This is the peer-reviewed (final) version of the following article:

Thiele J, Kollmann J, Markussen B, Otte A: Impact assessment revisited – improving the theoretical basis for management of invasive alien species. *Biological Invasions*, DOI 10.1007/s10530-009-9605-2.

The original publication is available at
http://www.springerlink.com/content/y541q8507gq33x12/.

Impact assessment revisited – improving the theoretical basis for management of invasive alien species

Thiele J[1*], Kollmann J[1], Markussen B[2], Otte A[3]

[1] University of Copenhagen, Department of Agriculture and Ecology, Rolighedsvej 21, 1958 Frederiksberg C, Denmark
[2] University of Copenhagen, Department of Basic Sciences and Environment, Thorvaldsensvej 40, 1871 Frederiksberg C, Denmark
[3] University of Giessen, Institute of Landscape Ecology and Resources Management, Heinrich-Buff-Ring 26–32, 35392 Giessen, Germany
[*]Corresponding author:
Jan Thiele, current work address: University of Münster, Institute of Landscape Ecology, Robert-Koch-Str. 26–32, 48149 Münster, Germany, Tel. +49 251 83 30075, Fax. +49 251 83 38338, Jan.Thiele@uni-muenster.de

Abstract

The theoretical underpinnings of the assessment of invasive alien species impacts need to be improved. At present most approaches are unreliable to quantify impact at regional scales and do not allow for comparison of different invasive species. There are four basic problems that need to be addressed: (1) Some impacted ecosystem traits are spatially not additive; (2) invader effects may increase non-linearly with abundance or there may be effect thresholds impairing estimates of linear impact models; (3) the abundance and impact of alien species will often co-vary with environmental variation; and (4) the total invaded range is an inappropriate measure for quantifying regional impact because the habitat area available for invasion can vary markedly among invasive species. Mathematical models and empirical data using an invasive alien plant species (*Heracleum mantegazzianum*) indicate that ignoring these issues leads to impact estimates almost an order of magnitude from the real values. Thus, we propose a habitat-sensitive formula for regional impact assessment that is unaffected by non-linearity. Furthermore, we make some statistical suggestions on how to assess invader effects properly and we discuss the quantification of the invaded range. These improvements are crucial for impact assessment with the overall aim of prioritizing management of invasive species.

Keywords: biological invasion, ecological impact, *Heracleum mantegazzianum*, invaded range, non-native species, quantification of regional impacts

Introduction

The impact of invasive alien species on ecosystem traits presents one of the major challenges of applied ecological research. Currently, scientists are trying to improve the theoretical basis for assessing the consequences of biological invasions (e.g. Reaser et al. 2007). Rigorous impact assessment is of vital importance for policy makers, nature conservation authorities and land managers who must decide whether to institute management programs for particular species. For sound decisions, it is necessary to quantify the impact of invasive alien species (McNeely et al. 2001), and given limited financial resources, the species have to be ranked according to their overall impact for setting management priorities (Hiebert 1997; Wittenberg and Cock 2001; Byers et al. 2002). While assessments of local effects of invasive species (e.g. on quadrats of some m^2) remain a key issue of impact assessment, we need to scale up to regional scales, because invaders, even if they show similar local abundance–effect patterns, may differ markedly in range size, proportion of impacted habitat within that range, and habitat specificity of their effects.

Parker et al. (1999) proposed a conceptual model for the quantification of regional impacts based on the linear equation, $I = R \times A \times E$, where I is the overall impact of the invader, R is the invaded range, A is the average invader abundance (number of individuals, biomass or other abundance measure per unit area), and E is the effect per individual or biomass unit (per-capita effect). This model integrates the major components of regional impacts, it provides the basic arithmetics and sets standards with regard to units of measurement. However, as Parker et al. (1999) already noted, the three axes of the impact model may be correlated and, then, the linear formulation becomes inappropriate. So far, no attempts have been made to estimate the measurement errors when applying the linear equation to concrete invasions where abundance and per-capita effect might be correlated.

Despite the scale of the management problems with invasive alien species there have been relatively few attempts to improve the theoretical basis for impact assessment. There is no solution available for how to deal with non-linear abundance–effect relationships, although recently some studies of economic impacts of invasive species applied non-linear impact functions (see Yokomizo et al. 2009). Further, there have been few suggestions on how to quantify the major impact components, i.e. range, abundance and effect, and thus the results of impact assessments can vary about one order of magnitude depending on the method chosen. Thus, there is a need for developing a consistent conceptual framework for impact assessment.

The following theoretical considerations and some empirical evidence focus on terrestrial animals and plants that impact ecosystem structure and function. Assessments of economical impacts use monetary currencies relying on somewhat different impact models and methods of quantification (e.g. Pimentel et al. 2001; Colautti et al. 2006; Cook et al. 2007; Juliá et al. 2007). However, we believe that the points discussed here could also be relevant to economical impact assessments.

The intention of the paper is to contribute to a more robust theory of impact assessment. We suggest some practical improvements, indicate directions for future research, and hope to stimulate some discussion among invasion biologists and ecologists. Specifically, our objectives are (1) to give an account of impacted ecosystem traits and their spatial additivity; (2) to elucidate the quantification of local effects under correlation of per-capita effect and abundance; (3) to discuss the delineation of the invaded range; and (4) to introduce an improved formula for calculation of regional impacts.

Impacted ecosystem traits

Invasive species can impact various ecosystem structures and functions at different levels of integration (Table 1). At the population level, for instance, demographic rates and genetic structure of native species can be affected (Williams and Crone 2006). At the community level, impacts can pertain to the abundance of resident species, community composition, species richness and soil seed bank (Meiners et al. 2001; Yurkonis and Meiners 2004; Mason et al. 2007). In the physical environment, invasive alien species can modify erosion processes, the availability of soil nutrients, and the water balance (Mack and D'Antonio 1998; Richardson and van Wilgen 2004; Gómez-Aparicio and Canham 2008). With regard to whole ecosystems, disturbance regimes, primary production, trophic interactions, pollinator services and a number of other ecosystem functions can be altered (Mack and D'Antonio 1998; Mack et al. 2000; Larson et al. 2006; Lopezaraiza-Mikel et al. 2007; Aizen et al. 2008; Nielsen et al. 2008).

Impacts can be assessed at different spatial scales, from single stands to the entire invaded range. If the aim is to quantify regional impacts, the question is whether or not effects on ecosystem traits concerned are spatially additive. For example, the biomass of native species that is displaced by an invasive alien species can be summed up over a number of invaded stands to yield a total regional impact in absolute figures of biomass. However, if the species richness of invaded vegetation is changed, it is not possible to sum up local impacts in terms of reduced species numbers in order to derive an absolute measure of regional impact. This is due to species being abstract categories that comprise a large (but unknown) number of individuals within a given range, rather than concrete entities, like a single individual or biomass unit. Thus, rigorous regional impact assessment in absolute numbers is limited to those ecosystem traits that are additive (cf. Table 1).

Quantification of local effects

Non-linearity of the abundance–effect relationship

The basic linear formula for quantification of regional impacts proposed by Parker et al. (1999) is based on average abundance multiplied with the effect per individual or biomass unit. This formula is valid if the per-capita effect (E) is constant and, hence, the effect per area (i.e. $A \times E$, where A is invader abundance) increases linearly with abundance (cf. Fig. 1). However, if E is a function of A, and thus this assumption is not met, then the basic linear formula will give wrong estimates of the per-area effect and, consequently, inaccurate accounts of impacts at the regional scale. More precisely, the mean of a non-linear function is not equal to the function of the mean.

The inaccuracy of using average abundance can be avoided by calculating the average local per-area effect ($\overline{P}$), i.e. the sum over all invaded stands ($i = 1 \ldots n$) of the product of abundance A_i and the per-capita effect E_i (being a function of A_i), then divided by the number of stands:

$$\overline{p} = \frac{\sum_{i=1}^{n} (A_i \times E_i)}{n} \quad \text{(eqn 1).}$$

Table 1 Structural and functional ecosystem traits impacted by invasive alien plant species at different levels of biological integration. Included are currencies for quantifying impacts and whether impacts are additive, i.e. can be summed up over several invaded sites, or not

Ecosystem traits	Currency	Additivity
Population		
Abundance	Individuals · area^{-1}	yes
Demographic rates	E.g. intrinsic growth rate (λ)	no
Genetic diversity	Diversity indices	no
Hybridization	Hybridization events	yes
Gene pool	Introgressed genes	yes
Community		
Species richness	Species · area^{-1}	no
Diversity	Diversity indices	no
Native biomass	kg · area^{-1}	yes
Primary productivity	kg · area^{-1} · a^{-1}	yes
Soil seed bank	Seeds · a^{-1}	yes
Abiotic environment		
Soil erosion	kg · a^{-1}	yes
Nutrient pools and supply rates	kg · area^{-1}, kg · area^{-1} · a^{-1}	yes
Water balance	l · a^{-1}	yes
Ecosystem		
Trophic interactions	Food web connections	no
Mutualisms	Mutualists	no
Disturbance regime	E.g. altered fire frequency	no
Pollinator services	Pollinator visits	yes

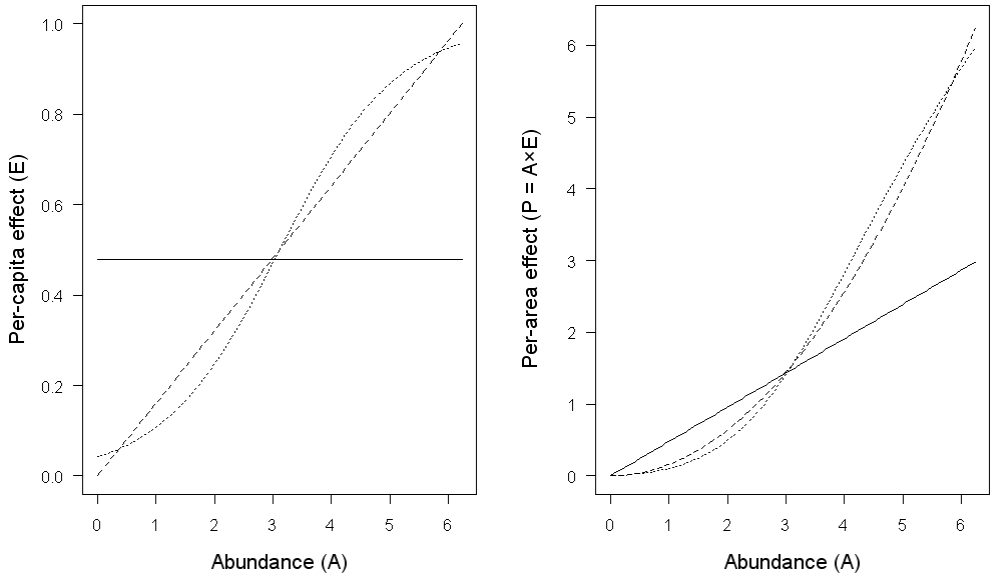
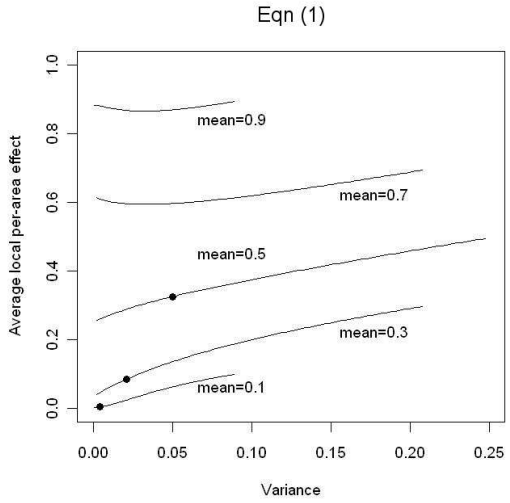


Fig. 1 Relationship between invader abundance and (a) per-capita effect (*E*), and (b) per-area effect ($E \times A$). The bold line represents the assumption implied in the basic linear impact formula (Parker et al. 1999) of constant per-capita effect and, consequently, linear increase of the per-area effect with invader abundance. In contrast, the other curves show linear increase (broken line) and sigmoid increase (dotted line) of the per-capita effect with invader abundance, which translates into a non-linear increase of per-area effect with invader abundance

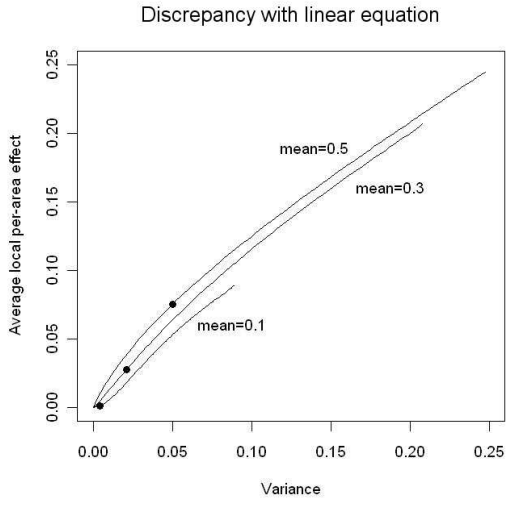
If there is a positive relationship between per-capita effect *E* and abundance *A*, the basic linear formula will underestimate the regional impact. Generally, the discrepancy between eqn (1) and the basic linear formula equals the covariance between *E* and *A*. We studied this discrepancy for three different cases of the abundance–effect relationship (see supplementary material):

1) For a constant per-capita effect *E* and, respectively, a linear increase of the local per-area effect with invader abundance, there is no discrepancy between the two formulas.

2) If *E* is a linear function of *A*, that is $E = \gamma_0 + \gamma_1 \times A$, then the discrepancy equals the product of the slope γ_1 and the variance of *A*. If the slope is positive, the basic linear formula underestimates the impact. Generally, the discrepancy increases linearly with the variance of the invader abundance.



(a)



(b)

Fig. 2 Results of impact computations based on a *positive sigmoid* relationship between the per-capita effect *E* and abundance *A* and on Beta distributions of the abundance (see Appendix S3, Figs. S1, S2). (a) The average local per-area effect of an invasive species calculated with eqn (1). The curves show that the average per-area effect depends on the mean and the variance of the invader abundance. (b) The underestimation of the average local per-area effect when using the basic linear formula (Parker et al. 1999) compared to eqn (1) based on the same sigmoid example. The three dots represent the Beta distributions shown in Fig. S1

3) If *E* is a positive sigmoid function of *A*, which might be a fairly realistic assumption, the result is similar to the positive linear function. Since the slope is positive, the basic linear formula underestimates the impact, and the magnitude of the discrepancy depends primarily on the variance of *A*. Secondarily, the magnitude of the discrepancy depends on other characteristics of the abundance distribution, such as the mean of *A*, if abundances follow e.g. Beta distributions (Fig. 2; see Appendix S3).

Abundance thresholds for adverse effects

A basic linear model of invader effects implies that impacts are present at all stand densities or, respectively, abundances of the invasive alien species. Yet it is conceivable that low local abundance of invasive species may have no substantial adverse effects. This can be shown for *Heracleum mantegazzianum* Somm. et Lev. (Apiaceae), a competitive-ruderal tall-herb which is highly invasive in Europe and North America (e.g. Thiele and Otte 2006; Pyšek et al. 2007). The analysis of plant species richness within 25-m² quadrats showed that open stands of the invader (i.e. cover percentage ≤50%) had no effect, whereas dominant stands significantly reduced species richness (Fig. 3).

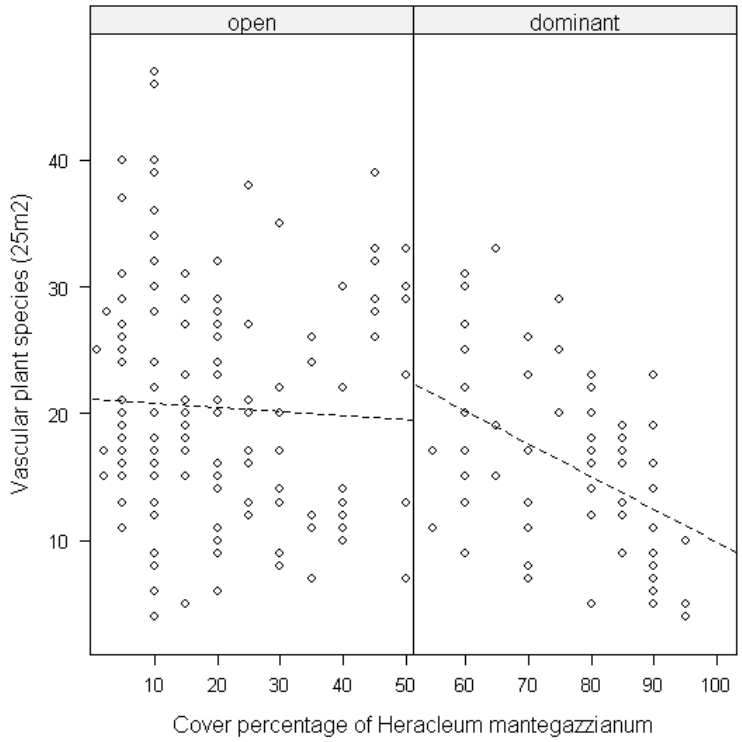


Fig. 3 Vascular plant species numbers of 25-m² quadrats (n = 202) in relation to cover percentages of the invasive *Heracleum mantegazzianum*. Species numbers decreased significantly with cover percentages within dominant stands of the invader (cover >50%; estimate = –0.26; $p < 0.001$), while there was no significant relationship in open stands (cover ≤50%; estimate = –0.03; $p = 0.536$). Data from Thiele and Otte (2007)

If there is an abundance threshold for adverse effects of an invader, then a linear model calculated for all of the invader's stands regardless of density might overestimate impacts. Yet the opposite can be true as well. In the example of *H. mantegazzianum*, a linear effect model including only the dominant stands yielded a much steeper slope, i.e. a stronger effect on species numbers, than a model for all stand densities (Fig. 4).

Consequently, the calculated impact was higher when basing the model on dominant stands and ignoring open stands.

For efficient management of invasive alien species it is important to detect effect thresholds. With thresholds present, it could be a reasonable option to institute control programs that keep the stand densities of the invader at or slightly below the impact threshold (cf. Byers et al. 2002), instead of conducting large-scale eradication programs which are likely much more cost-intensive.

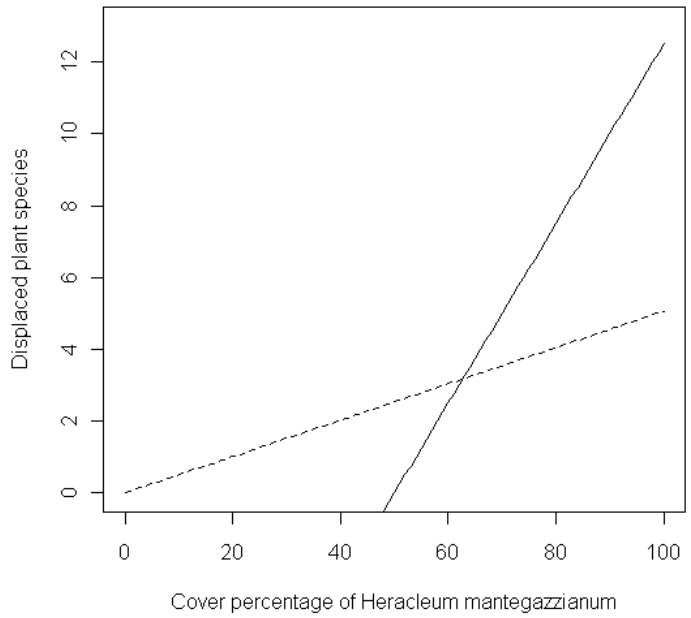


Fig. 4 Comparison of two effect models of *Heracleum mantegazzianum* on vascular plant species number in 25-m² quadrats based on regression analyses of empirical data (n = 202). The bold line shows the model for dominant stands (cover > 50%), while the broken line shows the model for all stands

Habitat specificity of effects

As many natives, invasive alien species may occur in more than one habitat type. Environmental variation among habitats can affect biomass, life-cycle duration, population growth and competitive interactions of the invader (Byers 2002; Thiele and Otte 2006; Hüls et al. 2007; Traveset et al. 2008). As a consequence, the effects an invader exerts on resident species, communities and ecosystems may change with habitat type (Griffen and Byers 2006; Hacker and Dethier 2006; Thiele and Otte 2007; Isermann 2008). While a species may be neutral or could have only a small effect in one habitat, it might become a hazard in another. There can also be habitat-specific abundance thresholds with respect to effects and, eventually, the spectrum of impacted ecosystem traits may vary with habitat type. Thus, we need to test for differences of invader effects between habitat types in order to assess effects correctly.

Testing the significance of effects

The quality of ecosystem traits that can be impacted by invasive species, such as biodiversity, resident biomass or nutrient pools, can vary among habitat types independently of the invader. At the same time, the variation of habitat quality can be

correlated with the abundances of the invader which could lead to statistical confounding. Hence, significance tests of effects that consider only the abundances of the invader but exclude environmental variation may be misleading.

For instance, the effect of *H. mantegazzianum* on species numbers was estimated in a simple linear regression as –0.083, i.e. a loss of 4.15 species at an increase of the invader by 50 cover-percentage points. Yet, a regression including habitat type as a co-factor yielded an effect estimate of –0.047, i.e. 2.35 species lost at an increase by 50 percentage points (Thiele and Otte 2007). Here, the model excluding environmental variation among habitats gave an almost twofold overestimate of the effect.

To account for the environmental variation that is independent of the invasive species, effects should be tested with models that include invader abundance as the main variate and habitat type as a co-factor as well as their interaction term (if significant). If there appear to be different abundance–effect relationships among habitats, then impact assessment should use separate effect estimates (slopes) for each habitat type.

For the estimation of effects, linear Gaussian models are often used. However, the ecosystem traits in question may not be normally distributed and, thus, may violate the assumptions of normal errors and homoscedasticity. For instance, species numbers are essentially count data which usually are Poisson-distributed. Cover-percentages represent proportion data that may be modelled with a binomial distribution or a Beta distribution (cf. Johnson et al. 1994). In such cases, the significance levels of effects in linear models (OLS, Gaussian GLM) may be erroneous. While it is possible to assess the magnitude of the effect with an ordinary linear model (given that there is a linear abundance–effect relationship), it is advisable to test the significance of the effect with the most adequate model under the given distribution of the data.

As the effects per individual or per biomass unit of an invader can vary with both the abundance of the invader itself and the type of habitat invaded, a thorough assessment may require a large sample of invaded sites. The samples should be either strictly random (cf. Rinella and Luschei 2007) or a complete survey in a predefined area, so that the sample sites are representative for the invader. As invader abundances are far from equilibrium close to invading fronts, the sampling should be confined to where the invader has been present for a longer period of time.

Assessment of invader abundance

The impact assessment of invasive alien species as proposed by Parker et al. (1999) is based on biomass or abundance (number of individuals) to quantify the stand density of the invader. Biomass is supposedly an excellent measure of stand density as it is strongly correlated with the amount of resources captured by the invader. Altering the availability of resources is, at least from a theoretical perspective, a precondition for effects on neighbouring species. Next to direct competition, the availability of resources can be modified through alteration of nutrient cycles (e.g. nitrogen fixation) or changes of the disturbance regime (Crooks 2002; Richardson and van Wilgen 2004). In addition, there can be direct allelopathic effects (Callaway and Ridenour 2004). In most cases, we would expect the magnitude of the effect to be related to the biomass of the invader, although some effects, such as reduced pollinator availability, may be less correlated with biomass.

Biomass, though, is tedious to sample and gauge, so that abundance estimates may be more practical, particularly in extensive field studies. However, plant biomass can vary vastly among individuals and habitats, and thus stands with the same invader biomass may reveal markedly different abundance estimates. Likewise, the assessment of effects on a per-capita basis, as required when using abundance estimates, is prone to

inaccuracies as the effects that individuals have will largely vary with body size. In the invasive *H. mantegazzianum*, we found, in fact, no significant correlation between invader abundance (i.e. number of individuals per quadrat) and total species richness or cover sum of resident species, although there were significant effects of the invader when using cover percentages. Thus, while abundance may be a good correlate of biomass density of animals that show less pronounced variation in body mass, we think it is not advisable to use abundance estimates in impact assessment of invasive plant species.

Hence, we would suggest using cover percentages in standardized quadrats as proxy for biomass. It appears reasonable to base the estimation of effects on cover percentages, both of the invader and the impacted communities. Empirical assessments of stand densities of the invader as well as the effects can be done using the same quadrats. This approach would allow for relatively quick and extensive field surveys with tens or hundreds of quadrats. Further, it would be possible to analyze existing vegetation relevés stored in large data bases (see for example Chytrý et al. 2008), to assess effects of invasive alien species on native species and communities.

Invaded range

How to delineate the invaded range?

For quantifying overall regional impact, we use the area of the invaded range to project the local effect to the regional scale. While it is mathematically straight forward to multiply range with the average per-area effect (eqn 1) to assess the overall impact of an invasive alien species, there can be substantial difficulties in the delineation of the invaded range itself.

Firstly, it is a non-trivial task to determine the outer limits of the range. Besides general difficulties in the delineation of species' ranges (Gaston 2003), uncertainties can arise about the status of a species (native, introduced) in different parts of its distributional range. Further, it is debatable whether to use the whole non-indigenous range of a species or whether to define the invaded range as the area where invasive behaviour is observed, i.e. strong spread and high stand densities (Davis and Thompson 2000). It would be logical to constrain the invaded range to the area where effects of the invader are evident, if sufficient empirical data were available from throughout the non-indigenous range.

Secondly, invasive alien species are usually confined to a few habitat types that only make up a subset of the habitats occurring within the total invaded range (R). In cases of species that invade patchy habitats with low coverage in the landscape, the area actually available for invasion and prone to impacts may be about an order of magnitude smaller than R. Thus, the proportion of available habitat within R may vary considerably between different invasive alien species. Therefore, the impacts of two invasive species cannot be compared based on an impact assessment that uses the total invaded range R. For comparable impact assessments, the range has to be narrowed down to the suitable habitat area (R_H) within R instead. In cases, where an invader impacts only a subset of the invaded habitat types, the area of the impacted habitat types (R_P) should be used, so that the range for overall impact assessment is:

$$R_P = \sum_{j=1}^{m} area_j \quad \text{(eqn 2)}$$

where $j = 1 \ldots m$ denotes the impacted habitat types.

Potential and current impact

The calculation of overall impact *I* based on R_P estimates the potential maximum impact that an invasive species can have given that it is able to invade the whole area of impactable habitat. While full invasion can be expected in contiguous habitats, invasion may be dispersal-limited in fragmented or patchy habitats (Thiele et al. 2008) and, thus, the real maximum invasion may comprise much less than 100% of the potentially available habitat area.

To rigorously compare invasions of species with different dispersal abilities invading habitat types with different configurations (contiguous or patchy), we would have to predict the maximum invasion success measured in terms of the invaded habitat range (R_I) at the end of the invasion process. This is naturally a complex and tedious task which can only be done with thorough model simulations of the species' population dynamics at landscape and regional scales. In the absence of such advanced solutions, a rough but comparatively easy and practical estimate of the maximum invasion of a species might be field surveys in invasion hotspots to calculate the proportional invaded habitat area (R_I) and the habitat saturation (R_S) (cf. Pyšek and Pyšek 1995; Thiele and Otte 2008).

How to quantify overall impacts at the regional scale?

Following from the above considerations, we would like to develop further the formula proposed by Parker et al. (1999) for the calculation of overall impacts on the regional scale (*I*). Instead of using the average abundance and assuming constant effect per individual or biomass unit, we propose to calculate the local per-area effect for a sample of invaded stands as $P_i = A_i \times E_i$, where the per-capita effect E_i is a function of invader abundance A_i (measurable as biomass or cover percentage) that is to be assessed from a representative sample of invaded sites ($i = 1 \ldots n$). Then, the average local per-area effect can be estimated as the arithmetic mean of the sites (eqn 1). In case that effect sizes differ between habitat types ($j = 1 \ldots m$), there should be made separate estimates of the effect function ($E_{ji} = f_j(A_{ji})$) and the average local per-area effect for each impacted habitat type ($\overline{P}_j$). The average local effects are then multiplied on the range of the respective habitat type R_j and, finally, the overall impact is calculated as the sum of these products over all impacted habitat types ($j = 1 \ldots m$). Thus, the formula for overall regional impact is:

$$I = \sum_{j=1}^{m} \left(R_j \times \frac{\sum_{i=1}^{n_j} (A_{ji} \times E_{ji})}{n_j} \right) \text{ (eqn 3),}$$

or in a more condensed form:

$$I = \sum_{j=1}^{m} (R_j \times \overline{P}_j) \text{ (eqn 4).}$$

Practical example

To test the applicability of the equations and considerations presented here, we calculated the impact of the invasive *H. mantegazzianum*, on the cover of resident vegetation, using the basic linear model and four impact models based on eqn 1 (Table 2). Field data were taken from a large data set collected during the EU-project 'Giant Alien' (Pyšek et al. 2007). The data set comprised 202 quadrats (25 m²) which where distributed among 20 landscape sections (1 km²) in different regions of central Europe. Cover percentages were estimated separately for the invader and different layers (tree,

shrub, herb etc.) of resident vegetation (for more details see Thiele and Otte 2006, 2008). Effects were tested with linear and second degree-polynomial regressions of resident cover percentage on the cover percentage of *H. mantegazzianum*. In this example, the impact models did not include significant non-linear terms. Thresholds were tested for by analysing subsets of the data with high or low invader cover percentages. For one habitat type (ruderal grassland) we found a significant effect threshold. For convenience, we set the total invaded range to 100 and used proportional values for available habitat areas that were measured from aerial photographs of 20 study areas covering 20 km².

The impact model using the average local per-area effect (eqn 1) of all habitat types and the total invaded range did not deviate much from the Parker model (Table 2, model 2a), because the effect models were linear in this case. However, habitat-sensitive models constrained to the invasible range differed by almost an order of magnitude from the basic models since only about a third of the area was suitable and some habitat types were not significantly impacted. The unit of the impact measure is area (e.g. km²) here, due to the impacted ecosystem traits under study being cover of resident vegetation. The basic models of Table 2 thus predicted a loss of 20 areal units of resident vegetation cover throughout a range of 100 areal units, whereas the most detailed model (2d) predicted a loss of 3 areal units. As regards other impacted ecosystem traits, the impact measure may take various different units.

Table 2 Impact assessments of an invasive plant species, *Heracleum mantegazzianum*, using the basic linear model (1; $I = R \times A \times E$) and different models based on the average per-area effect calculated with eqns 1 and 4 (2a–d; $I = R \times P$). Model 2a uses the total invaded range, whereas model 2b only uses the habitat area within the invaded range. Models 2c and 2d use habitat-sensitive estimates of range and effect (habitats without significant impact omitted), with model 2d also taking into account an effect threshold of 40% invader cover for the habitat type 'ruderal grasslands'. Values in italics were not used for calculations. In this example, the unit of the impact measure is area because we multiply range with the effect on resident cover per invader cover (i.e. the effect estimates are dimensionless)

Impact model		Range (proportional) (R)	Average cover percentage (A)	Effect estimate (E)	Average per-area effect (P)	Calculated Impact (I)
1	Basic linear formula	100	37.0	0.56	NA	**20.6**
2a	Total range	100	*37.0*	*0.56*	0.20	**19.9**
2b	Invasible range	33.7	*37.0*	*0.56*	0.20	**6.7**
2c	Habitat sensitive					
	Ruderal grasslands	4.0	*44.2*	*0.46*	0.19	0.76
	Tall-herb communities	5.7	*49.2*	*0.71*	0.35	2.01
	Woodlands	1.6	*23.2*	*0.72*	0.16	0.26
					Σ	**3.0**
2d	Habitat sensitive, w/ threshold					
	Ruderal grasslands	4.0	*44.2*	***0.72***	**0.21**	0.82
	Tall-herb communities	5.7	*49.2*	*0.71*	0.35	2.01
	Woodlands	1.6	*23.2*	*0.72*	0.16	0.26
					Σ	**3.1**

Implications and perspectives

More empirical research is needed to elucidate the relationship between invader abundance and the effects on different ecosystem traits. Yet the example of the relatively well studied *H. mantegazzianum* suggests that effect thresholds may not be uncommon in invasive alien species. Non-linear increase of per-area effects with

invader abundance was not found for impacts on the cover percentage of resident vegetation in the example presented here, but needs to be considered in effect modelling as the estimation error can be severe. The computations presented in Fig. 2 showed underestimates of the basic linear formula by ca. 33% and 25% compared to the robust formula (eqn 1) for the exemplary distributions of invader abundances with means of 0.3 and 0.5, respectively (cf. Fig. S1). For *H. mantegazzianum*, the variance of abundances was roughly twice as large (0.09) as for the distributions shown in Fig. S1 and, consequently, the estimation error would have been about 50%, given that the sigmoid increase of the per-capita effect models the effect of this species correctly. As the estimation error strongly depends on the variance of invader abundance (Fig. 2B) and variances may vary among species, the results of impact assessments using the basic linear formula are not comparable among species. Impact assessments become even more ambiguous, if there are no clear standards of how to delineate the invaded range, because the difference between total range and invasible (or impacted) range will often be as large as one order of magnitude. The practical example reveals that impact assessments ignoring these issues will be of little value for both scientific investigations as well as rankings of invasive species and setting management priorities.

For future research on impact assessment of invasive species, the most urgent question is about the abundance–effect relationship. Empirical studies considering a wide range of species and ecosystem traits are now needed to assess the complexity of invader effects and, where possible, to draw generalisations. It is important to study the whole array of invader abundances because, in the light of effect thresholds and non-linear abundance–effect relationships, it is not possible to extrapolate effect estimates made from a subset of the abundance array to higher or lower abundances. This is particularly important to consider in experimental studies of invader effects where abundances are controlled as part of the experimental design. For practical applications, impact assessments of invasive species need to be standardised with regard to the quantification of the invaded range. Further, it would be helpful to establish conventions about the way of quantifying invader abundance and to develop standard procedures for sampling and estimating effects.

Supplementary material

Appendix S1 Mathematical basis
Appendix S2 Discrepancy of eqn (1) and the basic linear formula
Appendix S3 Impact computations for sigmoid *f*
Figure S1 Beta distributions
Figure S2 Sigmoid function

References

Aizen MA, Morales CL, Morales JM (2008) Invasive mutualists erode native pollination webs. PLoS Biology. DOI:10.1371/journal.pbio.0060031

Byers JE (2002) Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. Oecologia 130:146–156

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. Conserv Biol 16:630–640

Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Front Ecol Environ 2:436–443

Chytrý M, Jarošík V, Pyšek P, Hájek O, Knollová I, Tichý L, Danihelka J (2008) Separating habitat invasibility by alien plants from the actual level of invasion. Ecology 89:1541–1553
Colautti RI, Bailey SA, van Overdijk CDA, Amundsen K, McIsaac HJ (2006) Characterised and projected costs of non-indigenous species in Canada. Biol Invasions 8:45–59
Cook DC, Thomas MB, Cunningham SA, Anderson DL, De Barro DJ (2007) Predicting the economic impact of an invasive species on an ecosystem service. Ecol Appl 17:1832–1840
Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166
Davis MA, Thompson K (2000) Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature for invasion ecology. ESA Bull 81:226–230
Gaston KJ (2003) The structure and dynamics of geographic ranges. Oxford University Press, Oxford
Gómez-Aparicio L, Canham CD (2008) Neighborhood models of the effects of invasive tree species on ecosystem processes. Ecol Monogr 78:69–86
Griffen BD, Byers JE (2006) Partitioning mechanisms of predator interference in different habitats. Oecologia 146:608–614
Hacker SD, Dethier MN (2006) Community modification by a grass invader has differing impacts for marine habitats. Oikos 113:279–286
Hiebert R (1997) Prioritizing invasive plants and planning for management. In: Luken JO, Thieret JW (eds) Assessment and management of plant invasions. Springer, New York, pp 195–212
Hüls J, Otte A, Eckstein RL (2007) Population life-cycle and stand structure in dense and open stands of the introduced tall herb *Heracleum mantegazzianum*. Biol Invasions 9:799–811
Isermann M (2008) Effects of *Rosa rugosa* invasion in different coastal dune vegetation types. In: Tokarska-Guzik B, Brock JH, Brundu G, Child L, Daehler CC, Pyšek P (eds) Plant invasions: human perception, ecological impacts and management. Backhuys Publishers, Leiden, pp 289–306
Johnson NL, Kotz S, Balakrishnan N (1994) Continuous univariate distributions, 2nd edn. John Wiley & Sons, New York
Juliá R, Holland DW, Guenther J (2007) Assessing the economic impact of invasive species: The case of yellow starthistle (*Centaurea solstitialis* L.) in the rangelands of Idaho, USA. J Environ Manage 85:876–882
Larson DL, Royer RA, Royer MR (2006) Insect visitation and pollen deposition in an invaded prairie plant community. Biol Conserv 130:148–159
Lopezaraiza-Mikel ME, Hayes RB, Whalley MR, Memmot J (2007) The impact of an alien plant on a native plant-pollinator network: an experimental approach. Ecol Lett 10:539–550
Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. Trends Ecol Evol 13:195–198
Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences and control. Ecol Appl 10:689–710
Mason TJ, French K, Russell KG (2007) Moderate impacts of plant invasion and management regimes in coastal hind dune seed banks. Biol Conserv 134:428–439

McNeely JA, Mooney HA, Neville LE, Schei P, Waage JK (2001) Global strategy on invasive alien species. IUCN on behalf of the Global Invasive Species Programme, Gland

Meiners SJ, Pickett STA, Cadenasso ML (2001) Effects of plant invasions on the species richness of abandoned agricultural land. Ecography 24:633–644

Nielsen C, Heimes C, Kollmann J (2008) Little evidence for negative effects of an invasive alien plant on pollinator services. Biol Invasions 10:1353–1363

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. Biol Invasions 1:3–19

Pimentel D, McNair S, Janecka J, Wightman J, Simmonds C, O'Connell C, Wong E, Russel L, Zern J, Aquino T, Tsomondo T (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. Agr Ecosyst Environ 84:1–20

Pyšek P, Pyšek A (1995) Invasion by *Heracleum mantegazzianum* in different habitats in the Czech Republic. J Veg Sci 6:711–718

Pyšek P, Cock MJW, Nentwig W, Ravn HP (eds, 2007) Ecology and Management of Giant Hogweed (*Heracleum mantegazzianum*). CAB International, Wallingford

Reaser JK, Meyerson LA, Cronk Q, De Poorter M, Eldrege LG, Green E, Kairo M, Latasi P, Mack RN, Mauremootoo J, O'Dowd D, Orapa W, Sastroutomo S, Saunders A, Shine C, Thrainsson S, Vaiutu L, (2007) Ecological and socioeconomic impacts of invasive alien species in island ecosystems. Environ Conserv 34:98–111

Richardson DM, van Wilgen BW (2004) Invasive alien plants in South Africa: how well do we understand the ecological impacts? S Afr J Sci 100:45–52

Rinella MJ, Luschei EC (2007) Hierarchical Bayesian methods estimate invasive weed impacts at pertinent spatial scales. Biol Invasions 9:545–558

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

Thiele J, Otte A (2007) Impact of *Heracleum mantegazzianum* on invaded vegetation and human activities. In: Pyšek P, Cock MJW, Nentwig W, Ravn HP, Wade M (eds) Ecology and management of giant hogweed (*Heracleum mantegazzianum*). CAB International, Wallingford, pp 144–156

Thiele J, Otte A (2008) Invasion patterns of *Heracleum mantegazzianum* in Germany on the regional and landscape scales. J Nat Conserv 16:61–71

Thiele J, Schuckert U, Otte A (2008) Cultural landscapes of Germany are patch-corridor-matrix mosaics for an invasive megaforb. Landscape Ecol 23:453–465

Traveset A, Brundu G, Carta L, Mprezetou I, Lambdon P, Manca M, Médail F, Moragues E, Rodríguez-Pérez J, Siamantziouras A-SD, Suehs CM, Troumbis AY, Vilà M, Hulme P (2008) Consistent performance of invasive plant species within and among islands of the Mediterranean basin. Biol Invasions 10:847–858

Williams JL, Crone EE (2006) The impact of invasive grasses on the population growth of *Anemone patens*, a long-lived native forb. Ecology 87:3200–3208

Wittenberg R, Cock MJW (2001) Invasive alien species: a toolkit of best prevention and management practices. CAB International, Wallingford

Yokomizo H, Possingham HP, Thomas MB, Buckley YM (2009) Managing the impact of invasive species: the value of knowing the density–impact curve. Ecol Appl 19:376–386
Yurkonis KA, Meiners SJ (2004) Invasion impacts local species turnover in a successional system. Ecol Lett 7:764–769