Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs

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Abstract

Questions: Are negative invasion–diversity relationships due to biotic resistance of the invaded plant community or to post-invasion displacement of less competitive species? Do invasion–diversity relationships change with habitat type or resident traits?

Location/species: Lowlands and uplands of western and southern Germany, *Heracleum mantegazzianum*; mountain range in central Germany, *Lupinus polyphyllus*; and coastal dunes of northwest Germany, *Rosa rugosa*.

Methods: We tested the significance and estimated regression slopes of invasion–diversity relationships using generalized linear (mixed effects) models relating invader cover and habitat type to species richness in different plant groups, stratified based on size, life cycle and community association.

Results: We found negative, positive and neutral relationships between invader cover and species richness. There were negative linear correlations of invader cover with small plant species throughout, but no negative linear correlation with tall species. Invasion–diversity relationships tended to be more negative in early-successional habitats, such as dunes or abandoned grasslands, than in late-successional habitats.

Conclusions: Invasion diversity–relationships are complex; they vary among habitat types and among different groups of resident species. Negative invasion–diversity relationships are due to asymmetric competitive displacement of inferior species and not due to biotic resistance. Small species are displaced in early-successional habitats, while there is little effect on persistence of tall species.

Keywords: Asymmetry; Biological invasions; Impact; Species richness; Succession.

Nomenclature: Haeupler & Muer (2000), Koperski et al. (2000), Wirth (1995)

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Introduction

Invasion biologists generally assume negative relationships between plant invasions and the diversity of the invaded plant communities. The hypothesis of biotic resistance predicts that the success of invasive plants, in terms of probability of establishment and abundance, is lower in species-rich communities (Levine et al. 2004). On the other hand, the local expansion of an invader may reduce the richness and diversity of resident species (Bímová et al. 2004; Wearne & Morgan 2004; Maskell et al. 2006; Isermann 2008b). Thus, the relationship between abundance of invasive species and resident diversity is relevant for the assembly and succession of plant communities.

Experimental studies have produced evidence for negative correlations between plant invasion and native diversity (see Levine et al. 2004), whereas observational studies have often found positive or neutral relationships (Bruno et al. 2004; Godfree et al. 2004; Houlahan & Findlay 2004; Essl & Dirnböck 2008). The variability of correlational patterns between invasive and native plant species has often been explained by co-variation of environmental factors and community diversity, leading to positive correlations at among-habitat scales, while correlations may be negative within habitat types (Shea & Chesson 2002; Davies et al. 2007; Fridley et al. 2007; Perelman et al. 2007).

Environmental factors may also control invader abundance, so that apparent invader effects may be confounded with environmental effects (Surrette & Brewer 2008). Therefore, it is necessary to assess correlations between the cover of invasive species and diversity of resident species (hereafter "invasion–diversity relationship") with models that control for environmental variation. Here, we are particularly interested in within-habitat relationships between invasive alien plants and resident diversity.

Although the species of a given plant community differ with respect to numerous traits, such as size and life cycle, surprisingly few studies have considered variation of the invasion–diversity relationship depending on the characteristics of the resident species. Yet relationships between established and arriving plants, such as competition or facilitation, may fundamentally depend on the species inherent characteristics. For example, asymmetrical competition may lead to the displacement of inferior species, while plants with a similar size to the invader may be unaffected (Isermann et al. 2007; Brewer 2008). Thus, invasion–diversity relationships may vary among invasive species and among different groups of resident species, calling for analyses based on ecological plant groups (Ortega & Pearson 2005; Perelman et al. 2007).

Invasion–diversity relationships may be nonlinear if establishment of native and invasive species is facilitated by the same environmental factors or processes, e.g. disturbances, or if moderate abundance of one species has a facilitative effect on the others. If such a positive association turns into a negative one at high invader abundance, e.g. through competitive displacement, the overall relationship becomes unimodal, i.e. diversity first increases and then decreases with invader abundance.

The aim of our study is to assess invasion–diversity relationships in different habitat types using three contrasting invasive plants. Specifically, we ask the following questions:

1. Are negative invasion–diversity relationships shaped by biotic resistance or by post-invasion displacement of resident species?
2. Do invasion–diversity relationships vary with characteristics of the resident species (size, life cycle, community association)?
3. Do invasion–diversity relationships vary among different habitat types?

Materials and Methods

Study species

We chose three invasive plant species that are widespread in Europe, have contrasting life histories, and can build up dominant stands with up to 90–98% cover. These species are the monocarpic plurennial tall herb *Heracleum mantegazzianum* Somm. et Lev. (Apiaceae), the perennial tall herb *Lupinus polyphyllus* Lindl. (Fabaceae) and the polycormic shrub *Rosa rugosa* Thunb (Rosaceae).

H. mantegazzianum originates from the Caucasus Mountains (Pyšek et al. 2007). The rosettes grow to a height of 1–1.5(−1.8) m, while the flowering stems grow up to 3.5(−5)-m high (Hüls 2005). In western and northern Europe, this species invades mesic grassland and disturbed ground, and mainly occurs in nitrophilous tall herb communities (Thiele & Otte 2006).

L. polyphyllus is native to Pacific North America. It has nitrogen-fixing root symbionts and thus increases plant available nitrogen at invaded sites. It reaches 0.7–1.1(−1.5)-m tall and spreads by seeds and rhizomes. The main invaded habitat types in central Europe include nutrient-poor acidic (*Nardus stricta*) grassland and mesic grassland in upland regions, which under the influence of *L. polyphyllus,* become dominated by nitrophilous tall herbs (Otte & Maul 2005).

R. rugosa is a native of the Pacific coasts of China, Japan and Korea. The species forms 1–1.5(−2)-m tall dense thickets (Bruun 2005). In northwestern Europe, it establishes particularly in coastal habitats, such as yellow and grey dunes and dune heath (Kollmann et al. 2007; Isermann 2008a), but also invades inland habitats (Thiele et al. 2009).

Field data

We collated vegetation relevés of the three invasive species from our own field studies. Data on *H. mantegazzianum* consisted of 202 relevés (25-m^2 plots) taken in 22 study areas in lowlands and uplands of western, central and southern Germany (2002–2003). The *L. polyphyllus* dataset comprised 80 relevés collected in two field surveys in the Rhön mountain range in central Germany in 1998 and 2001, using 25- or 100-m^2 plots. For *R. rugosa*, we used 63 relevés (16-m^2 plots) conducted on the East Frisian Islands of Spiekeroog, Norderney and Juist, northwest Germany, in 2001. We minimized sampling bias with respect to species richness (cf. Chytrý 2001) because plot locations were chosen according

to invader occurrences rather than the richness of plant communities, plot sizes were kept constant within field surveys, and only species within plots were recorded.

The datasets included species lists and cover–abundance estimates of vascular plants (in the *R. rugosa* dataset also bryophytes and lichens), cover–percentage estimates of the invaders and habitat classifications. From the vegetation relevés, we calculated species richness of different plant groups, based on size, life cycle and community association. We used the lower limit of the normal invader height range as the size threshold for "small" and "tall" species. Thus, for *H. mantegazzianum* and *R. rugosa*, all species > 1 m in height were classified as "tall", while for *L. polyphyllus* the threshold was 0.7 m. Further, we differentiated three life-cycle types (perennials, biennials, annuals), and distinguished community association based on the species' preferred vegetation classes (Oberdorfer 1983; Berg et al. 2004; see also http://www.floraweb.de) of the syntaxonomical classification (Braun-Blanquet 1964; Pott 1995). These sociological groups were not restricted to characteristic or differential species, but also included species known to be typical companions (see Supporting Information, Table SA1). Species typical of vegetation classes not sufficiently represented within the data were grouped as "other species." Some species were assigned to different groups for different invader datasets. If a vegetation class was not sufficiently represented in one of the datasets to allow for statistical analysis, the species were assigned to the "other species" group. If a species was typical for more than one vegetation class, it was assigned to the class that was represented by more species in the respective dataset.

We assessed the overall diversity of the sampled plant communities with the reciprocal of the Simpson *D* index. We focused these diversity assessments on the invaded herbaceous and dwarf shrub vegetation. Therefore, we excluded trees and tall shrubs, and in the *R. rugosa* dataset we also excluded bryophytes and lichens, from calculations of the reciprocal of Simpson's *D*.

Statistical analyses

Correlations between invader cover percentage and species richness in different plant groups were tested with generalized linear models (GLM) in *R* (*R-Development-Core-Team 2008*). We applied second-order polynomial models of invader cover in order to detect possible non-linear relationships. We accounted for environmental effects on diversity by including habitat type and its interactions with (squared) invader cover percentage into the regression models. The GLM were set up with Poisson distribution, and the significance of the predictor variables and interactions was assessed with sequential likelihood ratio tests (Type I tests) implying a hierarchy of the predictor variables: habitat type (HT) > invader cover (IC) > IC^2 > IC×HT > IC^2 ×HT. Non-significant predictors were excluded from the final models.

The reciprocal of Simpson's *D* was modelled with Gaussian GLM as it was near-normally distributed for *L. polyphyllus* relevés, and log-normally for the other invaders. The GLM of the *L. polyphyllus* dataset included the plot area (25 or 100 m^2) as another predictor, if significant, to account for species–area relationships. For the *R. rugosa* dataset, the models included a random site effect (modelled with *lmer* in *R*; Bates et al. 2008) because the plots were nested in 22 sites.

Results

Total species richness decreased linearly with *H. mantegazzianum* and *L. polyphyllus* cover, whereas there was a unimodal relationship with *R. rugosa* (Table 1). Slopes of total richness tended to be more negative in unmanaged open habitats (ruderal grassland, dunes) compared to both managed grassland and later successional stages, such as tall herb stands and scrub (Fig. 1). The reciprocal of Simpson's *D* diversity index decreased with *L. polyphyllus* cover, while negative correlations were restricted to single habitat types with *R. rugosa* (yellow dunes) and *H. mantegazzianum* (waste ground). In communities dominated by a few species, such as dune heath and scrub, *R. rugosa* tended to be positively associated with diversity.

The number of small species generally decreased with invader cover. However, *R. rugosa* cover only showed continuously negative correlations with small species in yellow and grey dunes, but not in dune heath and scrub. In contrast, "tall" species were either not related to invader cover (*L. polyphyllus*, *R. rugosa*) or they showed a unimodal relationship (*H. mantegazzianum*). The richness of bryophytes and lichens was independent of *R. rugosa* cover. Most often correlations with life-cycle types were negative, except for a unimodal association of annuals with *L. polyphyllus* and of perennials with *R. rugosa*. Negative correlations of *R. rugosa* with annuals were restricted to yellow and grey dunes.

Table 1. Correlations between cover of three invasive alien plant species (*Heracleum mantegazzianum*, *Lupinus polyphyllus*, *Rosa rugosa*) and total richness of resident vascular plant species, Reciprocal of Simpson's D diversity index, and species richness of different plant groups of vegetation relevé plots. Significance was tested with polynomial regression models that included habitat type, invader cover, squared invader cover and interactions of (squared) cover and habitat type.

Heracleum mantegazzianum Dependent variable	Habitat type (HT) (df = 4) P	Invader cover (IC) (df = 1) Effect	Invader cover (IC) (df = 1) P	IC×HT (df = 4) P	IC² (df = 1) Effect	IC² (df = 1) P	IC²×HT (df = 4) P
Total species richness	< 0.001	−	0.009	ns		ns	ns
Reciprocal of Simpson's D (log)	< 0.001		ns	0.008		ns	ns
Tall species	ns	+	0.033	ns	−	< 0.001	ns
Small species	< 0.001	−	0.013	0.012		ns	ns
Perennial herbs	< 0.001	−	0.020	ns		ns	ns
Biennial herbs	0.007	−	0.025	ns		ns	ns
Annuals	ns	−	0.041	ns		ns	ns
Mesic grassland species	< 0.001		ns	0.006		ns	ns
Nitrophilous (tall) herbs	< 0.001	+	0.006	ns	−	0.023	ns
Other species	< 0.001		ns	ns		ns	ns

Lupinus polyphyllus Dependent variable	Habitat type (HT) (df = 1) P	Invader cover (IC) (df = 1) Effect	Invader cover (IC) (df = 1) P	IC×HT (df = 1) P	IC² (df = 1) Effect	IC² (df = 1) P	IC²×HT (df = 1) P
Total species richness	ns	−	0.018	0.004		ns	ns
Reciprocal of Simpson's D	ns	−	0.002	ns		ns	ns
Tall species	0.001		ns	ns		ns	ns
Small species	0.006	−	0.003	ns		ns	ns
Perennial herbs	ns	−	0.007	ns		ns	0.003
Biennial herbs	ns		ns	ns		ns	ns
Annuals	0.036	+	< 0.001	ns		0.017	ns
Mesic grassland species	< 0.001		ns	ns	−	ns	ns
Nitrophilous (tall) herbs	< 0.001	+	< 0.001	< 0.001	−	0.016	ns
Nardus grassland and heath species	< 0.001	−	0.006	ns		ns	ns
Fen and bog-pool species	< 0.001	−	< 0.001	0.005		ns	ns
Other species	< 0.001		ns	ns		ns	0.047

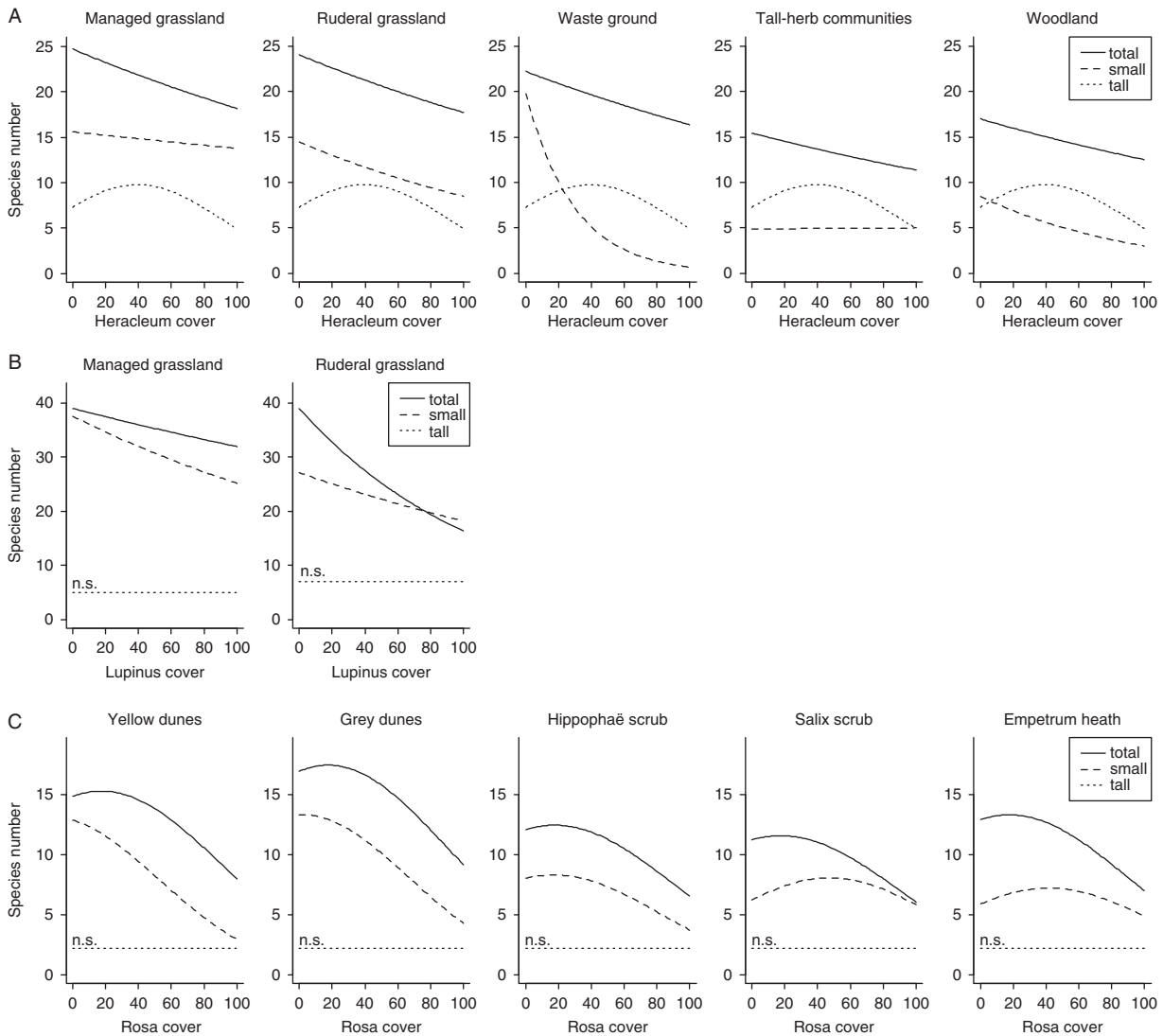| *Rosa rugosa* Dependent variable	Habitat type (HT) (df = 4) P	Invader cover (IC) (df = 1) Effect	Invader cover (IC) (df = 1) P	IC×HT (df = 4) P	IC² (df = 1) Effect	IC² (df = 1) P	IC²×HT (df = 4) P
Total species richness	0.023	+	< 0.001	ns	−	ns	ns
Reciprocal of Simpson's D (log)	0.019	−	0.046	0.010		ns	ns
Tall species	ns		ns	ns		ns	ns
Small species (w/o bryophytes and lichens)	0.007	−	< 0.001	0.013	−	0.026	ns
Cryptogams	< 0.001		ns	ns		ns	ns
Perennial herbs	0.002	+	< 0.001	ns	−	0.007	ns
Biennial herbs	0.016	−	0.005	ns		ns	ns
Annuals	0.003	−	< 0.001	0.008		ns	ns
Yellow dune species	0.006	−	< 0.001	ns		ns	ns
Grey dune species	< 0.001	−	< 0.001	ns		ns	ns
Nardus grassland and heath species	0.001	+	0.003	ns	−	0.014	ns
Mesic grassland	0.046		ns	ns		ns	ns
Scrub and sub-scrub	ns		ns	ns		ns	ns
Other species	ns		ns	0.048		ns	ns

Fig. 1. Relationships between cover of three invasive alien plant species [(**a**). *Heracleum mantegazzianum*, (**b**) *Lupinus polyphyllus*, (**c**) *Rosa rugosa*] and plant species richness (total richness, small and tall plants) in different habitat types. The log-transformed predictions of the Poisson GLM were back-transformed to real figures. There were significant interactions of habitat type and invader cover for small species in the cases of *H. mantegazzianum* and *R. rugosa*, and for total richness in the case of *L. polyphyllus* (Table 1).

Species of early-successional habitat types (yellow dunes, grey dunes, grassland) decreased with increasing cover of *L. polyphyllus* and *R. rugosa*, while *H. mantegazzianum* only tended to be negatively correlated with mesic grassland species on waste ground, but not in other habitat types. The species of dune heath were unimodally related to *R. rugosa* cover. Regarding the richness of plants typical of later successional stages, such as nitrophilous (tall) herbs, scrub and sub-scrub species, there were either unimodal trends or no significant relationship (*R. rugosa*). Species not typical of the invaded vegetation ("other species") were independent of invader cover.

Discussion

Complexity and competitive asymmetry of invasion–diversity relationships

The relationships between invader cover and resident species richness were highly variable among different groups of resident species and among the

three invasive species *H. mantegazzianum*, *L. polyphyllus* and *R. rugosa*. This shows that there is no simple rule relating invasive species to resident richness, but that invasion–diversity relationships depend in a complex way on characteristics of the species involved. Relationships can be positive, negative, unimodal or neutral, depending on the size and environmental preference of the species and on the type of invaded vegetation.

The contrasting results for "small" and "tall" species indicate that competitive asymmetry (sensu Connolly & Wayne 1996) plays an important role for invasion–diversity relationships. For small species the relationship was consistently negative, suggesting that they are displaced by tall invaders, probably through asymmetrical competition for light and space. In contrast, plant species of the same size class as the invaders generally did not incur competitive disadvantages. Only *H. mantegazzianum*, the tallest forb of central Europe, showed a significant unimodal relationship with tall resident plant species, which might be a sign of competitive displacement at very high invader cover percentages. Yet, in the reverse situation, this pattern could also be explained by facilitated invader dominance through the lack of resident competitors (Thiele 2007).

Biotic resistance or competitive displacement?

Although the invasion–diversity patterns were highly variable, all three invasive species were negatively associated with total resident species richness, at least at high invader abundances. There are two basic conceptual models that may explain the overall negative association of invader cover and species richness: biotic resistance or post-invasion competitive displacement of resident species.

The hypothesis of biotic resistance (Levine et al. 2004) predicts that resident species richness will restrict invader cover. Then, we would expect the relationship between invader cover and resident richness to be continuously negative, and slopes should be more negative with tall competitive species than with low-growing species, or more generally, slopes should be more negative with species similar to the invader. Alternatively, invader success may be independent of the original species richness, but displacement of resident species may occur when the invader cover increases. In this post-invasion displacement model the relationship could be either continuously negative or unimodal, as displacement will only occur at high invader cover. Further, we would expect slopes to be more negative

with low-growing and less competitive species, as these are more likely to be displaced than competitive residents (Isermann et al. 2007; Brewer 2008). In this study, correlations with small species were continuously negative, whereas relationships with tall species were either unimodal or neutral. Thus, our results support the post-invasion displacement model rather than biotic resistance.

Successional interactions of invasion–diversity relationships

The three invasive species studied here mainly invade habitat types that represent early-successional stages, such as open dune grassland, waste ground or anthropogenic mesic grassland. These habitat types are prone to successional change towards taller-growing vegetation such as tall herb stands, scrub and woodlands (Otte & Maul 2005; Thiele & Otte 2006; Isermann 2008a). For a good part, the variation of species richness among plots can be explained by differences in environmental conditions and successional stage, as can be seen from the often significant effect of habitat type (Table 1). The older successional stages tended to have significantly lower species numbers than the grasslands, which is in agreement with studies of successions on permanent plots or along chronosequences, where maximum species richness is usually found in intermediate successional stages (Isermann 2005).

In several cases, we found significant interactions of invader cover and habitat type, indicating that invasion–diversity relationships are variable among habitats and along successional series. Local expansion of the invaders appeared to reduce species richness and diversity in comparatively young habitat types, such as waste ground and recently abandoned anthropogenic grasslands where tall herbs invade, or open dune grasslands facing shrub and dwarf shrub encroachment. However, there was little negative effect in subsequent successional stages representing typical habitat types for the invaders, such as tall herb stands (*H. mantegazzianum*, *L. polyphyllus*) and scrub (*R. rugosa*). The differentiated analyses of species with different community association showed that it was primarily species typical of early successional habitat types that decreased. These results suggest that invasive species mediate successional change in vegetation structure, composition and diversity by introducing an additional vegetation layer (tall herb or shrub) into open habitat types. The invaders studied here, however, do not restrict parallel colonization by

native species that are typical of the same or a later successional stage as the invader, although negative effects on colonization rates have been found for other invaders (Yurkonis & Meiners 2004).

Conclusions

Invasion–diversity relationships are complex and depend on size, life history and community association of the resident species. Negative invasion–diversity relationships are shaped by asymmetric competitive displacement of inferior species due to local expansion of invasive species, whereas biotic resistance appears to play no role in our study systems. The three invasive species studied here clearly reduce the diversity of early successional plant communities, but have little effect on later successional stages.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Photo S1. Dominant stand of the invasive alien *Heracleum mantegazzianum* (Giant Hogweed) on abandoned grassland near Copenhagen, Denmark, in October 2008. The 3-m-tall flower stalks have died off giving space to the next cohort of vegetative adult plants that will flower next year (photo J. Kollmann).

Photo S2. *Lupinus polyphyllus* (Large-leafed Lupin) invades abandoned Crane's Bill-Yellow Oat meadows (Geranio–Trisetetum Knapp ex Oberd. 1957) and Mat-Grass pastures (Polygalo-Nardetum Oberd. 57) in the Rhön Biosphere Reserve, Central Germany, 700–900 m a.s.l. (photo A. Otte).

Photo S3. Large stands of the invasive alien *Lupinus polyphyllus* (Large-leafed Lupin) suppress species-rich grassland (Crane's Bill-Yellow Oat meadows (Geranio–Trisetetum Knapp ex Oberd. 1957) and Mat-Grass pastures (Polygalo-Nardetum Oberd. 57)) in the managed zone of the Rhön Biosphere Reserve, Central Germany, 700–900 m a.s.l., allowing nitrophilous tall-herb communities to arise (photo A. Otte).

Photo S4. The invasive alien shrub *Rosa rugosa* (Japanese Rose), flower and hips on the island of Amrum, Germany (photo M. Isermann).

Photo S5. Initial stages of *Rosa rugosa* (Japanese Rose) invasion on white dunes in northern Zealand, Denmark (photo J. Kollmann).

Photo S6. The invasive alien *Rosa rugosa* (Japanese Rose) forms extensive, dense thickets on coastal dunes. The picture shows invaded grey dunes on Langeoog, Germany, covered by about 2 ha of white and pink flowering *Rosa rugosa*, June 2008 (photo M. Isermann).

Table SA1. Sociological species groups and corresponding vegetation classes. Species assigned to different sociological groups for different datasets are marked: H, *Heracleum mantegazzianum* dataset; L, *Lupinus polyphyllus*; R, *Rosa rugosa*.

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