

Impact scores of invasive plants are biased by disregard of environmental co-variation and non-linearity

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Academic editor: Franz Essl | Received 2 March 2011 | Accepted 18 May 2011 | Published 5 October 2011

Citation: Thiele J, Isermann M, Kollmann J, Otte A (2011) Impact scores of invasive plants are biased by disregard of environmental co-variation and non-linearity. *NeoBiota* 10: 65–79. doi: 10.3897/neobiota.10.1191

Abstract

Prioritisation of high-impact species is becoming increasingly important for management of introduced species ('neobiota') because of their growing number of which, however, only a small fraction has substantial impacts. Impact scores for prioritising species may be affected by the type of effect model used. Recent studies have shown that environmental co-variation and non-linearity may be significant for effect models of biological invasions. Here, we test for differences in impact scores between simple and complex effect models of three invasive plant species (*Heracleum mantegazzianum*, *Lupinus polyphyllus*, *Rosa rugosa*).

We investigated the effects of cover percentages of the invasive plants on species richness of invaded communities using both simple linear effect models ('basic models') and more complex linear or non-linear models including environmental co-factors ('full models'). Then, we calculated impact scores for each invasive species as the average reduction of species richness predicted by basic and full effect models.

All three non-native species had negative effects on species richness, but the full effect models also indicated significant influence of habitat types. *Heracleum mantegazzianum* had uniform linear effects in all habitats, while effects of *L. polyphyllus* interacted strongly with habitat type, and *R. rugosa* showed a marked non-linear relationship. Impact scores were overestimated by basic effect models for *H. mantegazzianum* and *R. rugosa* due to disregard of habitat effects and non-linearity, respectively. In contrast, impact of *L. polyphyllus* was underestimated by the basic model that did not account for the strong interaction of invader cover and habitat type.

We conclude that simple linear models will often yield inaccurate impact scores of non-native species. Hence, effect models should consider environmental co-variation and, if necessary, non-linearity of the effects of biological invasions on native ecosystems.

Keywords

effect model, *Heracleum mantegazzianum*, impact assessment, *Lupinus polyphyllus*, management, non-native, prioritisation, *Rosa rugosa*

Introduction

Impacts differ in quality and quantity among introduced species ('neobiota'). Many non-indigenous species can be considered neutral, but some have severe implications for native biodiversity, ecosystems, human health and economy (Gaertner et al. 2009, Hejda et al. 2009, Goodenough 2010). Globally, roughly 1% of the introduced species have become invasive with substantial impacts (i.e. invaders sensu Davis and Thompson 2000), but this proportion varies among regions and is likely to increase with longer residence times (Williamson 1996, Richardson and Pysek 2006). The human and financial resources available for management of biological invasions do not allow controlling all invasive species. Hence, it is increasingly necessary to prioritise management of neobiota according to rankings of their impacts (Parker et al. 1999, Byers et al. 2002, Thiele et al. 2010a).

Different approaches have been taken to study the impact of invasive species. Regarding species richness of invaded communities, for instance, removal or seed-addition experiments have been used (Meffin et al. 2010), as well as comparisons of invaded and uninvaded sites (Adams and Engelhardt 2009, Hejda et al. 2009, Flory and Clay 2010, Maurel et al. 2010), multi-year studies of expanding margins of invasive stands (Brewer 2008), comparisons of different stages of invasion (Prévosto et al. 2006), and correlational studies of gradients of invader abundance (Isermann et al. 2007, Gooden et al. 2009). All these approaches have their pros and cons concerning inference about invader impacts (cf. Adams and Engelhardt 2009, Meffin et al. 2010).

For impact assessment, according to the framework provided by Parker et al. (1999), and expanded by Thiele et al. (2010a), it is advantageous to relate invader effects to direct measures of invader abundance or equivalent measures, because the density of stands of a specific invasive species and the consequent impacts may vary among invaded sites, forming continuous gradients. Further, the relationship of effect and invader abundance may be non-linear which may affect impact estimates and also management decisions (Yokomizo et al. 2009).

Relationships of invader abundance and ecosystem traits may be modified by environmental factors (Houlihan and Findlay 2004, Surrette and Brewer 2008), so that one actually has to deal with a triangular relationship. A negative correlation may partly be the result of environmental conditions facilitating the invasion, while constraining the ecosystem trait. For instance, disturbance events that destroy most biomass of a given plant community may reduce species numbers, but could increase the abundance of invasive plant species. So, a negative relationship of invader abundance and species richness among sites with different disturbance regimes may be caused by environmental factors, instead of being a genuine effect of the invader. Moreover, effects of

an invasive species on a particular ecosystem trait often vary among habitat types. For example, invasion of a tree species may decrease the cover of native herbaceous plants in a formerly treeless habitat, whereas it even could facilitate native species in forests, as has been shown for *Cinchona* spp. (Fischer et al. 2009, Jäger et al. 2009). Different or contrasting effects can be modelled as interactions of invader abundance and habitat type. Although it is important to include environmental variables into effect models of invasive species, the potential strength of the influence of environmental variation on impact scores has rarely been tested.

The aim of the present study was to assess to which extent impact scores of invasive species are affected by environmental variation, and by choice of a linear vs. non-linear effect model. We used empirical data of three invasive plant species for model building and calculation of impact scores. Richness of vascular plant species of invaded communities was chosen as response variable.

Methods

Study species and field data

We used three plant species, *Heracleum mantegazzianum*, *Lupinus polyphyllus* and *Rosa rugosa*, that are invasive and widespread in Europe; all three are able to form dominant stands with >90% cover (Thiele et al. 2010b).

Heracleum mantegazzianum (Apiaceae) is a monocarpic tall herb native to the Western Greater Caucasus. It invades mesic grasslands, waste ground, riverbanks, roadsides and forest edges where it forms tall-herb stands (Tiley et al. 1996, Pyšek et al. 2007).

Lupinus polyphyllus (Fabaceae) is a nitrogen-fixing perennial tall herb from Pacific North America that spreads by seeds and rhizomes. In Central Europe, it mainly invades unimproved and mesic grasslands in mountain areas and transforms them into tall-herb stands, especially when grassland management is abandoned (Otte et al. 2002, Otte and Maul 2005).

Rosa rugosa (Rosaceae) is a shrub originating from the Pacific coasts of East Asia. In Europe, it mainly invades coastal habitats, but it can also become invasive on inland habitats, such as *Calluna* heath (Bruun 2005, Kollmann et al. 2007, Isermann 2008, Thiele et al. 2009).

We estimated cover percentages of the invasive study species and recorded all vascular plant species on plots of 16, 25 or 100 m² (see Table 1) that were established in different communities invaded by the study species. In *H. mantegazzianum* all plots were situated inside of invaded areas, while in *L. polyphyllus* and *R. rugosa*, sampling also included areas adjacent to invaded stands, but still inside of the same plant community. Cover percentages of the invaders ranged between zero and (almost) 100% percent. Details on the datasets are given in Table 1.

The plots were assigned to habitat types based on plant communities of Central Europe (see Ellenberg 2009) or, in few cases, based on physiognomy, land use and

Table 1. Characteristics of the datasets used for effect modelling and for calculating impact scores.

	<i>Heracleum mantegazzianum</i>	<i>Lupinus polyphyllus</i>	<i>Rosa rugosa</i>
Plot size (m ²)	25	25, 100	16
No. of plots	202	80	63
Sampling years	2002, 2003	1998, 2001	2001
Invader cover (%)			
Minimum	1	0	0
Mean	37	22	44
Maximum	95	90	100
Study regions	Western, central and southern Germany (22 areas)	Central Germany (Rhön mountains)	Northwestern Germany (Spiekeroog, Norderney, Juist)

disturbance regime where assignment to plant communities by floristic composition was not feasible. Definitions of habitat types are given in the Supplement (Table A1).

Effect modelling

First, we calculated ‘basic’ effect models that only contained invader cover as predictor of species richness. For all three invaders, species counts within the plots clearly deviated from normal distributions. Thus, we used Generalized Linear Models (GLM) with (quasi-)Poisson distribution and log-link which fitted the data well.

Next, we looked for the best models of species richness considering invader cover, habitat type, squared invader cover and interactions of (squared) invader cover with habitat type, as potential predictor variables. We tested the significance of predictor variables with likelihood ratio tests, starting with the basic model (‘invader cover’) and adding one additional predictor variable at a time, in the aforementioned sequence. Only variables that significantly improved the model fit were included in the final effect model (‘full model’). All effect models were calculated with R 2.10.1 (R Development Core Team 2009).

The models of *L. polyphyllus* included plot size as an additional predictor variable to account for the possibility that 100-m² plots contained more species than 25-m² plots because of species-area relationships. For *R. rugosa*, we calculated Generalized Linear Mixed Models (GLMM) that included a random site effect to account for nest-ness of the plots. The GLMM were calculated with ‘lmer’ of the ‘lme4’ package in R.

Calculation of impact scores

We calculated impact scores by averaging predicted species loss over all sample sites using the basic and full models, thus yielding two impact scores per invasive species.

Impact scores were calculated as the difference between predicted species richness at zero invader cover and predicted richness given the actual cover of the invader, averaged over all plots for each invasive species (see Equ. 1).

$$\text{Equ. 1: } \frac{1}{n} \sum_{i=1}^n (\hat{y}_0 - \hat{y}_{x_i})$$

where \hat{y} = predicted species richness, x_i = invader cover of site i , and n = number of sample plots per invasive species.

For calculation of the predicted species richness, we used estimates of all predictor variables in the model. If habitat type was a significant predictor, we used estimates of all habitat categories in the calculations, even if the estimates of some categories did not differ significantly from zero according to the GLM t test or z test.

We calculated percentile (2.5–97.5%) confidence intervals for impact scores with bootstrapping using 10,000 resamples with replacement of same size as the original sample.

Results

We found different effect models for the three invasive species (Table 2, Figure 1). Models of *H. mantegazzianum* and *R. rugosa* contained main effects of habitat types, indicating that habitat types differed in species richness. Among habitat types invaded by *L. polyphyllus*, i.e. ruderal and managed grasslands, species richness differed not per se, but the relationship of invader cover and species richness interacted with habitat type (Figure 1c).

The three invaders had negative effects on vascular plant species richness of invaded communities, but the shapes of the relationships differed. *Heracleum mantegazzianum* had uniform linear effects in all habitat types, while the effects of *L. polyphyllus* were much stronger in ruderal than in managed grasslands. *Rosa rugosa* showed a non-linear relationship, so that species richness only was reduced at high cover percentages (Figure 1e). The details of the basic and full models (estimates etc.) are given in the Supplement (Tables A2–4).

Impact scores differed markedly between basic and full models (Figure 1). For the basic and full model of *H. mantegazzianum*, confidence intervals of impacts scores did not overlap, indicating that part of the apparent effect on species richness predicted by the basic model was, indeed, due to general differences in species richness between invaded habitat types. For *L. polyphyllus* and *R. rugosa*, impact scores calculated with full models were just outside the confidence intervals of the basic models, suggesting significant differences between model variants, but the confidence intervals overlapped by roughly 50%. Impact scores of *L. polyphyllus* tended to be higher when taking the stronger effect in ruderal grasslands into account, whereas impact scores of *R. rugosa* tended to be lower when considering non-linear effects and general differences in species richness between invaded habitat types.

Table 2. Components of ‘full’ effect models. P-values are taken from sequential Likelihood Ratio tests. Signs (–, +) indicate the relationship of (squared) invader cover with species richness; NS, not significant.

Variable	<i>Heracleum mantegazzianum</i>	<i>Lupinus polyphyllus</i>	<i>Rosa rugosa</i>
Invader cover	(–) < 0.001	(–) 0.018	(+) < 0.001
Habitat type	< 0.001	†NS	0.021
Squared invader cover	NS	NS	(–) 0.015
Habitat type x invader cover	NS	0.004	NS
Hab. type x squared inv. cover	NS	NS	NS

† Habitat type was marginally significant in sequential likelihood ratio tests when added after *L. polyphyllus* cover and before squared *L. polyphyllus* cover and the interaction terms ($p = 0.033$), but the main effect of habitat type did not improve the ‘full’ model that contained *Lupinus* cover and the interaction of cover and habitat type ($p = 0.833$).

Discussion

The case studies presented here show that effect models of invasive species may take various forms. Concerning impacts on biodiversity, models should consider environmental variation, because general biodiversity trends along ecological gradients may lead us to believe that impacts are higher than they actually are. However, underestimation of impacts may happen as well.

For instance, *H. mantegazzianum* invades managed grasslands, ruderal (abandoned) grasslands and tall-herb stands – these habitat types resemble, and quite often are, a successional sere (Thiele and Otte 2006). Along this sere, species richness generally decreases, while average cover of *H. mantegazzianum* increases. Only part of the decline in species richness is attributable to *H. mantegazzianum* that shades out lower growing grassland plants (Thiele et al. 2010b), while another part is due to generally lower species numbers in tall-herb stands compared to the grasslands that they replace during succession (Neuhäusl and Neuhäuslova-Novotna 1985). In other words, species numbers of tall-herb stands are low even if *H. mantegazzianum* covers only a minor proportion of the area. In contrast, impact of *L. polyphyllus* was underestimated using a simple model that included no potential interactions of invader cover and habitat type. In fact, reduction of species richness was much stronger in ruderal than managed grasslands. Hence, inclusion of the interaction term increased the impact score, although ruderal grasslands represented only 25% of the plots sampled.

Several recent studies have found that inclusion of environmental variables into effect models changed predictions of invader effects on biodiversity: apparent negative effects of *Lythrum salicaria* L. and *Rhamnus frangula* L. on richness of rare native species disappeared (Houlahan and Findlay 2004), negative correlation of *Lonicera japonica* Thunb. with species richness became less strong (Surrette and Brewer 2008), but on the other side, effect estimates of (native) *Hippophaë rhamnoides* increased, i.e. became

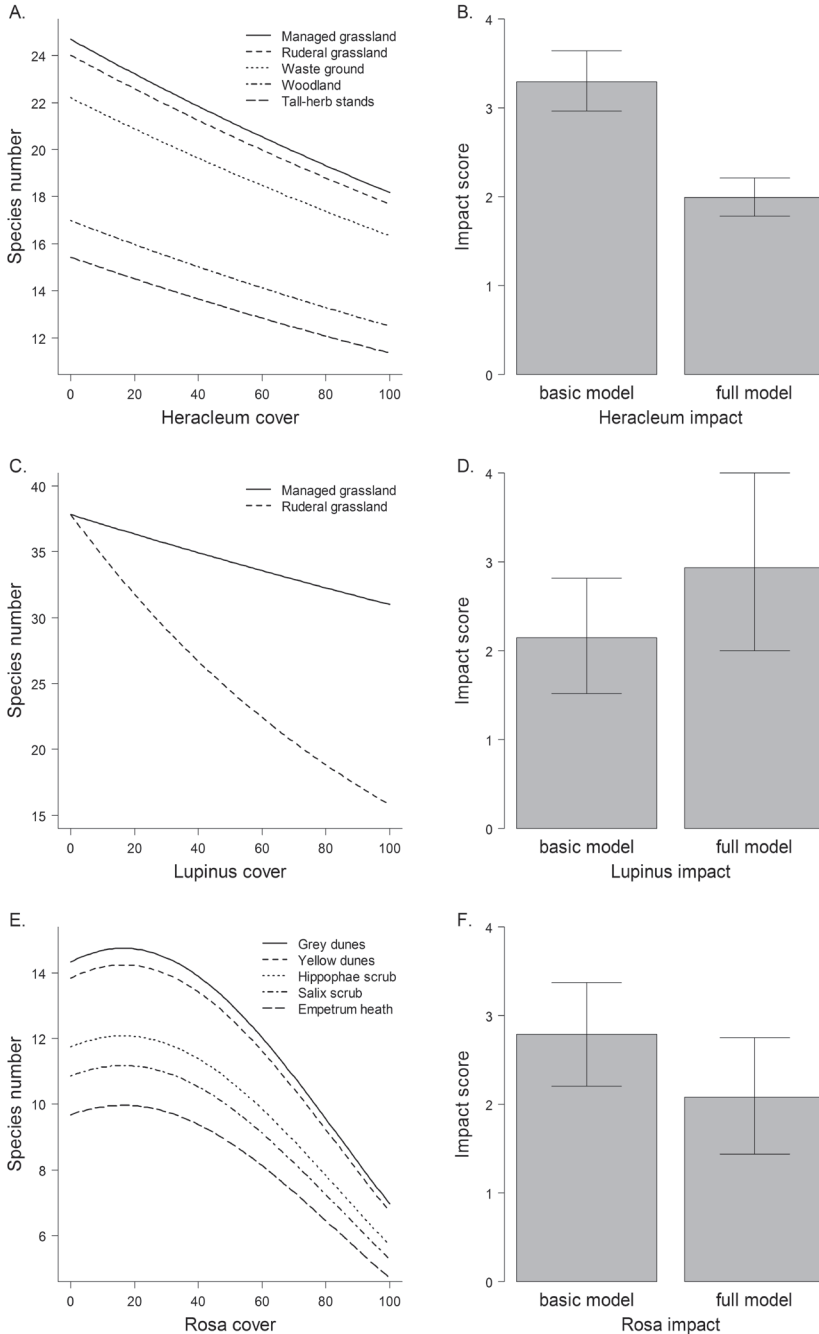


Figure 1. Effect models and impact scores. Left panels show the ‘full’ effect models of *Heracleum mantegazzianum* (A), *Lupinus polyphyllus* (C) and *Rosa rugosa* (E) that included habitat type as a co-factor and, if significant, non-linear terms of cover percentages of the invasive species. Right panels (B, D, F) show the corresponding impact scores calculated with ‘full’ models and with ‘basic’ models that only included a linear term of invader cover.

more negative, by up to 50% when including environmental co-variables (Isermann et al. 2007). Further, *Spartina anglica* C.E. Hubb. reduces native species richness in low-salinity marshes, while facilitating richness in mudflats (Hacker and Dethier 2006), and differences in impact on species richness among sites (Mediterranean islands) have been found for *Ailanthus altissima* (Mill.) Swingle and *Oxalis pes-caprae* L. (Vilá et al. 2006). Hence, it is the rule rather than an exception that disregarding environmental co-variation leads to biased estimates of invader effects on species richness.

Also non-linear relationships between invader abundance and biodiversity can substantially influence impact assessments. In the case of *R. rugosa*, the impact score was lower when introducing a quadratic term into the effect model, while inclusion of habitat type did not change the score much (basic model, 2.8; habitat model, 2.9; quadratic model, 2.1). A non-linear increase of effect with invader abundance will commonly lead to higher impact scores compared to a linear model (Thiele et al. 2010a), but the model of *R. rugosa* included both a negative quadratic and a positive linear term, so that in fact the non-linear model predicted a lesser effect. Non-linear effects on species richness were also found for the shrubs *Lantana camara* L. (Gooden et al. 2009) and *Hippophaë rhamnoides* (Isermann et al. 2007). These results suggest that non-linearity of abundance-effect relationships of invasive species should be considered in future impact studies.

Further advances of impact assessment and a deeper understanding of invader-diversity relationships could be expected from studies that take traits of the resident species into account, e.g. by modelling richness of functional plant groups or of species of high-conservation value. For the invaders studied here, it has been shown that different plant types – size classes, life forms, sociological groups – are affected differently (Thiele et al. 2010b). Regarding theory of biological invasions it would be interesting to investigate whether or not impact models could be generalised within groups of invasive species (e.g. life forms or strategy types). Another question is how to represent environmental variation in effect models. Here, we used habitat type as a co-factor which appears practical and useful, but might not be the optimal solution. The suitability of environmental properties and scaling of the variables (metric, categorical) will depend on both the invasive species and the ecosystem trait under study. Finally, multiple regression models, as applied here, account for main effects and interactions of invader and environment, but do not consider possible correlations among them. Thus, effect estimates may still be affected by spurious correlations. Further improvements could be achieved by more advanced models using, e.g., corrected path coefficients instead of regression coefficients.

Besides scientific approaches, impact assessment is grounded in normative definitions of impact or ecological damage. Not all negative relationships of invasive species with ecosystem traits necessarily have to be considered as damage, but definitions might focus on legal conservation resources or set thresholds discerning minor adverse effects from ‘significant’ damage (Bartz et al. 2010). In a normative sense, changes in species numbers may not directly quantify the ensuing damage (Ingo Kowarik, pers. comm.). Merging scientific and normative approaches into practical implementations

of impact assessment of invasive species remains a challenge for applied invasion biology and environmental planning.

Conclusions

Simple linear effect models may often yield inaccurate impact scores of invasive species. Hence, it appears to be advisable to consider somewhat more complex models that include environmental co-variables and, if applicable, non-linear effect terms. Models should preferentially be based on samples representing the full environmental gradient of invaded habitats and the full range of equilibrium abundances or cover percentages of the invasive species.

Acknowledgements

The study on *Heracleum mantegazzianum* by JT and AO was funded by the European Union within the project 'Giant Alien' (EVK2-CT-2001-00128). Research by JK benefited from a grant by the University of Copenhagen ('Centre for Invasive Species'). We thank Franz Essl and Ingo Kowarik for helpful comments on an earlier version of the manuscript.

References

- Adams SN, Engelhardt KAM (2009) Diversity declines in *Microstegium vimineum* (Japanese stiltgrass) patches. *Biological Conservation* 142: 1003–1010. doi: 10.1016/j.biocon.2009.01.009.
- Bartz R, Heink U, Kowarik I (2010) Proposed definition of environmental damage illustrated by the cases of genetically modified crops and invasive species. *Conservation Biology* 24: 675–681. doi: 10.1111/j.1523-1739.2009.01385.x.
- Brewer S (2008) Declines in plant species richness and endemic plant species in longleaf pine savannas invaded by *Imperata cylindrica*. *Biological Invasions* 10: 1257–1264. doi: 10.1007/s10530-007-9200-3.
- Bruun HH (2005) *Rosa rugosa* Thunb. ex Murray. *Journal of Ecology* 93: 441–470. doi: 10.1111/j.1365-2745.2005.01002.x.
- Byers JE, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Chornesky E, Hayes D (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* 16: 630–640. doi: 10.1046/j.1523-1739.2002.01057.x.
- Davis MA, Thompson K (2000) Eight ways to be a colonizer; two ways to be an invader: A proposed nomenclature scheme for invasion ecology. *Bulletin of the Ecological Society of America* 81: 226–230.

- Ellenberg H (2009) *Vegetation ecology of Central Europe*. Cambridge University Press, Cambridge, 731pp.
- Fischer LK, von der Lippe M, Kowarik I (2009) Tree invasion in managed tropical forests facilitates endemic species. *Journal of Biogeography* 36: 2251–2263. doi: 10.1111/j.1365-2699.2009.02173.x.
- Flory SL, Clay K (2010) Non-native grass invasion alters native plant composition in experimental communities. *Biological Invasions* 12: 1285–1294. doi: 10.1007/s10530-009-9546-9.
- Gaertner M, Den Breeyen A, Hui C, Richardson DM (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography* 33: 319–338. doi: 10.1177/0309133309341607.
- Gooden B, French K, Turner PJ, Downey PO (2009) Impact threshold for an alien plant invader, *Lantana camara* L., on native plant communities. *Biological Conservation* 142: 2631–2641. doi: 10.1016/j.biocon.2009.06.012.
- Goodenough AE (2010) Are the ecological impacts of alien species misrepresented? A review of the 'native good, alien bad' philosophy. *Community Ecology* 11: 13–21. doi: 10.1556/ComEc.11.2010.1.3.
- Hacker S, Dethier M (2006) Community modification by a grass invader has differing impacts for marine habitats. *Oikos* 113: 279–286. doi: 10.1111/j.2006.0030-1299.14436.x.
- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97: 393–403. doi: 10.1111/j.1365-2745.2009.01480.x.
- Houlahan JE, Findlay CS (2004) Effect of invasive plant species on temperate wetland plant diversity. *Conservation Biology* 18: 1132–1138. doi: 10.1111/j.1523-1739.2004.00391.x.
- Isermann M (2008) Classification and habitat characteristics of plant communities invaded by the non-native *Rosa rugosa* Thunb. in NW Europe. *Phytocoenologia* 38: 133–150. doi: 10.1127/0340-269X/2008/0038-0133.
- Isermann M, Diekmann M, Heemann S (2007) Effects of the expansion by *Hippophaë rhamnoides* on plant species richness in coastal dunes. *Applied Vegetation Science* 10: 33–42. doi: 10.1111/j.1654-109X.2007.tb00501.x.
- Jäger H, Kowarik I, Tye A (2009) Destruction without extinction: long-term impacts of an invasive tree species on Galapagos highland vegetation. *Journal of Biogeography* 36: 1252–1263. doi: 10.1111/j.1365-2745.2009.01578.x.
- Kollmann J, Frederiksen L, Vestergaard P, Bruun HH (2007) Limiting factors for seedling emergence and establishment of the invasive non-native *Rosa rugosa* in a coastal dune system. *Biological Invasions* 9: 31–42. doi: 10.1007/s10530-006-9003-y.
- Maurel N, Salmon S, Ponge J-F, Machon N, Moret J, Muratet A (2010) Does the invasive species *Reynoutria japonica* have an impact on soil and flora in urban wastelands? *Biological Invasions* 12: 1709–1719. doi: 10.1007/s10530-009-9583-4.
- Meffin R, Miller AL, Hulme PE, Duncan RP (2010) Experimental introduction of the alien plant *Hieracium lepidulum* reveals no significant impact on montane plant communities in New Zealand. *Diversity and Distributions* 16: 804–815. doi: 10.1111/j.1472-4642.2010.00684.x.

- Neuhäusl R, Neuhäuslova-Novotna Z (1985) Verstaudung von aufgelassenen Rasen am Beispiel von Arrhenatherion-Gesellschaften. *Tuexenia* 5: 249–258.
- Otte A, Maul P (2005) Verbreitungsschwerpunkte und strukturelle Einnischung der Stauden-Lupine (*Lupinus polyphyllus* Lindl.) in Bergwiesen der Rhön. *Tuexenia* 25: 151–182.
- Otte A, Obert S, Volz H, Weigand E (2002) Effekte von Beweidung auf *Lupinus polyphyllus* Lindl. in Bergwiesen des Biosphärenreservates Rhön. *Neobiota* 1: 101–133.
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1: 3–19.
- Prévosto B, Dambrine E, Coquillard P, Robert A (2006) Broom (*Cytisus scoparius*) colonization after grazing abandonment in the French Massif Central: impact on vegetation composition and resource availability. *Acta Oecologica* 30: 258–268. doi: 10.1016/j.actao.2006.05.001.
- Pyšek P, Cock MJW, Nentwig W, Ravn HP (2007) Ecology and Management of Giant Hogweed (*Heracleum mantegazzianum*). CAB International, Wallingford, 352pp.
- R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Richardson DM, Pyšek P (2006) Plant invasions: Merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30: 409–431. doi: 10.1191/0309133306pp490pr.
- Surrette SB, Brewer JS (2008) Inferring relationships between native plant diversity and *Lonicera japonica* in upland forests in north Mississippi, USA. *Applied Vegetation Science* 11: 205–214. doi: 10.3170/2008-7-18355.
- Thiele J, Otte A (2006) Analysis of habitats and communities invaded by *Heracleum mantegazzianum* Somm. et Lev. (Giant Hogweed) in Germany. *Phytocoenologia* 36: 281–320. doi: 10.1127/0340-269X/2006/0036-0281.
- Thiele J, Kollmann J, Rose-Andersen U (2009) Ecological and socio-economic correlates of plant invasions in Denmark: the utility of environmental assessment data. *Ambio* 38: 89–94. doi: 10.1579/0044-7447-38.2.89.
- Thiele J, Kollmann J, Markussen B, Otte A (2010a) Impact assessment revisited: improving the theoretical basis for management of invasive alien species. *Biological Invasions* 12: 2025–2035. doi: 10.1007/s10530-009-9605-2.
- Thiele J, Isermann M, Otte A, Kollmann J (2010b) Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs. *Journal of Vegetation Science* 21: 213–220. doi: 10.1111/j.1654-1103.2009.01139.x.
- Tiley GED, Dodd FS, Wade PM (1996) *Heracleum mantegazzianum* Sommier & Levier. *Journal of Ecology* 84: 297–319.
- Vilà M, Tessier M, Suehs CM, Brundu G, Carta L, Galanidis A, Lambdon P, Manca M, Médail F, Moragues E, Traveset A, Troumbis AY, Hulme PE (2006) Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. *Journal of Biogeography* 33: 853–861. doi: 10.1111/j.1365-2699.2005.01430.x.
- Williamson MH (1996) *Biological invasions*. Chapman & Hall, London, 256pp.

Yokomizo H, Possingham HP, Thomas MB, Buckley YM (2009) Managing the impact of invasive species: the value of knowing the density–impact curve. *Ecological Applications* 19: 376–386. doi: 10.1890/08-0442.1.

Appendix

Table A1. Definitions of habitat types. For descriptions of plant communities (syntaxa) see Ellenberg (2009).

Species	Habitat type	Definition
<i>Heracleum mantegazzianum</i>	Managed grassland	Pastures and meadows of well drained, fertile soils (typical Arrhenatheretalia communities)
	Ruderal grassland	Abandoned grassland, field margins, road verges and embankments (Arrhenatheretalia communities containing characteristic species of Galio-Urticetea and Artemisietea)
	Tall-herb communities	Tall-herb communities of fertile soils (Galio-Urticetea)
	Waste ground	Open communities of disturbed, non-agricultural sites (e.g. abandoned sand pits); floristic composition not matching any particular syntaxon
	Woodland	Communities dominated by trees; alluvial woodland (Alnion-glutinosa incanae, Salicion eleagni), copses and anthropogenic (semi-open) forests
<i>Lupinus polyphyllus</i>	Managed grassland	Unimproved Nardus grassland (Violion caninae) and montane grassland of more fertile soils (Polygono-Trisetion) with current or recent grassland management (mowing, grazing)
	Ruderal grassland	Unimproved Nardus grassland (Violion caninae) and montane grassland of more fertile soils (Polygono-Trisetion) without current land use containing characteristic species of tall-herb communities (Galio-Urticetea); subordinately sedge fens (Caricetum nigrae)
<i>Rosa rugosa</i>	Yellow dune	Mobile yellow dunes dominated by <i>Ammophila arenaria</i> (Ammophiletea: Elymo-Ammophiletum)
	Grey dune	Semi-fixed and fixed grey dunes with short, open grasslands (Koelerio-Corynephoretea), especially Corynephorion canescentis, Violo-Corynephoretum as well as herb-rich communities of the Tortulo-Koelerion
	<i>Hippophaë</i> scrub	<i>Hippophaë rhamnoides</i> scrub on semi-fixed grey dunes (Rhamno-Prunetea: Hippophao-Sambucetum)
	<i>Salix</i> scrub	<i>Salix repens</i> dominated scrub on dry fixed dunes (mainly brown dunes) mostly belonging to the Salici repentis-Empetretum (Empetrium nigri)
	<i>Empetrum</i> heath	<i>Empetrum nigrum</i> dominated heathlands on brown dunes (Empetrium nigri: Carici arenariae-Empetretum and Polypodio-Empetretum)

Table A2. Effect models of *Heracleum mantegazzianum* (Generalized Linear Models with quasi-Poisson distribution and log-link).

A. Basic model

Model component	Estimate	Std. Error	t value	Pr(> t)
Intercept	3.0596	0.0496	61.7	< 0.001
<i>H. mantegazzianum</i> cover	-0.0048	0.0011	-4.2	< 0.001

Null deviance: 842.0 on 201 degrees of freedom

Residual deviance: 771.7 on 200 degrees of freedom

B. Full model

Model component	Estimate	Std. Error	t value	Pr(> t)
Intercept	3.2064	0.0632	50.7	< 0.001
<i>H. mantegazzianum</i> cover	-0.0031	0.0012	-2.6	0.009
Habitat: ruderal grassland	-0.0276	0.0857	-0.3	0.748
Habitat: tall-herb stands	-0.4701	0.0888	-5.3	< 0.001
Habitat: waste ground	-0.1062	0.1132	-0.9	0.349
Habitat: woodland	-0.3745	0.1183	-3.2	0.002

Null deviance: 842.0 on 201 degrees of freedom

Residual deviance: 622.0 on 196 degrees of freedom

Table A3. Effect models of *Lupinus polyphyllus* (Generalized Linear Models with quasi-Poisson distribution and log-link).

A. Basic model

Model component	Estimate	Std. Error	t value	Pr(> t)
Intercept	3.5844	0.0765	46.9	< 0.001
<i>L. polyphyllus</i> cover	-0.0028	0.0012	-2.3	0.024
Plot size (25/ 100 m ²)	0.0017	0.0009	1.8	0.077

Null deviance: 282.8 on 79 degrees of freedom

Residual deviance: 234.3 on 77 degrees of freedom

B. Full model

Model component	Estimate	Std. Error	t value	Pr(> t)
Intercept	3.6334	0.0744	48.9	< 0.001
Plot size (25/ 100 m ²)	0.0012	0.0009	1.3	0.201
<i>L. polyphyllus</i> cover	-0.0020	0.0012	-1.7	0.089
Habitat: ruderal grassland	-0.0067	0.0023	-2.9	0.005

Null deviance: 282.8 on 79 degrees of freedom

Residual deviance: 210.6 on 76 degrees of freedom

Table A4. Effect models of *Rosa rugosa* (Generalized Linear Mixed Models with Poisson distribution and log-link, calculated with “lmer” of the “lme4” package in R).

A. Basic model

Model component	Estimate	Std. Error	z value	Pr(> z)
Intercept	2.5547	0.0659	38.8	< 0.001
<i>R. rugosa</i> cover	-0.0061	0.0011	-5.8	< 0.001

Null deviance: 113.6

Residual deviance: 79.3

B. Full model

Model component	Estimate	Std. Error	z value	Pr(> z)
Intercept	2.2515	0.2209	10.2	< 0.001
<i>R. rugosa</i> cover	0.0035	0.0041	0.9	0.391
Habitat: grey dunes	0.0348	0.1316	0.3	0.791
Habitat: <i>Empetrum</i> heath	-0.3572	0.1463	-2.4	0.015
Habitat: <i>Hippophaë</i> scrub	-0.1643	0.1486	-1.1	0.269
Habitat: <i>Salix</i> scrub	-0.2423	0.1907	-1.3	0.204
Squared <i>R. rugosa</i> cover	-0.4155	0.1684	-2.5	0.014

Null deviance: 113.6

Residual deviance: 61.8