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NEWS & VIEWS

ON THE NATURE OF THINGS: ESSAYS
New Ideas and Directions in Botany

Botany is the root and the future of invasion biology

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Although botanists have been at the center of invasion biology since its inception, few botanists identify as invasion biologists. Of those few, many primarily ally with associated disciplines such as weed science and agronomy. The modern field of invasion biology—the study of the introduction, establishment, evolution, and control of nonnative species—was formally established when zoologist Charles Elton proposed his biodiversity-invasibility hypothesis (Elton, 1958) and has since been largely dominated by zoologists. However, plants have proven to be tractable systems for both experimental and observational studies and have played an outsized role in addressing longstanding hypotheses in invasion biology (Fig. 1). Here, we briefly review the historic and contemporary contributions that botanists have made in invasion biology and argue that botanists will continue to play a critical role in revolutionizing invasion biology.

The work of botanists on plant invasions arguably began with 17th century Linneaus protégé, Pehr Kalm, first noting naturalized European species in North America. Early naturalists including Charles Lyell, Alfred Russel Wallace, and Charles Darwin commonly observed nonnative plants (Simberloff, 2013); Darwin's naturalization hypothesis, one of the first attempts to understand the invasion process, made use of these observations. Twentieth century botanists like Charles Baker and George Ledyard Stebbins avoided the terminology of invasion biology, but studied plant colonizations as natural evolutionary experiments and helped merge invasion biology with the modern synthesis (Barrett, 2015). In the 1980s and 1990s, botanists played consequential roles in understanding invasibility, inferring the population dynamics underlying invasions, and studying the consequences of invasions across communities, food webs, and ecosystems (Levine et al., 2003; Pyšek and Richardson, 2007). Many of these studies leveraged the experimental tractability of plants (i.e., immobility, flexible reproductive strategies, and easy propagation within manipulative experiments)—traits that continue to make plants uniquely pragmatic models for invasion research today. Genetic analyses of plant invasions during the 2000s overturned many long-standing assumptions of invasion dynamics, revealing that introductions are often repeated, admixture is frequent, and selection is common during invasions (Dlugosch and Parker, 2008; Colautti and Lau, 2015). Recently, advances in genomics have provided a more nuanced understanding of the invasion process. Below, we highlight four areas where plants are uniquely suited for studying invasions and where botanists have recently made consequential contributions to invasion biology: colonization dynamics, admixture, hybridization, and plasticity.

COLONIZATION DYNAMICS

Rather than simply determining whether invasions stem from single or multiple colonization events, recent genomic studies have

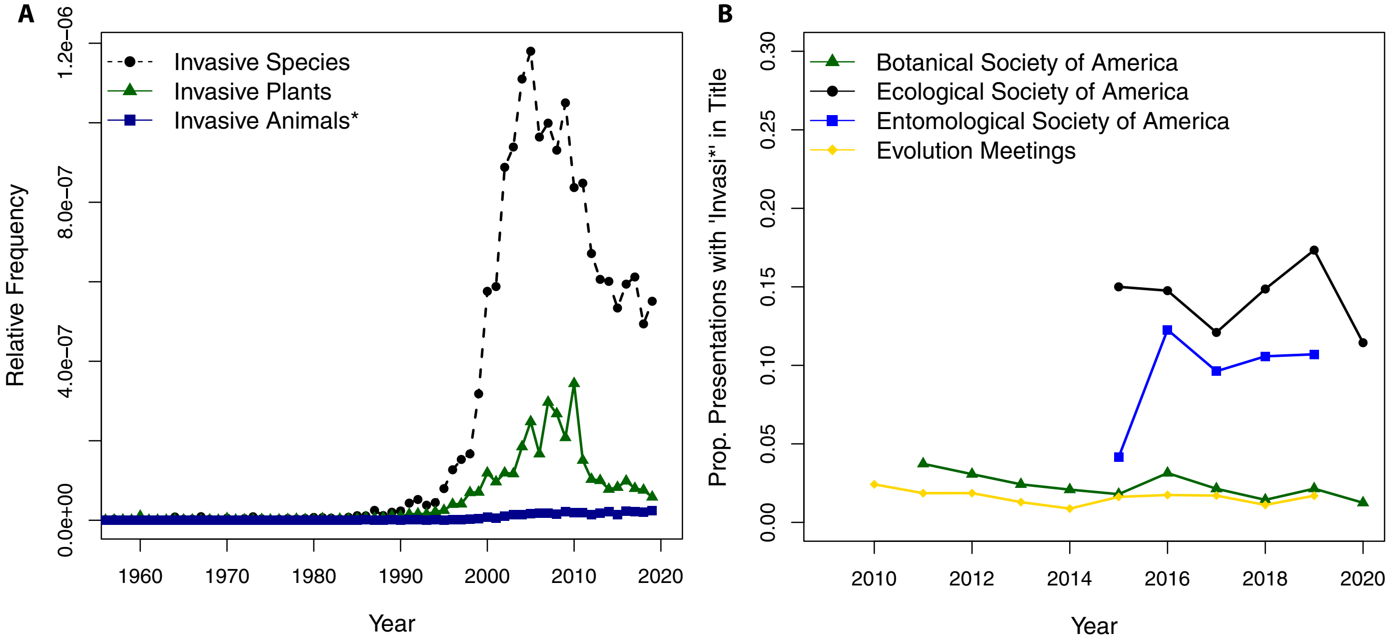

FIGURE 1. Plants are the most common invasive species found in books across the internet, but are underrepresented at botanical conferences relative to other organismal, ecological, and evolutionary biology conferences. (A) The relative frequencies of Google ngrams containing “invasive species” (black dotted line and circles), “invasive plants” (dark green solid line and triangles), or the sum of frequencies from several different animal taxa including “invasive insects”, “invasive animals”, “invasive fish”, “invasive birds”, “invasive amphibians”, and “invasive mammals” (blue solid line and squares). There were similar results for other synonyms (“exotic”, “foreign”). The term “weeds” was at least one order of magnitude more common in all years than any other search term likely due to its popular usage outside of science. (B) The proportion of total talks/posters containing the words invas* in the title across Botanical Society of America (dark green triangles), Ecological Society of America (black circles), Entomological Society of America (blue squares), and Evolution Meetings (gold diamonds). One caveat is that the term “weed” may be used instead of “invasive” in the title of posters or talks and could hide invasion biologist participation in either the Botanical Society of America or Ecological Society of America meetings.

begun to untangle the complex spatial and temporal context of colonization. For example, a *Mimulus guttatus* DC. invasion in the United Kingdom was once assumed to result from a single introduction from an Alaskan population. However, recent population genomic analyses reveal there were introductions from several genetically distinct native North American populations at multiple time points during the invasion (Vallejo-Marín et al., 2021). Invasions may lead to future introduction events. Recent studies in both *Mimulus guttatus* and *Ambrosia artemisiifolia* L. have documented “bridgehead” effects where invasive populations from one area led to an introduction into a second region (van Boheemen et al., 2017; Vallejo-Marín et al., 2021). The emerging consensus is that colonization is a dynamic and ongoing process that can repeatedly replenish or alter genetic diversity throughout an invasion.

ADMIXTURE

Unlike early hypotheses that suggested non-native populations were genetically depauperate, many invasive plant species show equal or greater levels of within-population genetic diversity in their invasive range compared to their native range. Increased genetic diversity in the introduced range is largely due to admixture among populations that were previously isolated in their native range. Furthermore, recent studies suggest that these novel genetic variants are ecologically important (Keller and Taylor, 2010). Hybrids between North American and European populations of *Phalaris arundinacea* L. have greater fitness in their invasive range (Lavergne and Molofsky, 2007), and admixture has driven local adaptation in invasive populations of *Spartina alterniflora* Loisel. in China (Qiao et al., 2019). Native populations of *Plantago lanceolata* L. are subject to ecological constraints that do not affect admixed non-native populations (Smith et al., 2020). These studies suggest invasive species are not simply preadapted to their introduced environment but can evolve ecologically important phenotypic novelty through admixture.

HYBRIDIZATION AND POLYPLOIDY

Novel variation in invasive plant populations can also stem from interspecific hybridization and polyploidy (Whitney et al., 2009; te Beest et al., 2012). For instance, hybridization between introduced *Sorghum halepense* Pers. and cultivated *Sorghum bicolor* (L.) Moench has resulted in introgression at several loci underlying traits including rhizome growth and seed size that likely facilitated invasion of *S. halepense* throughout the southeastern United States (Paterson et al., 2020). Polyploidy, the presence of more than two genome copies per cell, is often concomitant with hybridization and is more prevalent in plants than other taxa. Such genome duplication can increase heterozygosity, facilitate selfing, and increase phenotypic plasticity, all of which may promote invasibility (te Beest et al., 2012). For example, in Scotland, hybridization and polyploidization between two *Mimulus* species with native ranges on separate continents has generated individuals that are phenotypically divergent from both parent species (Meeus et al., 2020). Going forward, the mechanistic details that link genetic variants and gene dosage to phenotype and fitness are needed to understand exactly how hybridization and polyploidy can promote invasibility.

PLASTICITY

Plant studies have begun to provide evidence of the importance of phenotypic plasticity in invasions and the mechanisms underlying increased plasticity (Sultan et al., 2013; Bock et al., 2018). For example, the successful establishment of *Helianthus tuberosus* L. in riparian areas of Europe is associated with increased clonality through enhanced vegetative tuber formation, a plastic response to greater water availability that evolved further in the introduced range through selection at two loci (Bock et al., 2018). Recent work on epigenetic variation hints at additional mechanisms for generating plasticity for facilitating invasions, particularly for primarily asexual invaders like *Salvinia molesta* or *Fallopia japonica* (Mounger et al., In press [Preprint]). For example, genome-wide surveys of introduced *Fallopia japonica* populations grown in controlled greenhouse and reciprocal transplant experiments suggest variation in DNA methylation is far higher than genetic variation (Richards et al., 2012), potentially promoting success in diverse non-native habitats. The role of epigenetics in invasions is a direction ripe for research with many unanswered questions.

MOVING INVASION BIOLOGY FORWARD

The examples above demonstrate the significant contributions that botanists are making to invasion biology, but botanists are also well poised to overcome some of the mechanistic hurdles that have long encumbered invasion biology as a field. A major challenge has been inferring how the timing and strengths of different evolutionary forces can alter invasion trajectory and speed. Much of the difficulty in addressing this challenge stems from sampling limitations; inferences regarding the extent of genetic bottlenecks, prevalence and timing of admixture, and magnitude of selection typically result from comparisons of genetic variation between native and invasive populations for only a single time period. A more nuanced understanding of evolutionary processes underlying establishment and spread of invasions requires repeated sampling of invasive species throughout the course of an invasion. Botanists have two distinct advantages in implementing this approach. First, strong cooperation among herbaria, abundant collections, and robust digitization and databasing efforts make samples spanning the range and course of a plant invasion easy to access. Second, the increasing availability of community science observations and the relative ease of locating and resampling specific populations allows botanists to quickly ascertain, revisit, and collect populations at the forefront of invasions.

Combining herbarium collections and modern population genomic techniques allows for unparalleled assessment of changes across the genome throughout the entire time course of an invasion. While contemporary collections can be used to generate genomic data for any invasive species, herbaria tend to have plentiful collections of invasive species because these species are often conspicuous, abundant, and novel to the collector. Recent advances in genomic library design enable reduced-representation sequencing from small quantities of degraded DNA from preserved plant samples (e.g., Suchan et al., 2016), making genomic evaluation spanning the range and time course of an entire invasion tractable. Although there are some limitations to these data in terms of regional bias and lack of resampling from the same locations, this approach can greatly expand our ability to understand invasion dynamics across varied environments and taxa. Efforts to apply this approach to five focal invasive plant species are currently being coordinated by the Consortium for Plant INvasion Genomics (CPING, www.invasiongenomics.com).

Genomic studies of ongoing nascent plant invasions can provide similar time-course data sets while better allowing investigators to control the experimental design. However, identifying potential invaders early is difficult and may require decades of investment to track and sample invasion fronts. These disadvantages can be mitigated by integrating botanical databases with community science initiatives such as iNaturalist to identify potential invasive species soon after introduction and to identify new populations at the vanguard of invasions. Such observations are relatively easy for researchers to validate and collect as plants are sessile and populations are unlikely to become extirpated. Continuous tracking of invasions is not only useful for inferring information about colonization dynamics and admixture but can also provide important information on establishment rate and velocity of spread.

In summary, botanists have always been at the forefront of invasion biology, from early observations to contemporary hypothesis testing with modern tools. Plants have distinct advantages as experimental systems that have and will allow botanists to address novel questions in invasion biology. By embracing invasion biology as a field and leveraging our knowledge, historical resources, and new technologies, the botanical community can continue to revolutionize our understanding of invasive species.

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AUTHOR CONTRIBUTIONS

Brittany L Sutherland: Writing – original draft (equal); Writing – review & editing (equal). **Craig F Barrett:** Writing – review & editing (equal). **James B Beck:** Writing – review & editing (equal). **Maribeth Latvis:** Writing – review & editing (equal). **Michael R McKain:** Writing – review & editing (equal). **Erin M Sigel:** Writing – review & editing (equal). **Nicholas J. Kooyers:** Writing – original draft (equal); Writing – review & editing (equal).

All authors contributed to the drafting and revision of this manuscript.

DATA AVAILABILITY STATEMENT

Data for Fig. 1 are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.g1jwstqqg (Kooyers et al., 2020).

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