generated societal benefits (Ehrenfeld 2010) as well as the need for further assessments of these links and of their downstream effects. Nonetheless, overall our results suggest that the analysis of patterns for richness of the three life strategies (C–S–R) can provide relevant information for the anticipation of conflicts and/or impacts of alien species on ecosystem services, with positive implications for effective and socially relevant management of plant invasions.

## Applicability of the Approach to Support the Management of Plant Invasions

In this research, we proposed a framework to efficiently address the potential conflicts between patterns of alien invasive plant species invasion (expressed as patterns of alien species richness) and ecosystem services in a test region. By including a modeling approach to project patterns of alien species richness, also considering species richness by plant life strategies, our approach allows a deeper understanding of the environmental drivers underlying such patterns, including the major climate and landscape determinants of current distributions. In addition, the knowledge provided from ecological models is of uppermost application, as it allows exploring scenarios of climate and land use change and thereby deriving future projections (Thuiller and others 2007).

An operational approach to map targeted ecosystem services was also proposed in this study. Overall, we applied spatial sources of information, when available, and added expert knowledge (mainly from conservation biologists, hydrologists, and forest ecologists) whenever possible and necessary to select the relevant factors/proxies to map ecosystem services. We did this with the purpose of having a straightforward way to implement the mapping of ecosystem services, while optimizing the balance between time and cost. This procedure also ensures that the spatial outcomes on services provide relevant information needed for their application to both basic and applied research (Meyerson and others 2005).

We consider that by including such level of information in the analysis of potential conflicts between patterns for alien species and targeted ecosystem services, our approach provides an added-value to the ongoing research in this area, with relevant applications for landscape planning and management (Euliss and others 2011). Information derived from the application of our framework can be applied in local management of landscapes where conflicts between ecosystem services and alien species have been observed, by improving the knowledge related to drivers promoting alien invasions, but also for projecting specific actions to constrain the wide spread of such species. In addition, such information can be applied to the management of protected areas (for example, National Park or Natura 2000 network), where higher provision of biodiversity support services is expected, and conflicts with alien species should be avoided. In the case of our test region, the areas most devoid of alien invasions are coincident with those with higher values for provision of biodiversity support, and our results can be applied in their specific management plans, and included in a set of preventive measures, under scenarios of land use and climate changes.

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