

Release of invasive plants from fungal and viral pathogens

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Invasive plant species both threaten native biodiversity and are economically costly^{1–5}, but only a few naturalized species become pests^{2,4}. Here we report broad, quantitative support for two long-standing hypotheses that explain why only some naturalized species have large impacts. The enemy release hypothesis argues that invaders' impacts result from reduced natural enemy attack^{2,4,6–10}. The biotic resistance hypothesis argues that interactions with native species, including natural enemies, limit invaders' impacts^{6–8}. We tested these hypotheses for viruses and for rust, smut and powdery mildew fungi that infect 473 plant species naturalized to the United States from Europe. On average, 84% fewer fungi and 24% fewer virus species infect each plant species in its naturalized range than in its native range. In addition, invasive plant species that are more completely released from pathogens are more widely reported as harmful invaders of both agricultural and natural ecosystems. Together, these results strongly support the enemy release hypothesis. Among noxious agricultural weeds, species accumulating more pathogens in their naturalized range are less widely noxious, supporting the biotic resistance hypothesis. Our results indicate that invasive plants' impacts may be a function of both release from and accumulation of natural enemies, including pathogens.

Although the enemy release hypothesis (ERH) is commonly assumed to be a principal explanation for plant invasiveness^{4,7}, reviews have concluded that evidence for it is equivocal^{8,9}. Few data quantify the degree to which naturalized plants are released from natural enemies relative to their native range^{8–11}. In addition, a central prediction of the ERH—that naturalized plants that are more completely released from enemies have greater impacts—remains untested. Similarly, although some assumptions of the biotic resistance hypothesis (BRH) are supported^{8,11,12}, no study has tested whether naturalized plants experiencing greater attack by native enemies have lesser impacts. To test whether naturalized plants' release from and/or accumulation of pathogens explains their degree of impact, we compiled geographic data on plant associations with viruses and biotrophic foliar/floral fungi from published compendia and governmental or academic databases (see Methods). We focused on pathogens because they are ubiquitous and can be potent regulators of host populations^{10,13–15}.

Overall, each plant species was infected by 77% fewer fungus and virus pathogen species in its naturalized range than in its native range (general linear model: $F_{1,472} = 369.84$, $P < 0.0001$). We tested whether this decrease could be explained by changes in plant geographic range size¹¹, estimated by geographic prevalence. Pathogen species richness increased with greater plant geographic prevalence in both ranges, and more so in plants' native than in their naturalized ranges (range \times geographic prevalence interaction: $F_{1,415} = 54.81$, $P < 0.0001$). In addition, the intercept of this relationship was also greater in the native range (native, 0.57 ± 0.14 (mean \pm s.e.); naturalized, 0.012 ± 0.022). For all possible values of geographic prevalence ($0 \leq$ geographic prevalence ≤ 1), therefore, pathogen species richness was greater in plants' native ranges than in their naturalized ranges after controlling for the relationship between richness and range size.

We predicted viruses to be less easily escaped than fungi because they are more commonly systemic, seed-transmitted and asymptomatic than are fungi, and generally have broader host ranges¹⁶. As expected, plants were infected by 84% fewer fungi and 24% fewer viruses in their naturalized ranges than in their native ranges (Figs 1 and 2). Plants' greater release from fungi than viruses caused the composition of their pathogen assemblages to shift. The percentage of associated pathogen species that were fungi decreased from 88% in plants' native ranges to 61% in their naturalized ranges (Fig. 2; paired t -test: $t_{119} = 6.2$, $P < 0.0001$). We also predicted that plants heavily used by humans would be less released from pathogens because they probably have been introduced more times and at higher abundances than other species. Release from fungi was more

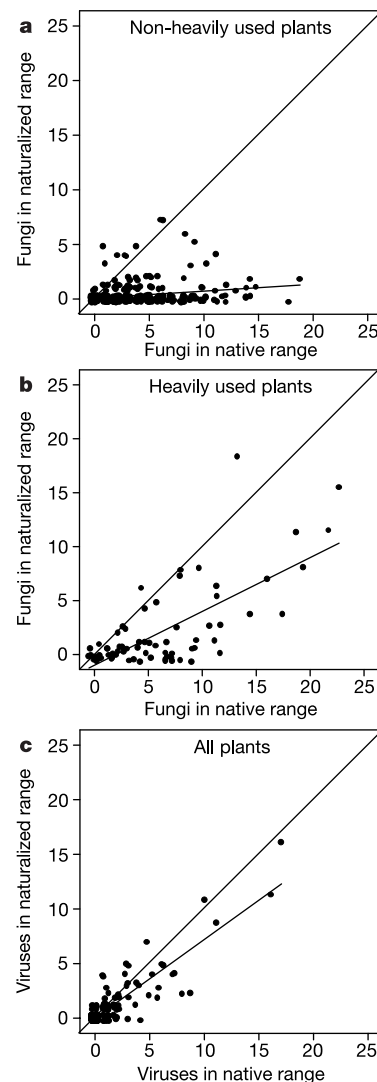


Figure 1 Net release of introduced plant species from fungal and viral pathogens. Each circle represents one host species; slight random noise was added to species with identical values to render each one visible. **a**, Release of the 401 plants not heavily used by humans from fungal pathogens. Number in naturalized range = $0.040 + 0.082 \times$ (number in native range); $\chi^2 = 62$, $P < 0.0001$, $R^2 = 0.135$. **b**, Release of the 72 plants heavily used by humans from fungal pathogens. Number in naturalized range = $0.042 + 0.34 \times$ (number in native range); $\chi^2 = 144$, $P < 0.0001$, $R^2 = 0.488$. **c**, Release of all 473 plants from viral pathogens. Number in naturalized range = $0.021 + 0.71 \times$ (number in native range); $\chi^2 = 164$, $P < 0.0001$, $R^2 = 0.809$.

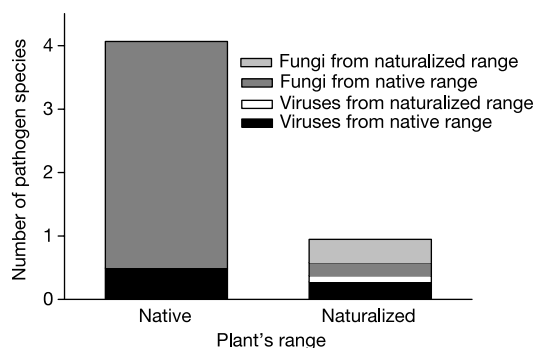


Figure 2 Composition of pathogen assemblages in the plant's native and naturalized ranges in terms of pathogen type and origin.

complete for plants not heavily used by humans than for heavily used species (Fig. 1a, b; Poisson ANCOVA: $\chi^2 = 73$, $P < 0.0001$), but release from viruses was not influenced by human use ($\chi^2 = 0.10$, $P = 0.75$). These patterns of pathogen release (Fig. 1) were general across plant species life histories, growth forms and phylogenetic histories. Controlling for host perenniality, growth form (graminoid, woody or herb), family (Asteraceae, Brassicaceae, Fabaceae, Poaceae or other) or monocot versus dicot did not increase the model fit by more than 2%.

Although the total costs and impacts of invasive species are relatively well quantified^{3,5}, attributing these totals to individual species remains challenging^{5,17}. We used plants' status as noxious weeds as an indicator of their economic costs because 95% of economic costs of US invasive plants are agricultural⁵ and states list plants as noxious weeds primarily on the basis of their agricultural impact¹. Many states and non-governmental organizations separately list invasive plants that degrade natural areas¹, providing an analogous indicator of plants' environmental impact. Among noxious weeds, species that experienced more complete pathogen release were more widely noxious (Fig. 3a), suggesting that greater release from pathogens increases invasive plants' economic costs,

and strongly supporting the ERH. Similarly, among plants listed as natural area invaders, species that experienced more complete pathogen release were more widely invasive (Fig. 3b). But this relationship was not robust to exclusion of the least released species (exclusion yielded, $\chi^2 = 3.0$, $P = 0.084$, $R^2 = 0.030$), providing more limited support for the ERH's prediction that more complete pathogen release increases invaders' environmental impact.

Pathogen release is the net result of two opposing forces: plants' 'escaping' pathogens from their native range during introduction, and subsequently 'accumulating' pathogens native to their naturalized range (release = escape - accumulation). Noxiousness might have increased with greater pathogen release (Fig. 3a) either because more noxious plants escaped more pathogens, or because they accumulated fewer pathogens, or both. Noxiousness increased with greater pathogen escape (Fig. 4a), implying that pathogens limit plant populations in their native range^{10,14,15} and supporting the idea that classical biocontrol can mitigate the costs of noxious weeds^{18–20}. In plants' naturalized ranges, fungi and viruses accumulated from those ranges comprised 49% of the pathogen assemblage (Fig. 2), indicating potential for biotic resistance despite plants' strong net release. Consequently, noxiousness also decreased with greater pathogen accumulation (Fig. 4b), supporting the BRH and the idea that native pathogens can be effective biocontrol agents^{12,18–20}. Thus, noxiousness is a function of both escape and accumulation of pathogens.

Control of potential pests by natural enemies is a chief ecosystem service²¹. Our results illustrate the breadth of this service: pathogens seem to both reduce the frequency with which naturalized plants are listed as noxious agricultural weeds (Fig. 4b) and prevent native plant populations from becoming pests (refs 14, 15, and Fig. 4a). Our results also suggest that invaders become more widely problematic, in part, because their introduction disrupts their associations with pathogens, thereby eroding the ecosystem service of pest control provided by pathogens and other natural enemies.

Together with similar results for animals²², our study shows that naturalized species are generally strongly released from pathogens. In addition, more completely released invasive plants are more

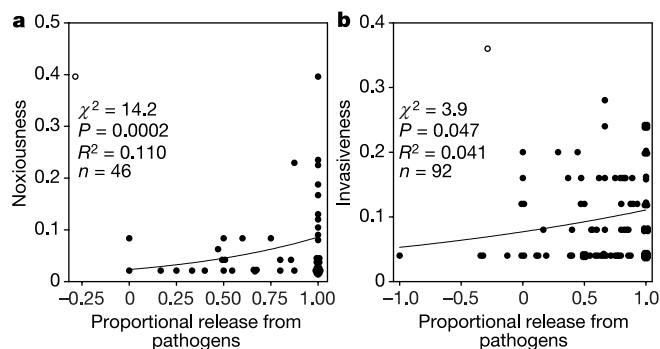


Figure 3 More complete release from pathogens increases the degree of noxiousness and invasiveness in the naturalized range. More complete release was measured by the difference in number of associated pathogen species between native and naturalized ranges divided by number associated in the native range. **a**, Degree of noxiousness in the naturalized range, measured by the proportion of states in which the pathogen is governmentally declared noxious; **b**, degree of invasiveness in the naturalized range, measured by the proportion of groups listing the species as an invasive problem in natural areas. Each circle represents one plant species; slight random noise was added to species with identical values to render each one visible. A highly influential outlier, *S. halepense* (Johnsongrass), was excluded from statistical analyses and is shown as an open circle (Methods).

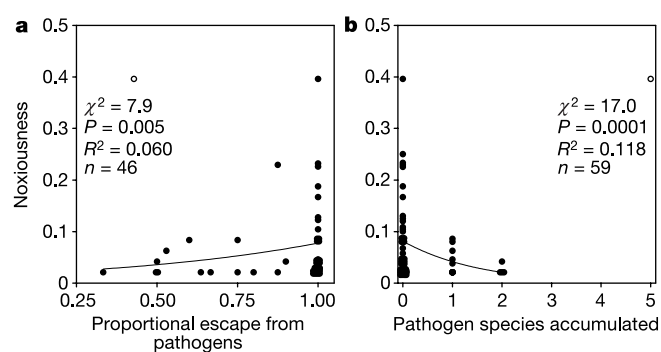


Figure 4 Decomposition of the effect of net release on noxiousness into the effects of escape from pathogens and accumulation of pathogens native to each plant's naturalized range. **a**, Escape from pathogens, measured as the proportion of pathogens from each plant's native range not occurring in its naturalized range; **b**, accumulation of pathogens native to each plant's naturalized range. The effect of pathogen accumulation was robust to removing all species that accumulated two pathogens from the analysis. Sample size is greater in **b** than in **a**, because plants with no pathogens reported in their native range, and therefore no potential for escape, were excluded from **a**. Each circle represents one plant species; slight random noise was added to species with identical values to render each one visible. A highly influential outlier, *S. halepense* (Johnsongrass), was excluded from statistical analyses and is shown as an open circle (Methods).

widely listed as problematic invaders of agricultural and natural ecosystems, strongly supporting the ERH. Although these correlations are not strongly predictive and exclude one outlier species, they were detected despite several limitations. We lacked data on pathogens' prevalences within populations, their distributions among plant populations within each geographic range, and the relative effects of different pathogens. We also lacked data on release from the natural enemies usually considered to be the principal agents of release and resistance for plants, herbivores^{8,9} and root pathogens^{10,14,15}, although release from these enemies could be correlated with release from pathogens quantified here. Therefore, additionally quantifying release from herbivores and other pathogens may explain much of the remaining variation in invasive plants' impacts. Our results point to a strong role for natural enemies in plant invasions; a more complete consideration of the diversity of invaders' natural enemies will better identify the extent of this role. □

Methods

Data collection

We focused on biotrophic foliar and floral fungi and all viruses of plants naturalized to the United States from Europe because this was the only combination of pathogens, plants and introduction route for which comprehensive data over two large geographic areas was available. In addition, plants naturalized to the United States from Europe are of interest in themselves because they are so numerous and important: they comprise 41% of the 4,100 plants naturalized to the United States and, on the basis of this percentage, have annual economic costs of US\$14 billion⁵. Similarly, the pathogens included comprise many of the world's most economically important groups¹⁶.

We compiled data on plant species in the US Department of Agriculture (USDA) Plants Database (<http://plants.usda.gov>) list of species naturalized to the United States (that is, those species not native to the United States but surviving in wild populations without human intervention). We used a random number generator to choose 1,165 of the 4,100 species listed on 17 January 2001. For each of these species, we determined whether its native range included part of Europe (species listed as from the 'Mediterranean' were included) using published floras from the naturalized range. For the 474 species native to Europe, we compiled data on growth form, perenniality and taxonomy from the USDA Plants Database. We excluded the one randomly chosen gymnosperm species, leaving 473 species in 69 families.

From the same database, we compiled the number of states in which each plant was governmentally declared a noxious weed and used this as an indicator of economic costs. For noxiousness, we report analyses including all states declaring a plant noxious, but results were similar when excluding prophylactic declarations of noxiousness. To estimate environmental damage resulting from each species, we counted the number of groups (state and regional exotic pest plant councils, state governmental agencies, the National Park Service and the Nature Conservancy) citing each species as an invasive problem in natural areas. These citations were compiled by the Alien Plant Working Group of the Plant Conservation Alliance, a consortium of US governmental agencies in cooperation with non-governmental groups (<http://www.nps.gov/plants/alien/list/all.htm>). Geographic prevalences in plants' native and naturalized ranges were defined as plants' proportional incidence in 39 European geographic regions²³ and in the 49 continental United States, respectively. Some species existing in naturalized populations are also cultivated by humans. We determined whether each species is or has been heavily used by humans (that is, a crop, silvicultural species or source of animal fodder) using ref. 24.

For each species, we counted the associated rust, smut and powdery mildew pathogens in the plant's native and naturalized ranges listed in the USDA Fungus-Host Distributions database (<http://nt.ars-grin.gov/SBMLweb/Databases/Home.htm>). This database includes the data from numerous published compilations, including refs 25–27, and thus was regarded as a complete source of information on smut and powdery mildews in both Europe and the United States, and on rusts in the United States. The database did not include the authoritative compilations of European rusts^{28,29}, however, so we collected data from these texts directly. We counted the number of viruses of all types associated with each species in its native and naturalized range listed in the Virus Identification Data Exchange project database (<http://image.fs.uidaho.edu/vide>). We included only viruses known to infect each plant naturally, thereby excluding associations based only on experimental inoculations. We conservatively assumed that pathogens listed as occurring in both native and naturalized ranges followed the same path of introduction as their host, originating in the plant's native range.

Analysis

We used SAS Insight 8.0 for statistical analyses. Models with number of pathogens as the dependent variable were analysed assuming a Poisson response distribution and the identity link function, with two exceptions. The Poisson distribution could not be fit when testing whether number of pathogen species differed between native and naturalized ranges, and whether range size explained this difference, so a normal distribution was assumed. These two models treated species as block and range as the factor. Logit regressions were used for binomial response variables (noxiousness and invasiveness). All

χ^2 statistics are type III Wald tests. We report unadjusted R^2 values. All species were included in each analysis and figure unless otherwise stated. The range size analysis included all 420 species for which geographic prevalences were available. We considered that *Sorghum halepense* was an outlier (and thus excluded it) in analyses of noxiousness and invasiveness (Figs 3 and 4), because it has caused the most damage to US agriculture of plants in our dataset³⁰, and therefore the pathogens in its naturalized range have probably been more completely enumerated.

The observed release from pathogens could have resulted from pathogens being less studied in plants' naturalized than in their native ranges. This hypothesis predicts that better studied plant species, such as those governmentally declared noxious¹, should have more associated pathogen species. But plants designated as noxious weeds in at least one state had no more pathogens in their naturalized ranges than did other plants ($\chi^2 = 0.0035$; $P = 0.95$), suggesting that pathogen release was not an artefact of sampling effort.

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