



Allelopathy is pervasive in invasive plants

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Abstract Invasive species utilize a wide array of trait strategies to establish in novel ecosystems. Among these traits is the capacity to produce allelopathic compounds that can directly inhibit neighboring native plants or indirectly suppress native plants via disruption of beneficial belowground microbial mutualisms, or altered soil resources. Despite the well-known prevalence of allelopathy among plant taxa, the pervasiveness of allelopathy among invasive plants is unknown. Here we demonstrate that the majority of the 524 invasive plant species in our database produce allelochemicals with the potential to negatively affect native plant performance. Moreover, allelopathy is widespread across the plant phylogeny, suggesting that allelopathy could have a large impact on native species across the globe. Allelopathic impacts of invasive species are often thought to be present in only a few plant clades (e.g., Brassicaceae). Yet our analysis shows that allelopathy is present in 72% of the 113 plant families surveyed, suggesting that this

ubiquitous mechanism of invasion deserves more attention as invasion rates increase across the globe.

Keywords Allelopathy · Invasion · Phylogenetic analysis

Introduction

Allelopathy, the production of chemicals by a plant species that can affect neighboring plants or soil microbes, has been long acknowledged as an important functional trait that can alter neighbor plant performance and ultimately plant community structure. Anti-plant allelopathic compounds can directly affect neighboring plant tissues, disrupting germination, and seedling or adult plant growth (reviewed in Zhang et al. 2020). Indeed, a recent meta-analysis focused on the direct allelopathic effects on plants demonstrated that neighbor plant performance was reduced by 25%, on average (Zhang et al. 2020). However, anti-microbial allelopathic compounds can also alter soil nutrient availability (Zhang et al. 2019), or directly kill microbial cells in the soil, resulting in the disruption plant-microbial mutualisms (Hale and Kalisz 2012) that are fundamental for plant resource acquisition (Fletcher and Renney 1963; Kelsey and Locken 1987; Stachon and Zimdahl 1980; Yamamoto 1995; Hale et al. 2011). Therefore, the average effects

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of allelochemicals on neighbor plant performance is likely even greater if we include the indirect effects of plant–microbe mutualism disruption (Hale and Kalisz 2012) for the many plant species that rely on microbes in nutritional mutualisms [e.g. ~ 70% of all land plants participate in arbuscular mycorrhizal fungal mutualisms (Smith and Read 2008; Parniske 2008; Soudzilovskaia et al. 2020)].

Because of these potential detrimental effects on neighbor plant's fitness, allelopathy has gained prominence in the field of invasion biology as part of the arsenal of potential trait weapons in the novel weapon hypothesis (Callaway and Aschehoug 2000; Callaway and Ridenour 2004; Inderjit et al. 2008). Non-native invaders are known to influence nutrient fluxes, availability and uptake (Ehrenfeld 2010; Zhang et al. 2019), which change the physiology and population growth rate of native species (Bialic-Murphy et al. 2019), alter the abundance of species within a community (Roche et al. 2020) and can even change stable states of entire ecosystems (reviewed in Wardle et al. 1998). Despite clear negative effects on individual plant species and their communities, the importance of allelopathy as a common trait of many invaders rather than a few well-studied examples is unknown. Thus, it remains unclear the extent to which allelopathy is one of the key traits in the arsenal that increases exotic invasion success.

Here we present data on the allelopathic potential of 524 known invasive plant species gleaned from three datasets in an attempt to shed light on the ubiquity of allelopathy across plant invaders. We ask two fundamental questions: (1) How common is allelopathy a trait of known invasive plant species? (2) Is the propensity to produce allelopathic chemicals phylogenetically conserved?

We identified the 524 invasive plant species across three datasets: 81 impactful invasive plants identified in Pyšek et al. (2012), 19 species from Zhang et al. (2019), and 330 from the International Union for Conservation of Nature (<https://www.iucn.org/>) list of global plant invaders. When not available in the original publication, we queried each plant species name AND allelopath* in google scholar (Supplemental Table 1). The search was completed on June 08, 2020. Species were categorized as allelopathic if a direct or indirect effect of the allelochemical was reported in at least one site where the invader was studied. Using this pooled dataset, we then calculated

the percentage of invasive plants that were categorized in the literature as allelopathic. Allelopathy has not been tested in all invasive species in our database. We treated missing observations as no evidence of allelopathy and thus our results represent a conservative estimate of allelopathy prevalence.

In addition, we created a plant phylogeny of our 524 species using Phylomatic based on the Zanne et al. (2014) plant phylogeny. These species represent 113 plant families across Angiosperms and Gymnosperms. To assess if the propensity to produce allelopathic chemicals was phylogenetic conserved, we calculated Pagel's λ using the `fitDiscrete` function in the `Geiger` package in R v. 3.5. Values of Pagel's λ can range between 0 (no phylogenetic signal) to 1 (trait evolution = Brownian motion) indicating a trait is highly conserved.

Results

Allelopathy occurred in 51.4% of the invasive species in our database. This high rate of incidence indicates that allelopathy is a prevalent trait of successful invaders and likely explains an important component of the biotic impacts on native plant and their associated beneficial microbes in invaded communities. Interestingly, the capacity to be allelopathic was not phylogenetically conserved ($\lambda = 0.000$, $P > 0.050$; Fig. 1) and is found in 72% plant families across the Gymnosperms and Angiosperms (both Monocots and Dicots).

Publication bias and missing data

Allelopathy has not been tested in all invasive plants in our analyses. Despite the guidelines for testing and validating potentially allelopathic compounds suggested by Blair et al. (2009) not everyone measures allelopathy the same way, or on the same plant stages and the degree to which the same species expresses allelopathy can differ across studies (Zhang et al. 2020). Further, plants species synthesize a wide array of compounds. Given the wide range of potentially allelopathic chemicals that plants produce, there are likely to be diverse mechanisms that underlie the success of an allelopathic invader ranging from direct plant inhibition to altered soil chemistry to disruption of beneficial plant-microbial mutualisms belowground

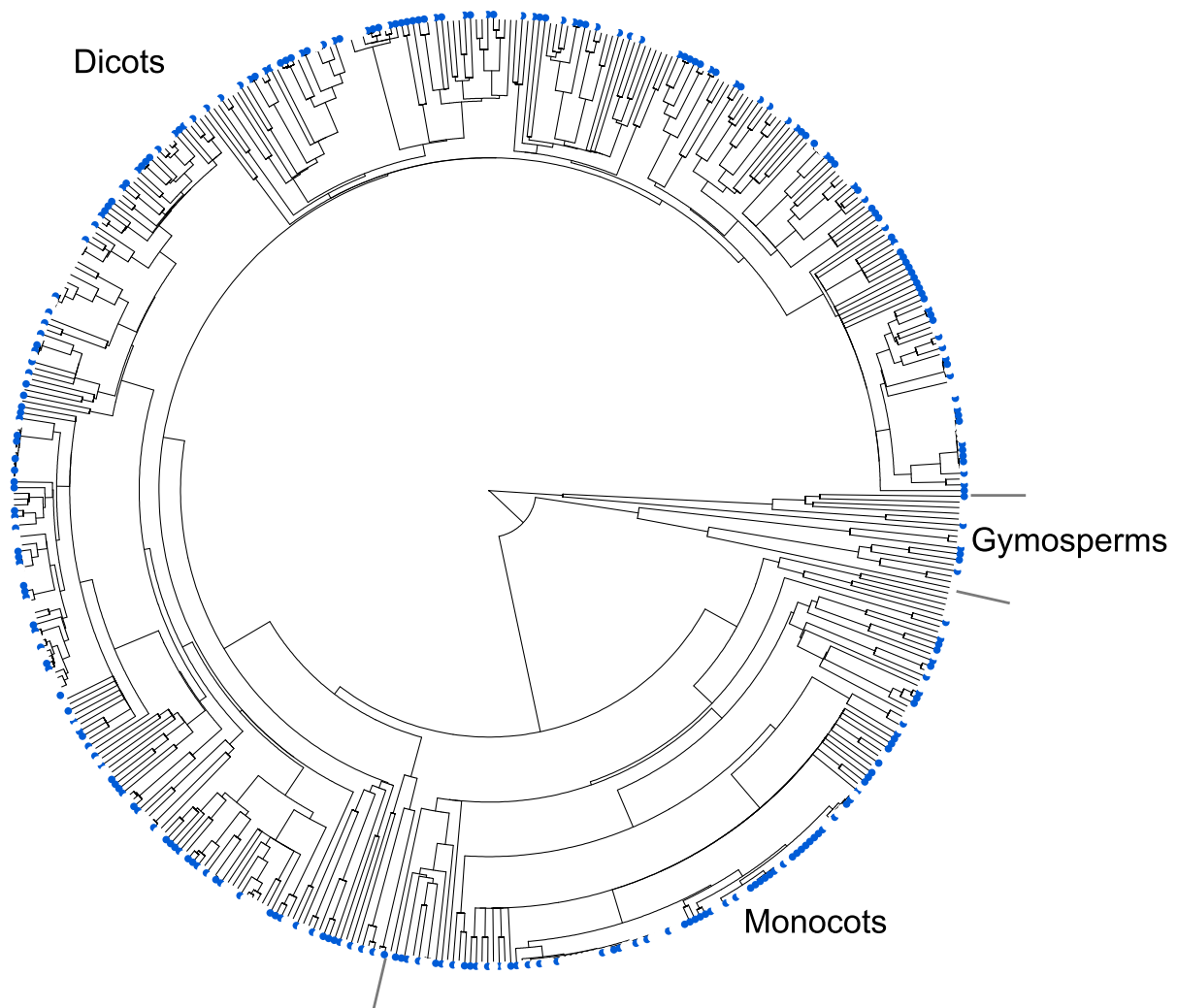


Fig. 1 Phylogeny of 524 invasive plant species included in this study. Blue color indicates allelopathic species. Allelopathy is spread throughout the plant phylogeny in all major lineages

(Hale and Kalisz 2012). Therefore, the degree to which the same species expresses allelopathy can differ across studies (Zhang et al. 2020). Most studies test for direct effects on the plants (Zhang et al. 2020) and do not test for beneficial plant–microbe mutualism disruption (e.g., reduction in biomass or diversity of beneficial belowground microbial symbionts), likely because it is easier to study direct effects. Despite these differences, our analyses confirm that allelopathy is an important characteristic of invasive plant species. We acknowledged that the prevalence of allelopathy in non-invasive plant species would provide a relevant comparison, but this information is currently unavailable and is beyond the scope of our study.

Discussion and conclusion

Invasive species are among the greatest threats to native plant biodiversity (Gaertner et al. 2009; Powell et al. 2011; Vilà et al. 2011) and the prevalence of invasive plants is increasing (MEA 2005). Despite this threat to native biodiversity, the mechanisms underlying invasion are still not well resolved. Here we demonstrate that allelopathy is a common invasion mechanism across the plant phylogeny, present in every lineage examined. Given that not all invasive plants in our database have been tested, it is likely that allelopathy in invasive species is even greater than we report here. While model allelopathic invasive plants

(e.g., *Alliaria petiolata* (garlic mustard); *Fallopia japonica* (Japanese knotweed)) have received the bulk of study and notoriety in invasion literature, our analysis suggests allelopathy is a widespread mechanism of invasion success. Future research aimed at demonstrating the prevalence of direct (e.g., plant-plant inhibition) versus indirect pathways (e.g., inhabitation of native plant-microbial interactions) of allelopathy is necessary to mediate the detrimental effects of invasion in native ecosystems.

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Availability of data and material: published online data from three datasets Pyšek et al. (2012), Zhang et al. (2019), and the International Union for Conservation of Nature (<https://www.iucn.org/>) list of global plant invaders. Code availability (software application or custom code) Phylomatic code Zanne et al. (2014).

Compliance with ethical standards

Conflict of interest Not applicable.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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