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# No universal scale-dependent impacts of invasive species on native plant species richness

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A growing number of studies seeking generalizations about the impact of plant invasions compare heavily invaded sites to uninvaded sites. But does this approach warrant any generalizations? Using two large datasets from forests, grasslands and desert ecosystems across the conterminous United States, we show that (i) a continuum of invasion impacts exists in many biomes and (ii) many possible species–area relationships may emerge reflecting a wide range of patterns of co-occurrence of native and alien plant species. Our results contradict a smaller recent study by Powell *et al.* 2013 (*Science* **339**, 316–318. (doi:10.1126/science.1226817)), who compared heavily invaded and uninvaded sites in three biomes and concluded that plant communities invaded by non-native plant species generally have lower local richness (intercepts of log species richness–log area regression lines) but steeper species accumulation with increasing area (slopes of the regression lines) than do uninvaded communities. We conclude that the impacts of plant invasions on plant species richness are not universal.

## 1. Introduction

An unsettling paradox in terrestrial plant ecology has emerged: alien plant invasions often increase regional plant diversity without causing extinctions of native plant species [1]. In the absence of empirical evidence of continuing plant invasions causing extinctions, some studies have used forecasting models to calculate a growing 'extinction debt' [2]. Such forecasts may assume that mounting extinctions are an inevitable consequence of negative interactions with invading plants and that weaker factors contribute to native species persistence (e.g. adaptations, dispersal, long-lasting seed banks). However, the levels of uncertainty of ecological forecasts may be difficult to quantify, owing to uncertainties in future climates, unpredictable disturbances, species adaptations and the effects of trade and transportation bringing in enemies to alien and native species alike [3–5]. Models of plant extinction debt would be more convincing if there were extensive empirical evidence of native plant extinctions caused by direct or indirect interactions with alien plant species. This consideration has spawned a fervent quest by biologists to survey native plant extirpations and extinctions in sites of extreme invasions where species loss might be expected to occur first [6,7].

In their haste to observe plant extinctions, some biologists might be tempted to rely on field data on extirpation (a local-scale species disappearance or, perhaps, a temporary species absence). Plant populations, however, are dynamic and often ephemeral [8], and long-term, detailed, large-scale studies of invaded plant communities are very rare. Perhaps for these reasons, a growing number of invasion studies use a haphazard (or subjective) sampling design to compare heavily invaded and uninvaded sites to investigate the impact of invasions on local plant species presence and abundance.

Comparing heavily invaded and uninvaded paired sites sounds simple. But are the effects of invasive species that black and white? Powell *et al.* [6] reported

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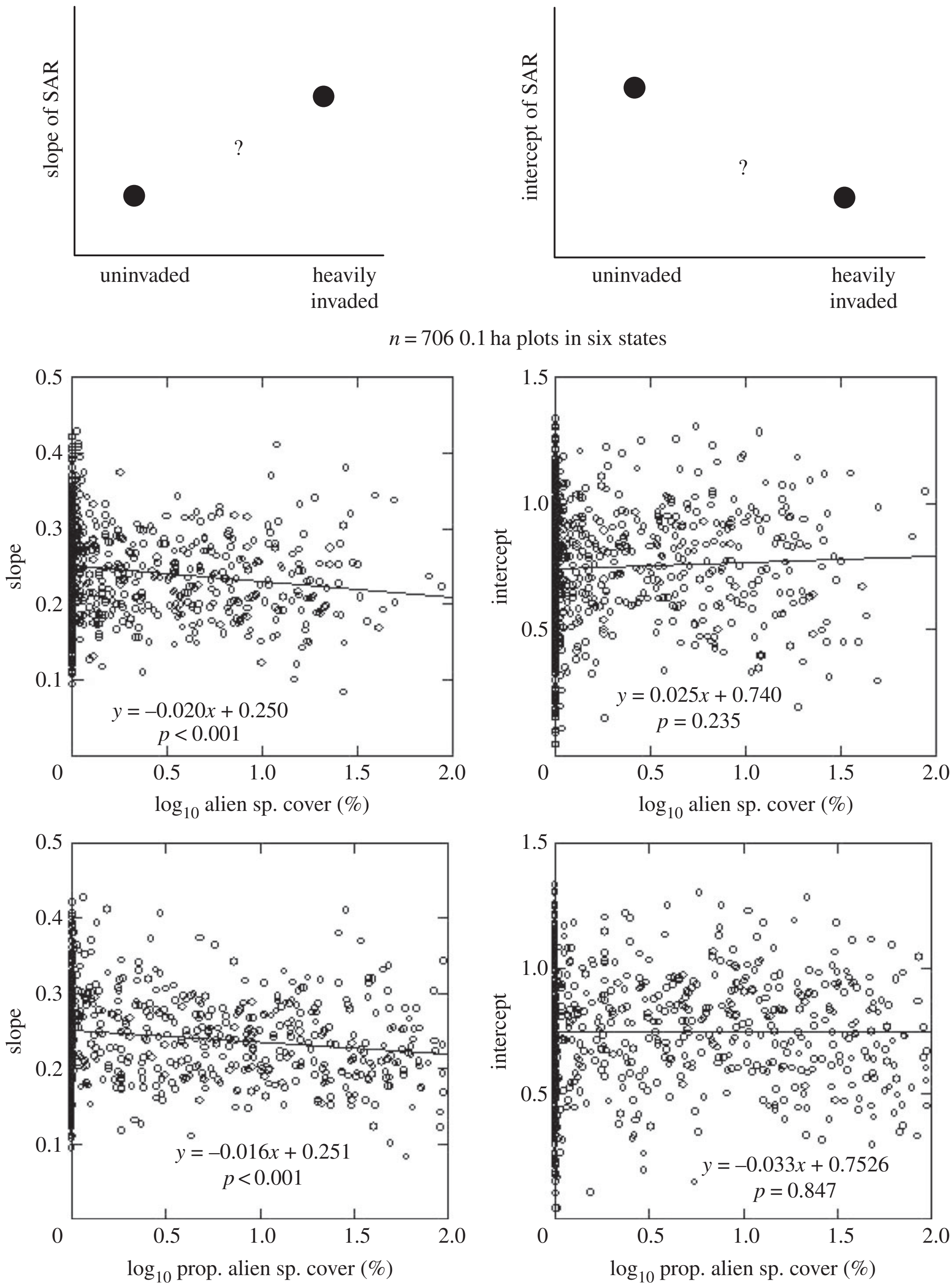


**Figure 1.** Expected results based on Powell *et al.* [6] (top panel) compared to measured SARs along a continuum from uninvaded to heavily invaded sites in a randomly selected set of $n = 706$ 0.1 ha Modified-Whittaker vegetation plots in grasslands, shrublands and forests in six states (Colorado, Utah, Wyoming, South Dakota, Montana and Minnesota).

a 'universally' lower intercept and steeper slope of the species–area relationship (SAR) in invaded communities relative to uninvaded communities across biomes. However, the authors subjectively included only three alien species that could achieve dominance and they 'haphazardly chose three disparate, forested biomes from across the United States that are experiencing established but ongoing invasions'. They also 'chose species with disparate growth forms and physiology across biomes in order to explore possible generality of their effects on diversity' ([6]; p. 316]).

We wondered whether any universal generalizations might emerge from subjective and haphazard sampling. Would results be similar in other biomes with a mix of alien species (which is often the case)? In addition, we wondered whether a continuum of invasion severity exists in most biomes. If there were a continuum of invasion severity, would we see a continuum of impacts? We present two large independent datasets of invasion continuums in 11 US states to address these questions.

## 2. Material and methods

### (a) Modified-Whittaker plots

This dataset comprises 706 plots in forest, grassland and desert biomes. They sample riparian zones, upland sites, grazed and ungrazed sites, and some sites affected by wildfires [9–11]. The plots are randomly located and numbers vary by state: Utah (379), Colorado (274), Wyoming (42), South Dakota (20), Montana

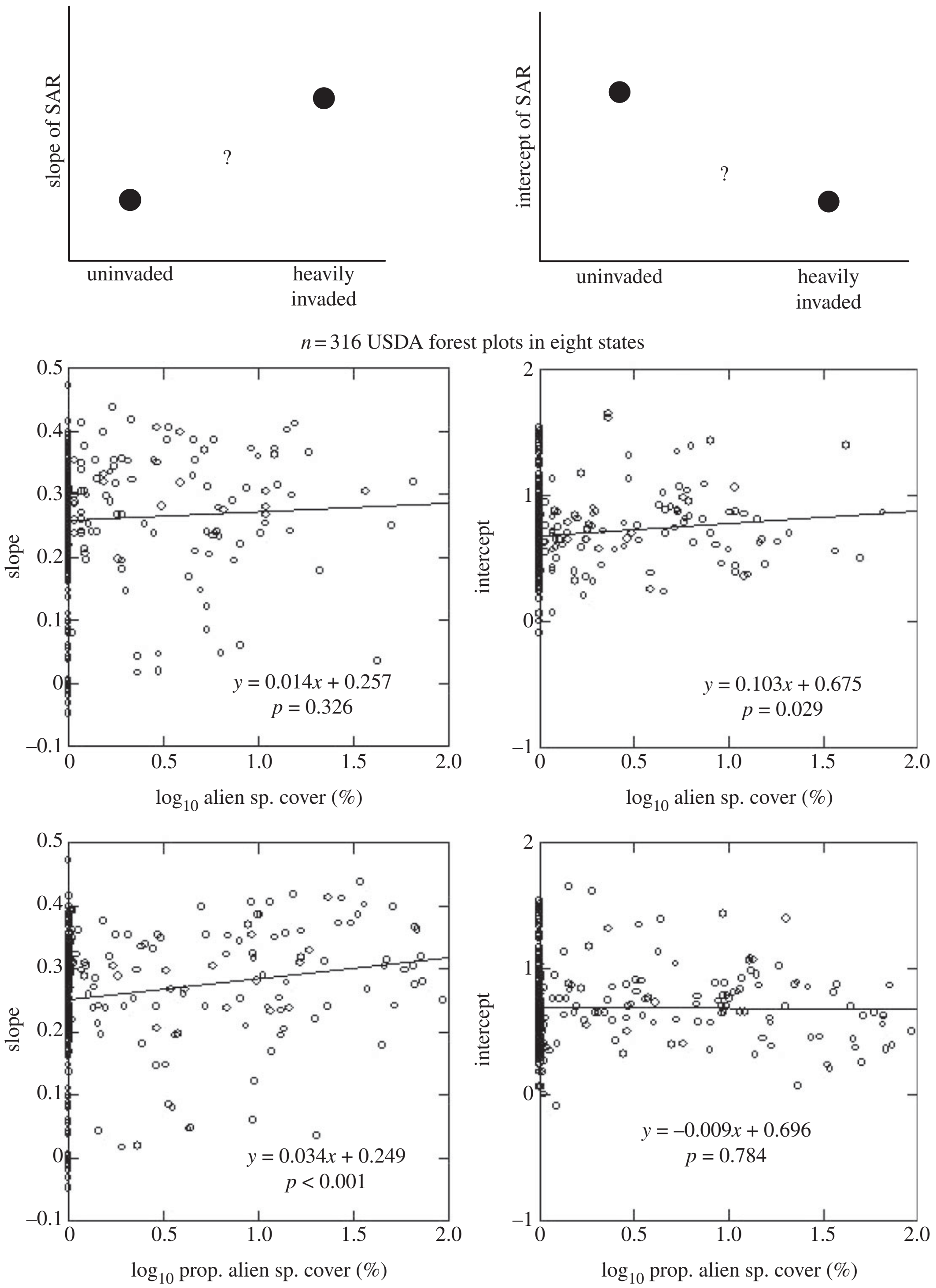


**Figure 2.** Expected results based on Powell *et al.* [6] (top panel) compared to measured SARs along a continuum from uninvaded to heavily invaded sites in a systematic sampling of $n = 316$ USDA forest plots in Colorado, Delaware, Michigan, Oregon, Pennsylvania, Virginia, Washington and Wyoming.

(14) and Minnesota (4). Each plot is $20 \times 50$ m (1000 m$^2$), within which are ten 1 m$^2$ subplots. Plots were sampled between 1995 and 1999. Foliar cover was visually estimated for all vascular species within plots and subplots to the nearest per cent.

## (b) USDA forest service's forest health monitoring plots

This dataset was obtained from 316 large (672 m$^2$) vegetation-monitoring plots in forested areas in eight states, which are part of the USDA Forest Service's Forest Health Monitoring Program [12]. The plots are *systematically* spaced throughout forested habitats in the US (one every 63 942 ha) and the numbers vary by state: Colorado (33), Delaware (39), Michigan (71), Oregon (44), Pennsylvania (81), Virginia (15), Washington (12) and Wyoming (21). Each plot consists of four 168 m$^2$ subplots, with three 1 m$^2$ quadrats in each subplot. Thus, each 672 m$^2$ plot yielded data on mean species richness at the 1 m$^2$ scale, and mean foliar cover and total species richness at the 672 m$^2$ plot scale, to assess SARs. All the plots were sampled between 1997 and 2001 in the summer. Species richness results have been published [13] but coefficients of SARs have not yet been reported for these data.

## (c) Statistical analysis

We transformed all species richness and cover values with a $\log_{10}$ transformation ($\log_{10}(X+1)$) prior to analysis to determine the slope and intercept of species–area curves. We used either $\log_{10}$ combined cover of all alien species or $\log_{10}$ proportion of combined alien species cover as the independent variable. In our figures, each data point represents one plot (i.e. $n = 706$ Modified-Whittaker plots in figure 1; $n = 316$ USDA plots in figure 2). In each figure, the $y$-coordinate is the slope or intercept of the SAR within each plot based on the number of native and alien species recorded in the 1 $m^2$ subplots and entire plot; the $x$-coordinate is either the $\log_{10}$ of alien species foliar cover or the $\log_{10}$ proportion of alien species foliar cover, based on the averages of cover values in the replicated 1 $m^2$ subplots within each of the larger plots. All analyses were conducted using SYSTAT v. 12.0 [14].

## 3. Results

We found extreme variation among plots, and a slight, but significant, *negative* relationship between the slope of the species–area curves and alien species cover among the Modified-Whittaker plots (figure 1). We found no significant relationship for the intercept values of the species–area curves (figure 1), where a negative relationship was expected based on Powell *et al*. [6].

For the USDA Forest Service plots, there was a significant *positive* relationship between the proportion of alien species cover and the slope of the species–area curve, but no significant relationship between alien species cover and slope (figure 2). Contrary to expectations, we found a significant *positive* relationship between the intercept values of the species–area curves and alien species cover. We found no significant relationship between the intercept values of the species–area curves and the proportion of alien species cover (figure 2).

Both of these large datasets contained individual plots with more than 70% cover of alien species. However, in both datasets, alien species were absent from more than 70% of the sample plots, and less than 1% of the plots had more than 90% cover of alien plants. In both datasets, we found an inverse-J shaped distribution of alien species cover by plot, such that heavily invaded sites might be expected to be very rare in many biomes.

## 4. Discussion

Our two large, unbiased datasets revealed only a small fraction of heavily invaded sites in an ocean of uninvaded and poorly invaded sites. Powell *et al*. [6] used extreme sites (heavily invaded plots versus uninvaded plots) to establish a false dichotomy. We found no evidence to support the universality of their findings on the slopes and intercepts of species–area curves. Instead, we found that invasion impacts are unlikely to be as universal as Powell *et al.* suggest. Invasion impacts vary in space and time owing to species traits [15], time since invasion, soil fertility, disturbance, species interactions and many other factors [1,11]. The continuum of plant invasion severities may allow for native plant species to coexist with alien species and persist in many landscapes [1].

It is impossible to extrapolate the results from subjective and haphazard studies. Statisticians and many ecologists have long warned about haphazard sampling in ecological studies [16], even if several such study sites reveal similar patterns [17]. What such studies may provide, however, are worst-case scenarios. Using Powell *et al*. [6] approach, it can be shown that impacts of expanding dominant species on local plant species richness can be even more drastic in terms of both species richness–area regressions intercepts and slopes [18,19].

In summary, it might be difficult to suggest universal ecological patterns or processes from subjective sampling or haphazard sampling of extreme sites in a few study areas. Given the current broad scale patterns our data show, we see inconclusive evidence of invasion intensity altering species–area curves at meaningful scales (figures 1 and 2). Invasion may have some locally strong effects, but those effects may be overestimated by the types of studies that Powell *et al*. [6] conducted. While local displacement of a native species by an alien species may not be desirable, we cannot assume that highly local extirpation leads to regional extirpation [1]. Though heavily invaded sites remain a major concern for conservation, we cannot assume that all uninvaded sites will be heavily invaded in the future. Abundance of invasive plant species is not constant. It may increase, fluctuate or even crash completely [20–24]. While we cannot assume that extirpation leads to extinction, we argue that targeted invasive species control efforts and properly designed monitoring of native biodiversity at large spatial scales are essential to save native species [25]. We find ourselves in agreement with Gilbert & Levine [2], who conclude that 'the relatively short time since invasion in many parts of the world is insufficient to observe the full impact of plant invasions on native biodiversity'.

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