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OPINION ARTICLE

The Human Release Hypothesis for biological invasions: human activity as a determinant of the abundance of invasive plant species [version 1; peer review: 2 approved]

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Abstract

Research on biological invasions has increased rapidly over the past 30 years, generating numerous explanations of how species become invasive. While the mechanisms of invasive species establishment are well studied, the mechanisms driving abundance patterns (i.e. patterns of population density) remain poorly understood. Invasive species typically have higher abundances in their new environments than in their native ranges, and patterns of invasive species abundance differ between invaded regions. To explain differences in invasive species abundance, we propose the Human Release Hypothesis. In parallel to the established Enemy Release Hypothesis, this hypothesis states that the abundance of invasive species may be partly explained by the level of human activity or landscape maintenance, with intermediate levels of human activity providing optimal conditions for high abundance. The Human Release Hypothesis does not negate other important drivers of species invasions, but rather should be considered as a potentially important additional or complementary mechanism. We illustrate the hypothesis via a case study on an invasive rose species, and hypothesize which locations globally may be most likely to support high abundances of invasive species. We propose that more extensive empirical work on the Human Release Hypothesis could be useful to test its general applicability.

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report

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Any reports and responses or comments on the article can be found at the end of the article.

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Introduction

Biological invasions can threaten ecosystems¹, economies², and human health³. The Scientific Committee on Problems of the Environment (SCOPE) put biological invasions on top of its research agenda in 1983⁴. Since then, the field of invasion ecology has rapidly gained momentum. The number of publications dealing with biological invasions has increased a hundredfold in less than two decades⁵. Several journals are partly (e.g. *Diversity and Distributions*, *Natural Areas Journal*) or fully (e.g. *Biological Invasions*, *Invasive Plant Science and Management*, *NeoBiota*) devoted to research, management and policy issues related to invasive species. However, despite a growing body of knowledge on biological invasions, difficulties remain in predicting invasion success⁶.

Within Europe, the distribution of people is strongly related to the number of alien species. Presumably, this reflects that biological invasions are aided by human transport and that species establishment is facilitated by human disturbance⁷. Nevertheless, at the global scale, the proportion of widely distributed alien plant species (relative to all species) is far lower in Europe than in North America – despite Europe's long history of trade and therefore a longer residence time of alien plants⁸. The observation that Europe serves as a global contributor of alien plant species, whereas North America seems to be a better recipient, has sparked the concept of biological resistance, which explains invasion success or failure in relation to the traits of the native flora⁹. An additional important consideration, which has not been assessed to date, could be that Europe also has a higher proportion of landscapes that are actively managed by humans than, for example, the Americas, Australia and Africa¹⁰. To date, approaches to predict invasion patterns in response to anthropogenic global change have focused on (i) the extent of novel ecosystems¹¹, and (ii) alien species richness¹².

In this paper, we propose that the abundance of an alien species in a given landscape can be (at least partly) explained by the level of active landscape maintenance by humans. We term this hypothesis the Human Release Hypothesis. As discussed in detail below, the Human Release Hypothesis states that the abundance of invasive species may be partly explained by the level of human activity or landscape maintenance, with intermediate levels of human activity providing optimal conditions for high abundance. Unlike the Disturbance Hypothesis and the Intermediate Disturbance Hypothesis, which explain patterns of establishment of invasive species¹³ and patterns of native species diversity respectively¹⁴, the Human Release Hypothesis specifically addresses patterns in the abundance of alien species that are already established in particular areas outside their native ranges.

We first discuss how the Human Release Hypothesis fits into the context of other key hypotheses in invasion ecology. We then illustrate the hypothesis via a case study on a global invader, the sweetbriar rose (*Rosa rubiginosa* L.). Finally, we assess how the Human Release Hypothesis may be integrated into biological invasion research, and we hypothesize which locations worldwide may be particularly prone to supporting high abundances of invasive species.

The Human Release Hypothesis

According to Richardson *et al.* (2000)¹⁵, an invasive terrestrial plant species is a naturalized alien species that produces reproductive

offspring, often in very large numbers, at considerable distance from parent plants, and thus has the potential to spread over extensive areas. A key question in invasion ecology is how the interaction of species traits with environmental characteristics predicts invasion success, including both establishment and abundance in the new environment⁶.

Catford *et al.* (2009)¹⁶ summarized 29 leading hypotheses predicting invasion success and integrated them into the PAB-framework (Figure 1). This framework considers the size and frequency of introductions (i.e. propagule pressure, P), ecosystem invasibility based on abiotic characteristics of the new environment (A), and biotic characteristics of an invasive species and its recipient community (B). In this framework, human influence on the invasion process is recognized primarily during the establishment stage. For example, human action can increase propagule pressure¹⁷ and multiple introduction events make establishment more likely, because species have a higher chance to encounter suitable environmental conditions¹⁸. Multiple introductions of the same species also can lead to higher genetic diversity¹⁹. However, examples exist of successful invaders with low genetic diversity²⁰, and stemming from single or few introduction events, suggesting that propagule pressure is only one of many variables explaining invasion patterns²¹.

With respect to abiotic conditions, invasion is facilitated if species are pre-adapted to their new environment, for example due to a similar climate in the new environment²². Like propagule pressure, pre-adaption is not a necessary precondition for successful invasion, because climatic niche shifts have been reported for invasive species²³. Disturbance events also provide windows of opportunity for invasive species²⁴. Many invasive plant species are adapted to exploit temporarily favourable conditions through their short life cycles, rapid growth, high reproductive allocation,

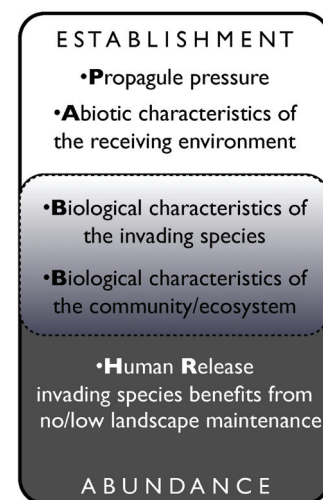


Figure 1. Incorporating our hypothesis into the PAB framework. The establishment and abundance of invasive plant species are explained by different mechanisms, which have been summarized by Catford *et al.* (2009)¹⁶ in the PAB framework (see text for details). However, the biological characteristics of a given invading species and of its new environment only partly explain the abundance of established invasive populations. We argue that additional insights can be gained via the Human Release Hypotheses, which can complement the existing PAB framework.

persistent soil seed banks and rapid germination (the Ideal Weed Hypothesis)²⁵.

Finally, biotic characteristics of the recipient community may involve the absence of natural enemies. The Enemy Release Hypothesis explains invasion success as a function of alien species having escaped their natural enemies, allowing them to allocate resources to growth and reproduction rather than defence²⁶. This would make alien plants stronger competitors. In the context of the Intermediate Disturbance Hypothesis, which proposes higher species diversity at intermediate frequencies or intensities of disturbance (see Wilkinson, 1999)¹⁴, alien plants are likely to have the greatest impact on community diversity when resources become limited and plant diversity is highest, by co-opting more resources²⁷.

In parallel to the Enemy Release Hypothesis, here, we propose the Human Release Hypothesis. It describes a situation where alien species have escaped relatively higher levels of human landscape maintenance that is characteristic within their native ranges. Changing patterns of land use are widely recognized to increase opportunities for introduced species to establish and spread²⁸, but already prevailing patterns of land use intensity also should be expected to influence the populations of species – both in their native and introduced ranges. This is because highly intensive land use by humans (such as in many parts of Western Europe) often corresponds to high levels of active landscape maintenance – which translates into little available habitat for both native and introduced species, as well as high levels of active weed control. At the other end of the spectrum of human land use intensity, we hypothesize that pristine natural habitats also offer few windows of opportunity for alien

species to establish (the Biotic Resistance Hypothesis)²⁹. Thus, we hypothesize that the abundance of invasive species should be highest in between these two extremes – namely in extensively used landscapes characterized by frequent fallowing, low levels of weed control, high heterogeneity, and many disturbed edges of small farmland patches³⁰. Such landscapes are where “human release” should contribute to optimal conditions for invasive species to establish large populations.

While existing hypotheses explain the establishment and naturalization process of invasions, little work has attempted to explain the (potential) abundance of invasive species in their new environments. Part of this gap may be effectively addressed by the Human Release Hypothesis (Figure 1).

Case study on an invasive rose

To illustrate the plausibility of the Human Release Hypothesis, we present findings at two scales on the invasion success of *Rosa rubiginosa*, a shrub native to Eurasia and invasive in Australia, New Zealand, South Africa, North and South America (see Dataset 1 and Supplementary Figure S1). First, we synthesize previous cross-continental case studies that compared plant performance between invasive populations in Central and Southern Argentina with native populations in Spain and Germany (for more details see Zimmermann *et al.*, 2012)³¹. Second, we compare climatic conditions as well as land use and human population density between invasive and native *R. rubiginosa* populations at a global scale. In combination, our findings suggest the Human Release Hypothesis may be a useful complementary hypothesis to other existing hypotheses in invasion biology (Table 1).

Table 1. Hypothesis for the invasion success as they apply to *Rosa rubiginosa* in Argentina. (^aCavallero & Raffaele 2010, ^bZimmermann *et al.* 2010, ^c2011, ^d2012, ^eHirsch *et al.* 2011, ^fpresent publication).

Hypothesis	Mechanism	Case study	
Propagule Pressure	Multiple introductions into new range make establishment more likely and secure high genetic diversity	Genetic diversity in invasive populations very low, small number of introduction events ^{b,e}	REJECTED
Favorable environmental conditions	Species benefits from climatic or edaphic conditions, or vegetation characteristics in new range	Structure of vegetation matrix did not differ between ranges, edaphic conditions not favourable in invasive populations and climatic conditions vary greatly within the introduced range ^{d,f}	
Enemy Release	Invasive species allocates resources no longer needed for defence to growth and reproduction	Damaged or infested leaf area high in invasive and native range ^d	
Evolution of Increased Competitive Ability	Selection favours genotypes which have allocated resources, which are no longer needed for defence to adapting and enhancing competitive ability	Individuals from both ranges same growth rates in common garden experiments ^d	
Ideal Weed	Invasive species share traits that facilitate invasions	Ideal weed traits of study species: high phenotypic plasticity, clonal growth, asexual reproduction ^{b,d}	CONFIRMED
Disturbance	Disturbance events open window of opportunity for invasive species	Species occurs in invasive range across habitat types after anthropogenic or natural disturbance ^{a,c}	
Human Release	Invasive species benefits from low levels of landscape maintenance	Trimming or removal of individuals only in native range, individuals in invasive range older, in invasive range lower number of people/km ² as well as less residential areas and less cropland area than in native range ^{d,f}	PROPOSED

Rosa rubiginosa has successfully invaded a range of ecosystems within Argentina, covering a major climatic gradient, but exhibiting low levels of genetic diversity^{32,33} (Figure 2a). Low genetic diversity suggests that multiple introduction events constituting particularly high propagule pressure cannot explain the species' invasion success. Despite lower genetic diversity, populations of *R. rubiginosa* are considerably smaller in Spain and Germany than in Argentina (Figure 3) – native populations consist of 5 to 20 individuals whereas invasive populations consist of hundreds of individuals³¹. In addition to propagule pressure, abiotic and biotic variables also cannot fully explain the invasion success of *R. rubiginosa*. In Argentina, the species neither benefits from favourable soil conditions nor from reduced biotic resistance³¹.

Moreover, a global climatic analysis shows that *R. rubiginosa* also does not depend or benefit from pre-adaptation to the climate of its new environment (Figure 2b). We developed two climatic envelope models based on BioClim parameters and the occurrence of native and invasive populations respectively using the maximum entropy method³⁴ (MAXENT, see Appendix 1 and 2 in the Supplementary

material). We detected a significant differentiation of realized niches between invasive and native populations (Schoener's $D=0.31$, $p<0.0001$; Figure 2b). Furthermore, back-projection of the climatic niche based on invasive populations points to a southern European origin. However, genetic analyses tracked the native origin of invasive Argentinean, Chilean, Australian and New Zealand populations to Central Europe^{32,33}. Key climatic predictors therefore do not point to a climatic advantage in the invasive range, but instead indicate that *R. rubiginosa* is able to thrive under a wide range of conditions (Supplementary Figure S2 and Supplementary Figure S3).

The Ideal Weed and Disturbance Hypotheses (Table 1) partly explain the invasion success of *R. rubiginosa* in Argentina^{31,35,36}. However, the Enemy Release Hypothesis failed to explain abundance patterns – natural enemies appeared equally harmful to the species in the native and introduced ranges³¹ (Table 1). By contrast, in the invasive range, anthropogenic disturbances such as logging and burning create windows of opportunities for the rose to establish, but just as importantly, disturbance events are then followed by decades of abandonment that enable the species to become abundant.

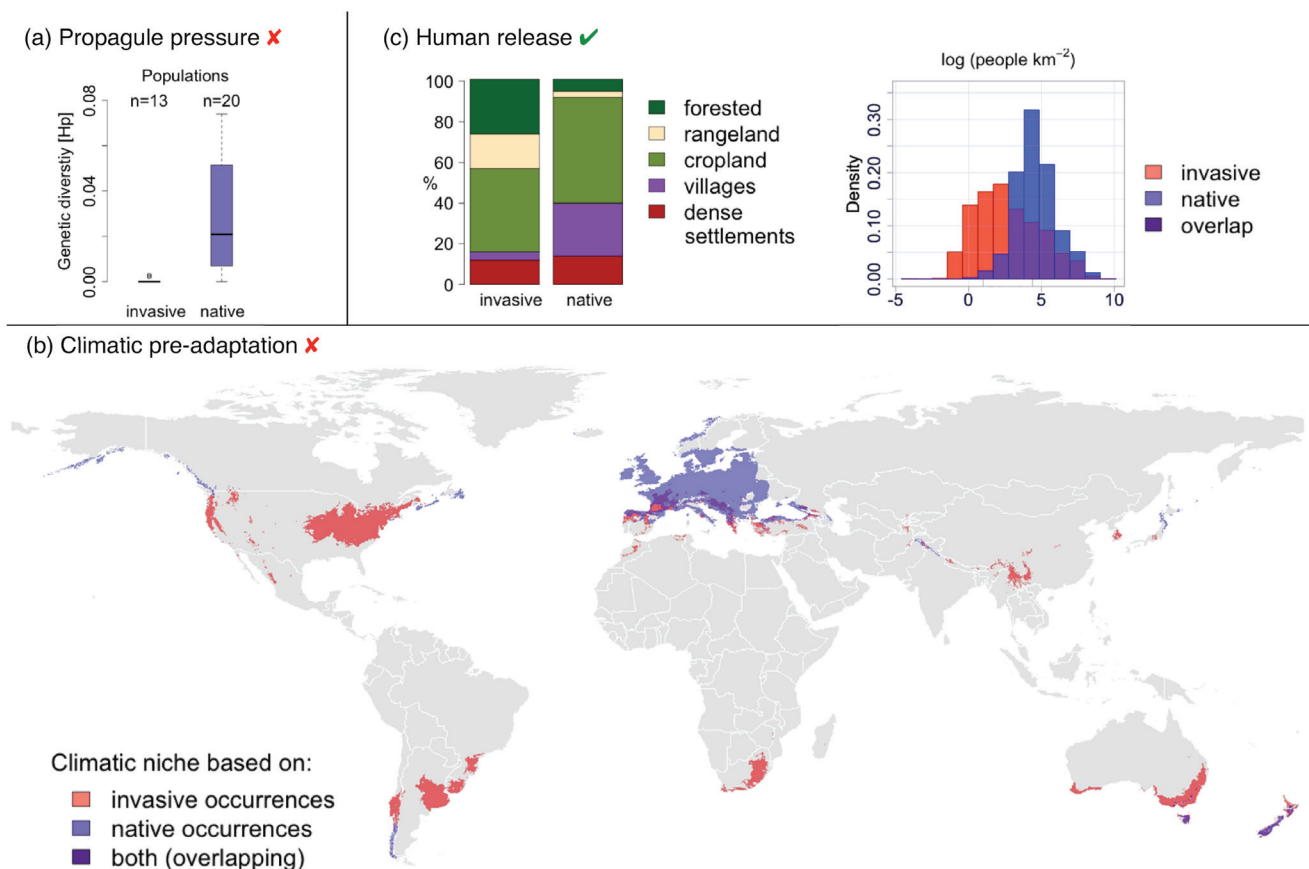


Figure 2. *Rosa rubiginosa* benefits from human release. (a) Genetic diversity in *Rosa rubiginosa* is higher in its native Spanish and German populations than in the introduced populations in Argentina, suggesting the species did not benefit from multiple introductions (for details see Zimmermann *et al.* 2010)³². (b) The species does not benefit from a climatic pre-adaptation to the new range. The world map shows the species' climatic niche based on the species' native distribution (blue) and the invasive distribution (pink). Overlap of climatic niches (purple) is minimal. (c) *Rosa rubiginosa* appears to benefit from "human release" in its new range. The barplot shows the global proportions of different anthropogenic biomes¹⁰ according to the location of invasive and native sweetbriar rose populations. The native range has a larger proportion of residential areas and a higher human population density (log people/km²). Only 0.56% of the invasive range is wildlands, and only 0.03% of the native range.



Figure 3. Invasive *Rosa rubiginosa* populations in Argentina (a, b) and native populations in Germany (c) and Spain (d). In parts of Argentina, single disturbance events have offered windows of opportunity for the species to establish populations, some of which have remained undisturbed for 30 years or longer (a)^{31,36}. The low level of human landscape maintenance means that populations can expand over vast areas and consist of hundreds of individuals (a, here along the whole visible lakeside in Patagonia). (a) For our study area in Patagonia we predicted that 36% of the area (5000 km²) was threatened by *R. rubiginosa* invasion, across a precipitation gradient from 1400 mm/annum (mountains in the far background) to 600 mm/a³⁶. In Argentina *R. rubiginosa* shrubs have time to grow to their full size (b), by contrast, many native landscapes are regularly maintained; shrubs are regularly trimmed and mostly grow in hedgerows (c, Germany). Furthermore, in Germany and Spain, fewer habitats are available in landscapes dominated by agriculture and urban areas (d, Spain).

Having considered a wide range of existing hypotheses (Table 1), we found that additional insights into the invasion patterns of *R. rubiginosa* may be gained by the Human Release Hypothesis. This is because a key difference between native and introduced environments appears to be the level of active landscape maintenance. In the case study, we observed frequent trimming or removal of individuals only in Spain and Germany and not in Argentina, and individuals and populations in Argentina were significantly older than their native counterparts^{31,36}. At the global scale, our analysis revealed a similar pattern (albeit at a coarser resolution; 2.5 × 2.5 arc min, Figure 2c). Native *R. rubiginosa* populations occur in areas with higher proportions of cropland, residential areas and human population densities than invasive populations (Figure 2c). These conditions very likely correspond to a high degree of landscape maintenance, and hence little available habitat for *R. rubiginosa* in its native range.

Integrating the Human Release Hypothesis with other explanations

A key premise of this paper is that existing hypotheses that predict invasion success can be effectively complemented by the Human Release Hypothesis (Figure 1). Our own data, of course, focused only on one species – which is enough to pose a hypothesis, but far too little to test its general usefulness. To that end, we see two research priorities that should be addressed to further scrutinize the Human Release Hypothesis so that, if appropriate, it can be integrated into invasive species management. First, additional species should be studied in both their native ranges and in different parts of their introduced ranges. Such comparisons would be useful to test the drivers of invasive species abundance and to validate (or refute) invasion patterns derived from modelling approaches^{11,12}. An important first clue that the Human Release Hypothesis may be relevant could be whether invasive individuals of a given perennial species are significantly older than individuals within the native range. Second, it may be useful to further investigate the relationship between landscape maintenance and human land use intensity, how it manifests in different regions, and if generalizations are possible at the global scale. The frequency of weeding and trimming, as well as the prevalence of fallowing, are just two of many potential indicators for the level of active landscape maintenance.

Dataset 1. *Rosa rubiginosa* L. occurrence data (occurrences_R. rubiginosa.csv, 416 kb)

1 Data File

<http://dx.doi.org/10.6084/m9.figshare.1002067>

Evidently, the Human Release Hypothesis is still in its infancy, and it would be unwise to make bold management recommendations on its basis. Based on our analysis to date, preliminary insights that are relevant to managing invasive species are: (i) sparsely populated areas may face a higher risk of biological invasions than more densely populated areas; (ii) extensively managed rangelands may be more susceptible to high abundances of invasive species than intensively managed croplands; and (iii) high abundances of invasive species at landscape and regional scales could be facilitated by long periods of fallowing or land abandonment³⁷.

Data availability

figshare: Dataset 1. Rosa rubiginosa L. occurrence data (occurrences_R.rubiginosa.csv, 416 kb). Doi: [10.6084/m9.figshare.100206738](https://doi.org/10.6084/m9.figshare.100206738)

Author contributions

HZ and HvW conceived the study. HvW and PB performed the climatic niche model and PB performed the climatic niche equivalency test. JF and HvW contributed substantially to the framing of the

manuscript. EW compiled the geographic distribution of the study species. HZ wrote the first draft of the manuscript and contributed to the data analysis and data collection, and all authors contributed substantially to revisions.

Competing interests

No competing interests were disclosed.

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Supplementary material

<https://f1000researchdata.s3.amazonaws.com/supplementary/3740/7d02646a-def8-4980-adf8-fd60fb4d75a5.pdf>

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Melisa Giorgis

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This manuscript presents a simple and interesting hypothesis about how human activities could drive the increase in abundance of invasive species. It is based on two important observations; 1. Invasive species have in general higher abundances in their new environment than in the native ranges, and 2. The patterns of invasive species differ between invaded regions. The authors realized that human land management activities explain the difference in abundance of species, between both the invader and native range and between different invader regions. Specifically they put a new role for “human activities” into the second stage of plant invasion ([Diez & Edwards, 2006](#)). I think that it is an interesting hypothesis, which provides a new vision and background for future research on invasion ecology and conservation management. Finally, I have some suggestions that may help to a better understanding of this article and future development.

1. The need for a clear definition of “active landscape maintenance by human”. The authors at the end mention the frequency of weeding and trimming, as potential indicators of active landscape maintenance. But could human maintenance be defined as any human activity developed in order to sustain the same physiognomy, structure, floristic composition or/and biomass? “Active landscape maintenance” is for me too general. If active landscapes involve just the maintenance of biomass, it could be defined as “disturbance” in the context of “intermediate hypothesis”. But perhaps it might be more than just biomass.
2. Did this hypothesis explain the species abundance in both the native and the invaded range? Please check the third paragraph in the introduction with the third paragraph in the page four. From the manuscript I understand that it explains the abundance in both situations.
3. In the second paragraph of the introduction: I don't find the aim of the last line. Moreover, the author could improve the first paragraph after the subtitle The Human Release Hypothesis, because I also don't understand the logic among that paragraph. It seems to be two important sentences (important), but I don't find any cohesion between them. It is also quite hard to understand what the paragraph aims for.

4. Future context. 1; how this hypothesis works for different life forms (competitor; stress-tolerator; ruderal plant strategy). I find really interesting thinking of this. Maybe the context of Fig. 1 of [Diez and Edwards \(2006\)](#) is a good scene. 2; the manuscript focus on Europe as the principal and the only example, but maybe Asia is another possible example. On one hand it provides a great amount of invasive species and on the other hand it has a higher proportion of dense settlements. Species like *Cotoneaster*, *Ligustrum* and *Pyracantha* that are native from Asia are the most invasive species in the earth and cover at least in Argentina, an significant portion of landscape.

Competing Interests: No competing interests were disclosed.

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Author Response 09 Dec 2014

Heike Zimmermann, Leuphana University, Lüneburg, Germany

Thank you for your thorough and helpful review. We have incorporated all the minor comments concerning typos and wording. For our response to the mayor comments please see below:

1. We included a more detailed explanation of landscape maintenance. The key difference between "disturbance" and "maintenance" is the time scale. Disturbance can be a single event but maintenance is defined as "work that is done to KEEP something in good conditions".

See [Introduction](#): "We define intermediate levels of human activity as activity patterns defined by sporadic disturbance events that are followed by long periods lacking active management, such as fallowing or abandonment. In contrast, regions with high levels of human activity frequently experience active management, such as weeding, hedge trimming or mowing of field margins."

See section [The Human Release Hypothesis in the context of other invasion hypotheses](#): "Thus, we hypothesize that the abundance of invasive species should be highest in between these two extremes – namely in extensively used landscapes characterized by frequent fallowing, low levels of weed control, high heterogeneity, and many disturbed edges of small farmland patches³². Such landscapes are where "human release" should contribute to optimal conditions for invasive species to establish large populations."

2. Yes, it does explain the abundance in both ranges. We clarified this now further in the [Introduction](#): "Finally, we propose that the Human Release Hypothesis can also explain why some species that are highly abundant in their invasive range have relatively low abundance in their native range."

3. We re-wrote this paragraph and hope it is now comprehensible:

"To date, extensive data on the abundance of invasive alien species is widely lacking. Existing approaches to predict invasion patterns in response to anthropogenic global change have focused primarily on the development of novel ecosystems¹¹ and alien

species richness¹². Based on this, it is now widely acknowledged that systems containing high numbers of alien species tend to be those created and sustained by humans."

4. Future context. We now included a paragraph on how our hypothesis applies to different life strategies, and we encourage to investigate how comparisons between species from Asia and their invasive range could fit to our hypothesis.

See section The Human Release Hypothesis in the context of other invasion hypotheses: "Disturbance events also provide windows of opportunity for invasive species²⁶ and are often the result of human activity. Many invasive plant species are adapted to exploit temporarily favourable conditions through their short life cycles, rapid growth, high reproductive allocation, persistent soil seed banks and rapid germination (the Ideal Weed Hypothesis)²⁷. All these traits are also of advantage in systems where frequent weeding or mowing is practiced. Therefore, species pursuing this competitive ruderal strategy could profit twofold from Human Release."

See last section: "We generated our hypothesis based on findings in Europe, however many invasive plant species on the American continent originate from Asia^{42,43}, thus it would be interesting to test our hypothesis based on land use patterns from these regions. "

Competing Interests: No competing interests were disclosed.

Reviewer Report 23 May 2014

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Christoph Kueffer

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This is an interesting concept paper. It touches upon two timely research problems in invasion science: (i) how to better incorporate the role of humans into invasion theory, and (ii) how to improve the predictability of the abundance of invasive alien species (instead of only occurrence).

The key idea of the proposed 'human release hypothesis' seems that land management intensity – especially of abandoned or extensively used habitat – can explain differences in the abundance of a species between its native and alien ranges because the abundance of the species might be reduced in the native range through more intensive management of such land and associated cutting of the species. This is an interesting idea because it states that the presence of humans and their effects on landscapes can reduce invasion spread in opposition to traditional thinking that sees human land use mainly as a driver of invasions. The authors propose for instance that differences in land management coverage and intensity might explain why Europe is less invaded than regions with a higher proportion of wildlands such as North America or Australia.

The argumentation of the article fits also well with recent thinking in biodiversity conservation that emphasizes that permanent conservation intervention will in the future increasingly be necessary to maintain threatened biodiversity and ecosystem services in an era of global change; and that this will require building on synergies with other land use practices (such as weeding through agricultural practices in buffer zones around protected areas).

Competing Interests: No competing interests were disclosed.

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

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