
7-2019

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Citation Details

Published as: Cruzan, M. B. (2019). How to Make a Weed: The Saga of the Slender False Brome Invasion in the North American West and Lessons for the Future. BioScience, 69(7), 496–507.

How to Make a Weed – The Saga of the Slender False Brome Invasion in the North American West and Lessons for the Future

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Abstract

Historical herbarium collections and genetic analyses indicate that slender false brome (*Brachypodium sylvaticum*) was first introduced in test gardens in Oregon in the early 1900s as part of the USDA's plant introduction program. A small number of naturalized populations were established, but it was not until several decades later that this alien species became an aggressive invader. The Oregon invasive strains of false brome were generated as a consequence of mating among genetically divergent lineages. The resulting hybrid populations contained high levels of genetic variation that fueled the evolution of specific adaptations to the Pacific Northwest climate, and ultimately generated genetically superior lineages. Although the false brome invasion has caused significant ecological and economic harm and is expected to continue spreading across western North America, understanding the circumstances that have promoted its success may provide valuable lessons for the management of native plants under pressure from global climate change.

Keywords: Adaptation, hybridization, inbreeding depression, invasive species, range expansion.

Invasive species cause massive harm to human and ecological systems worldwide. The numbers and abundance of introduced plants and animals across regions varies, but nearly every part of our planet has been subjected to some impact from alien species (Turbelin et al. 2017). The invasive species crisis is a direct consequence of human activities. Many invaders have been introduced by accident as they are transported by commerce and tourism, but more often than not, introductions have been purposeful, and usually with the best intentions in mind (Hulme 2009, Reichard and White 2001). In spite of our propensity to carry alien hitchhikers as we travel, the prevalence of invasive species is surprising; it is actually quite difficult for any plant or animal to survive and reproduce after introduction to a foreign region. An outstanding case is the European starling, which was introduced to New York City in 1890 through efforts of the American Acclimatization Society, whose goal was to introduce birds from the writings of Shakespeare in the New World. Many attempts to introduce starlings and other European birds failed before an introduction of 60 starlings succeeded in establishing a stable population in Central Park (Cooke 1928). From this small foothold, starlings have increased in numbers and spread across the continent, and now number more than 200 million.

In spite of some dramatically successful invasions by organisms such as starlings, more often than not, plants and animals that have been moved from their native range to foreign regions are doomed to failure. This is generally true because the habitable region for any particular species is usually limited to narrow climatic zones, so much of the planet is inhospitable for them. Even if an alien species is fortunate enough to find itself in a compatible environment, it is likely to face stiff competition and predation from natives, as well as novel sets of pathogens (collectively referred to as biotic resistance) that may conspire to thwart its establishment and contribute to its rapid demise (Levine et al. 2004). The idea that a large proportion of introduced species will never become naturalized (establishing self-sustaining populations) or invasive (capable of aggressive growth causing ecological or economic harm) has come to be known as the ”tens rule” (Williamson and Fitter 1996), which predicts that about one in 10 introduced species are likely to become naturalized, and one in 10 of those will typically become invasive. Of course, processes governing the success of introduced species are more complex than this simple rule would suggest. For example, success rates tend to be much higher on islands, and are generally higher for mammals compared to plants (Vander Zanden 2005), but it is generally true that successful invaders represent a small fraction of the original introductions. Introduced species developing into invaders are capable of displacing native vegetation and creating economic costs (Pimentel et al. 2000, Pimentel et al. 2005, Ricciardi et al. 2011); however, it is also of interest to ask whether there are particular characteristics of species or conditions of their introduction that improve the chances of invasion success, and whether successful invaders can provide us with lessons we can apply to facilitate the persistence of native species facing challenges from global climate change.

Introduced Plants Provide Accessible Examples for the Study of Invasion Success

One of the most numerous groups of invasive species are plants (often referred to as “weeds”). While not all weeds (defined as unwanted and often aggressive plants) are alien plants, it is also true that not all introduced plants become weedy invaders. The idea that some plants make much better invaders than others dates back to the work of Herbert Baker in the mid-1900s

(Baker 1965, Cheptou 2012). Baker suggested that plants that were particularly adept at colonizing new locations were typically able to reproduce autonomously – either through self-fertilization or asexual reproduction – and were more often annuals or short-lived perennials. These ideas fit well with widely accepted views on ecological succession, where annuals and herbaceous perennials were considered to be typical of pioneer species colonizing sites after the destruction of mature vegetation. But it appears that the same rules do not always apply to invasive species. Although much effort has been made to understand the primary features that render some plants more invasive than others (Rejmanek and Richardson 1996), few generalities have emerged (Barney and DiTomaso 2008, Moles et al. 2008). There are some notable examples of invasive annual plants such as cheatgrass (*Bromus tectorum*) in arid regions of North America, but many more invasive species are long-lived perennials, including the wheel cactus (*Opuntia robusta*) in Australia, and woody shrubs and trees such as Japanese honeysuckle (*Lonicera japonica*) and Chinese tallow (*Triadica sebifera*) in eastern North America. The fact that many invasions appear to represent unique stories has made it difficult to establish character profiles for invasive plants and to predict a species' potential for future invasion.

While it has been difficult to identify plant characteristics that predict invasion potential, it may be the case that the number and size of introductions, and the resulting levels of genetic diversity, may have more influence on the chances of successful establishment, and perhaps whether a species eventually becomes invasive. Newly introduced species generally take some time before they begin to spread and become invasive. This lag period has often been attributed to population growth; populations need to become relatively large before they can export large numbers of migrants for the colonization of new territory (Williamson 1996). On the other hand, a growing body of evidence suggests that this delay may represent a period of rapid adaptation to the conditions in the invaded range (Dormontt et al. 2011, Prentis et al. 2008). This idea is difficult to reconcile with accepted views of colonization after long-distance dispersal, which is thought to typically result in low levels of genetic variation that would limit the potential for adaptive evolution. In contrast, it is often true that the most aggressively invasive species have high levels of genetic variation, indicating that their success is a consequence of multiple introductions from the native range (Bossdorf et al. 2005, Dlugosch and Parker 2008, Mack 2005). The increase in genetic variation after multiple introductions could promote adaptation to novel conditions, in which case we may consider the potential for invasion success to be consequence of evolution after introduction.

Here, I describe the introduction and range expansion of the slender false brome (also false brome; *Brachypodium sylvaticum*; https://www.cabi.org/isc/datasheet/9890; Fig. 1), which is an invasive species that is actively undergoing range expansion. This perennial bunchgrass is an aggressive invader of forest understories that is rapidly spreading and causing ecological harm by displacing native species in several regions of California, Oregon, and Washington in western North America. I first describe the historical introduction of this species, and the ecological and evolutionary processes that have led to its success. I conclude by applying the principles we have gleaned from studies of the slender false brome to the management of native species that are under pressure from global climate change.

The Slender False Brome Introduction

The saga of the invasion of slender false brome begins in the late 1800s, when success stories of plant and animal introductions fueled the enthusiasm for substantial efforts to collect seeds from around the world. One of the earliest purposeful introductions of an alien species occurred in 1888, when the California citrus industry was threatened with collapse by an infestation of cushiony scale insects (*Icerya purchase*), which had been accidentally introduced from Australia. Investigation of the natural predators of this pest led to the introduction of a species of ladybird beetle (the vedalia beetle, *Rodolia cardinalis*), which successfully controlled the scale insects and was one of the first examples of the effective use of a biological control agent (Majerus 1994). This example motivated efforts to introduce other potentially useful species, especially foreign plants. During the late 1800s, the USDA Seed Distribution Program was established to introduce varieties of crops and other agriculturally important species. This effort was expanded to include the collection and distribution of lesser known species with the establishment of the Office of Foreign Seed and Plant Introduction (Griesbach 2013). Collectors from this agency scoured the globe in search of plants they thought could have economic value, and local range managers grew these alien species in test gardens to assess their potential use in horticulture and agriculture. As part of this effort, scientists in Eugene and Corvallis apparently planted slender false brome from several locations in Europe in test gardens to evaluate their suitability to improve Oregon rangelands for the support of cattle production (Rosenthal et al. 2008). This effort was ultimately abandoned, perhaps because the hairy leaves of this grass proved distasteful to cattle, but range managers had unknowingly initiated a perfect storm for the creation of an aggressively invasive grass.

By planting false brome from different geographic regions in the same garden, managers had inadvertently promoted hybridization among genetically divergent strains. Mixing among these varieties elevated levels of genetic variation available for selection to act on, and generated the novel invasive hybrid lineages that are now spreading across the Pacific Northwest. Genetic analyses have revealed that the Oregon invasive lineages are the result of interbreeding among plants from England, Spain, Italy, and other parts of Europe, and correspond closely with the genetic profiles of accessions from these regions maintained by the USDA Western Regional Plant Introduction Station (https://www.ars.usda.gov/pacific-west-area/pullman-wa; Rosenthal et al. 2008). There are no written records of when test gardens of false brome were established, but plant introduction efforts continued from around 1900 until the early 1930s, so it is reasonable to assume that false brome was introduced into Oregon during this time. We know from herbarium records that false brome was first collected in Oregon in 1939, and it remained isolated near its points of introduction in Eugene and Corvallis for many decades (Fig. 2). The Oregon climate is classified as temperate Mediterranean, which has drier summers and cooler, wetter winters compared to the temperate maritime and Mediterranean climates in Europe (Marchini et al. 2018a). Consequently, the introduced varieties of false brome were not a good match for Oregon climates. But these newly introduced plants apparently gained a foothold, and began the process of adaptation to their new home, which was facilitated by intermixing among genetically divergent strains from across Europe. By the 1990s, the invasion of Oregon forest understory habitats began in earnest; false brome now occupies over 10,000 acres of wildlands across the state. But this saga has not yet come to a conclusion because, based on environmental niche modelling, false brome is expected to continue spreading until it occupies forest understories across vast regions of the Pacific Northwest (Fig. 3).

The Slender False Brome Invasion

Recent studies of false brome have revealed how selection modified these plants to generate the invasive hybrid strains. By growing plants from native source regions with invasive false brome under controlled conditions, Marchini et al. (2018a) determined that Oregon invasive hybrids differ from their European progenitors for a number of traits that have improved their ability to thrive during long dry summers (Fig. 4). Simply showing that characteristics of the invasive plants differ from European varieties would not be adequate to demonstrate evolutionary adaptation to the Oregon climate, because such changes could be due to accidents of introduction and early survival (genetic drift; Leinonen et al. 2013). Marchini et al. (2018a, 2018b) circumvented this problem by comparing the trait differences to genetic variation based on DNA sequence variation as measured by genetic markers (microsatellite markers) that were not subject to the effects of natural selection. Plants from source regions in Europe were grown with plants from Oregon in controlled environments and trait differences between these two regions were compared to the degree of difference expected in the absence of selection based on the microsatellite markers. These analyses demonstrated that a number of anatomical and physiological characteristics of the Oregon invasive false brome had changed to a greater degree than expected if variation were due to random changes in genetic composition occurring during introduction. They also showed that the direction of change matched expectations from what we know about how plants adapt to arid conditions (Fig. 4). The majority of trait changes for the invasive variety appear to have occurred prior to the invasion of large regions of forest understory, so this example supports the idea that invasive species can undergo adaptive evolution during the lag phase of the invasion process.

Reconstructing the story of range expansion of false brome from historical herbarium collections and from patterns of variation in genetic markers reveals that the rapid spread of false brome in Oregon has been assisted to a large extent by humans (Ramakrishnan et al. 2010). From its original introduction points in Eugene and Corvallis, false brome spread south into the Rogue River Valley and north through the Willamette Valley (Fig. 2). Much of the early spread of this invasive species appears to have occurred through logging activities, and false brome continues to be abundant in regions that have a history of logging. From pioneer populations established after logging, false brome continued its invasion with the assistance of vehicle traffic, recreational activities, and domestic dogs (Arredondo et al. 2018, Holmes et al. 2010). In detailed analyses of plants in the Clackamas Watershed near Portland, Oregon, Arredondo et al. (2018) uncovered patterns of genetic variation that are consistent with the movement of recreationists among frequently visited fishing spots, boat ramps, and launching sites for rafters. Observations indicate that the seeds of false brome are easily caught in recreationists' shoes and the fur of their dogs, but wild animals such as deer are also known to be dispersers of false brome in Europe (Heinken and Raudnitschka 2002). The dependence on humans for transport and the creation of suitable habitat is supported by the association of false brome with human-mediated disturbance (Taylor and Cruzan 2015, Taylor et al. 2015).

Consequently, false brome is commonly found near vehicle pull-outs, along road verges and hiking trails, and in other areas where natural vegetation has been destroyed.

Humans are ideal dispersal agents for the spread of invasive plants such as false brome because our habitual movements concentrate seed deposition in specific locations (directed dispersal; Howe and Miriti 2004). In the case of false brome, human activities serve to disrupt the vegetation and leaf litter that would normally thwart the establishment of this invader (Holmes et al. 2010, Taylor et al. 2015). In a natural forest, a thick layer of leaf litter presents an effective barrier to the establishment of weeds. Once this barrier is disturbed or removed, conditions are perfect for weed establishment and growth. While native bunchgrasses such as Columbia brome (*Bromus vulgaris*) and others occur at much lower densities in the same types of habitats, false brome has an advantage over native species, in that it produces many more seeds. This confers higher propagule pressure, which is thought to be important for the spread and dominance of invasive species (Lockwood et al. 2005). The enormous number of seeds produced facilitates the rapid colonization of any patch of bare soil that becomes available (Taylor and Cruzan 2015, Taylor et al. 2015). We humans not only move seeds around as they attach to our clothing and vehicles, but our activities often create just the right type of opportunities for weeds to become established and thrive.

As false brome seeds are inadvertently transferred to new locations, the range of this species continues to expand, but not all source populations have equal invasion potential. Genetic analyses by Ramakrishnan et al. (2010) have shown that the largest populations, which may be more vigorous as a consequence of their higher genetic diversity, serve as sources for local invasions. In contrast, the newly established populations tend to be small, have low genetic diversity, and contribute little to the colonization of new sites (Fig. 5). The reduced invasion potential of small, newly established populations is likely due to inbreeding (Marchini et al. 2016). False brome is capable of reproducing by self-fertilization, but like all outbreeding organisms, populations of this species have sustained substantial numbers of deleterious mutations (genetic load). Deleterious recessive mutations are expressed as harmful traits only when they are homozygous (i.e. two copies are present in the genome). Consequently, when inbreeding occurs (i.e. when closely-related individuals mate), larger proportions of the genome become homozygous, and more of these harmful genetic variants are expressed, leading to lower fitness of inbred offspring (inbreeding depression). This is a particularly critical problem for a newly invasive species, because as it expands its range, new populations are often established from one or a few seeds; the potential for inbreeding is high. This results in a reduction in genetic variation and the capture of a subset of genes that travel with the leading edge of a species' range (gene surfing; Hallatschek and Nelson 2008). Thus, the process of geographic spread leads to increased inbreeding at the edge of the range, and the invasion may become stalled due to the effects of inbreeding depression.

While inbreeding would normally slow the range expansion of an invader, the multiple introductions that originally allowed false brome to establish in the Pacific Northwest may have afforded it another advantage that is beginning to increase its invasion potential. In small, inbred populations at the range edge, selection can eliminate harmful mutations in a process called “purging.” The success of purging depends on having genetic exchange among populations to infuse them with healthy levels of genetic variation that can facilitate the elimination of deleterious recessive alleles when combined with inbreeding and selection against inbred individuals (Whitlock et al. 2000). Analytical models by Whitlock et al. (2000) and simulations by Marchini et al. (2016) have shown that purging is most effective with low levels of gene flow and selection in inbred populations. In the case of false brome, inbred populations at the range edge exhibit evidence of purging of deleterious mutations (Marchini et al. 2016). Once invasive populations have eliminated most of their harmful mutations, the newly colonized populations will no longer suffer from inbreeding depression, so we expect that the rate of invasion will begin to accelerate (Fig. 6). The simulations conducted by Marchini et al. (2016) have demonstrated that this process is highly dependent on the initial amounts of genetic variation, so introducing false brome to Oregon from multiple locations not only allowed false brome to become better adapted, it also provided the necessary genetic variation for this invader to escape the debilitating effects of inbreeding depression, and consequently to increase its invasion potential. While some degree of purging is evident in several leading edge populations of false brome (Marchini et al. 2016), we currently do not know how effective this process has been across the range of this species, or how much it has contributed to its invasion success.

When species are introduced into foreign locations, they are likely to encounter novel sets of pathogens, predators, and potentially beneficial organisms that can affect their success. One hypothesis for the success of alien plants suggests that, because pathogens that may limit population growth in the native range are absent in the introduced range, reduced damage from herbivores and pathogens in the introduced range increases invasion potential (the enemy release hypothesis; Keane and Crawley 2002). While introduced species appear to have lower herbivore and pathogen damage in some cases (Bossdorf et al. 2005), false brome populations in the native and invaded range displayed similar levels of damage from generalist herbivores and pathogens (Roy et al. 2011), indicating that the increased vigor of the invasive lineages of this species was not due to enemy release. In contrast, the story of false brome’s relationships with fungal mutualists is more complicated. On the one hand, the loss of a fungus that normally inhabits leaf tissue of plants (fungal endophyte) in the native range appears to have increased the vigor of plants in the invaded range (Vandegrift et al. 2015). On the other hand, soil fungal mutualists (mycorrhizal fungi) in the invaded range appear to increase the growth, leaf nitrogen content, and competitive ability of invasive false brome (Workman and Cruzan 2016). Apparently, the loss of an endophytic mutualist and the adoption of a novel mycorrhizal mutualist, in addition to the evolution of well-adapted and genetically superior strains, are contributing to the success of invasive false brome in its new home in the Pacific Northwest of North America.

The Best Way to Make a Weed

Humans have been unwitting partners throughout the false brome invasion in Oregon. Not only did we first introduce this plant, but we and our domestic animals act as the perfect means to transport seeds to locations where false brome can thrive. Ecological and genetic studies of false brome reveal a story of how a species that is benign in its native range can undergo rapid evolution to become an aggressive invader. The information we have gathered from this invasion has provided important insights into prudent management of this and other invasive species by controlling the most vigorous source populations. The false brome story provides important lessons, not only on the processes responsible for the evolution of invasive species, but also for our understanding of how native plants and animals will have the best chances of surviving challenges from changing climates.

If the false brome story is typical for invasive species that have emerged over the last century, then we would expect this to be reflected by similarities of some primary characteristics across invasions. For example, it is quite common for alien species to remain rare for some period after naturalizing and before they become more widespread (Williamson 1996). While these lag periods have often been considered to be due to demographic processes, the observed pattern of extended periods of low abundance followed by rapid range expansion does not fit well with strictly demographic or ecological explanations (Crooks 2005). This pattern, combined with the observation that many of the most aggressive invaders are marked by relatively high levels of genetic variation in the invaded range, suggests that lags in abundance may well be periods of evolution and adaptation of newly naturalized populations. For example, Chinese tallow tree, kudzu, reed canary grass, and cheatgrass in North America, the wheel cactus in Australia, and others, have unexpectedly high levels of genetic variation in their introduced ranges (reviewed in Cruzan 2018 page 299, Novak and Mack 2016).

The potential for adaptation to novel environments may be elevated further if alien populations are established by introductions from different geographic regions of the native range, which could enhance evolutionary potential as a consequence of hybridization (also referred to as admixture) among genetically divergent lineages (Dormontt et al. 2011, Ellstrand and Schierenbeck 2000, Pfennig et al. 2016). Hybridization is thought to be responsible for the origin of several invasive lineages, including smooth cordgrass hybrids (*Spartina*) in Central California (Ayres et al. 1999, Sloop et al. 2011), and reed canary grass (*Phalaris arundinacea*), which is displacing other wetland species across North America (Lavergne and Molofsky 2007). This idea – that hybridization can act as an evolutionary stimulus – has been recognized by plant biologists since the mid-1900s (Anderson and Stebbins 1954). The potential for hybridization to promote adaptation and diversification has been demonstrated in such cases as Darwin's finches (*Geospiza*) in the Galapagos (Grant and Grant 2016) , and the rock rose (*Piriqueta*) in Florida (Cruzan 2005). The importance of hybridization is becoming more widely accepted with the accumulation of genetic evidence for historical admixture in a wide range of species, including many types of plants and animals, and even humans (Payseur and Rieseberg 2016, Stringer 2012).

Observations of lag periods and evidence of multiple introductions in many invasive species suggest a generalized scenario for many successful invaders (Fig. 7). In the first stage, individuals are imported from multiple locations in the native range (Stage 1). After establishing, these plants begin interbreeding to generate hybrid offspring (Stage 2). Not all of the original colonizers and hybrids will be well-adapted, so they will be subjected to selection in their new environment. Strong selection has demographic consequences, so we may expect naturalized populations to go through a period of low abundance (population bottleneck; Stage 3). Once well-adapted hybrids begin to emerge, the rate of range expansion will begin to increase (Stage 4), but the invasion may become stalled due to inbreeding at the expanding range edge (Fig. 6). With adequate levels of genetic variation and continued mixture among separate invading lineages, mutations may be purged (Fig. 7, Stage 5), resulting in an accelerated invasion as newly colonized populations escape the detrimental effects of inbreeding depression (Fig. 6).

This scenario of hybridization after multiple introductions may be common for many invasive species, but it is certainly not universal. In fact, there are a number of cases where introduced species were apparently "pre-adapted" to the environments they encountered in their new homes. For example, an independent invasion of false brome near Stanford University in California originated from a single location in Italy (Rosenthal et al. 2008). The spread of this invasion has been limited compared to the ones in Oregon, but there are other examples of extremely successful invasions that have limited genetic diversity. One of the most dramatic of these is the invasion across a wide swath of North America by a single clone of Japanese knotweed (*Fallopia japonica*). This species is able to exploit a relatively wide range of habitats because of its ability to adapt through non-genetic changes in methylation of the genome, referred to as epigenetic changes, rather than the acquisition and fixation of novel variation in DNA sequences (Richards et al. 2010). Another example of a very successful invasion is the water hyacinth (*Eichhornia crassipes*), a floating aquatic plant that is represented by just a few clones over broad regions of North America and Asia (Zhang et al. 2010). There may be many other examples of successful invasion as a consequence of pre-adaptation and by rapid evolution after multiple introductions, and much more work is required before we can fully appreciate the wide range of mechanisms used by plants to succeed in challenging environments.

Lessons for the Future

Although starlings, false brome, and many other invasive species are considered to be pests, understanding the circumstances that create a successful invader may offer valuable information to the management of native species as they face the challenges of global climate change. Virtually all species have undergone changes in their geographic range at some point in the past, and many of the processes occurring during range shifts are the same that determine the success of invasive species. For example, following the last ice age, temperate plant species in the Northern Hemisphere underwent range expansions from their southern glacial refugia (Clark et al. 1998, Hewitt 1999, Webb 1981). These species encountered many of the same difficulties as newly-introduced alien species; with the exception of tundra species living at the edge of retreating ice sheets, northward migrants were only able to shift their distribution by invading established plant communities. Hence, vegetation at each longitude was gradually replaced by more southerly species as fire, insect infestations, diseases, and other disturbances created openings for colonization and establishment. It is likely that turnover in vegetation in response to contemporary climate change will occur in much the same manner, as disturbances enable range shifts and replacement of existing plant communities (Dale et al. 2001).

The climate change event that native plants and animals are currently facing is unprecedented in a number of ways. In addition to being more rapid, modification of landscapes and destruction of habitat by human activities have imposed additional challenges that were not present during historical episodes of climate change (Nogués-Bravo et al. 2018). Extensive regions have been modified for agriculture, urbanization, and transportation, resulting in the separation and isolation of fragments of natural habitat. The process of habitat fragmentation not only erected additional barriers for dispersal and range shifts, but may also have compromised the evolutionary potential of species as population sizes have shrunk (population bottlenecks), leading to increased inbreeding and the loss of genetic variation (Vranckx et al. 2012, Young et al. 1996). This is a particularly important point because the level of genetic diversity is a strong predictor of evolutionary potential and the ability to adapt to novel conditions (England et al. 2003, Lavergne and Molofsky 2007). During historical climate change events, most species were capable of moving or adapting, but the impediments to dispersal and loss of genetic diversity that many native species face today may require additional measures to maintain current levels of biodiversity.

It is generally true that habitat changes with geographic distance; if you move from any particular point on the landscape, you will soon encounter different environments due to changes in the microclimate along with proximity to water features (e.g., wetlands, waterways, lakes, and oceans), the local topography, elevation, and longitude. Consequently, any species that is distributed over a region of some size is likely to be genetically heterogeneous as specialized lineages (e.g., ecotypes, races, and varieties) occupy different portions of the geographic range. Ernst Mayr (1947, page 280) captured this idea succinctly when he said that "All geographical races are also ecological races, and all ecological races are also geographical races." It is notable that, in the case of slender false brome and many other invasive species, their ability to become established and expand their ranges appears to be a direct consequence of admixture among genetically divergent geographic lineages (Pfennig et al. 2016). So perhaps our blunders with species introductions around the world ultimately provided us with a valuable lesson for the future; the best chances for adaptation and range shifts in native species may come from the same type of admixture that has generated so many invasive species (Hamilton and Miller 2016, Whiteley et al. 2015).

Today, the genetic signatures of historical range expansion are still evident, and tell stories of opportunities for hybridization and admixture for many species (Hewitt 1999, Maskas and Cruzan 2000, Soltis et al. 1997). The lessons we can glean from historical range expansions, and the processes responsible for persistence and adaptation of invasive species, suggest that new strategies may be needed to sustain biodiversity under the challenging conditions imposed by contemporary climate change. The ecological processes involved in range shifts are difficult to study because we do not have examples of native species that have recently undergone range expansion. So ironically, invasive species may be our best chance for studying the processes of colonization and establishment responsible for changes in geographic distribution. Information on the ecological and evolutionary progression of invasion will be extremely valuable as we are faced with many difficult management decisions for the rescue and remediation of native species in decline from the pressures of climate change (Groves et al. 2002, Pfennig et al. 2016). So maybe we should take some hope for the survival of native species under pressure from climate change from the lessons we have learned from invasive species that were able to adapt to novel conditions within a century or less. On the other hand, implementing any plan to encourage admixture will require substantial shifts in our conservation goals. For many decades we have focused on individual entities – species, distinct varieties within species, and the biological communities that they occupy – as the primary targets of our conservation efforts. The way that we have defined biological diversity, and have even written laws in some countries (e.g., the Endangered Species Act in the USA), are based on taxonomically defined species, and exclude or devalue individuals of hybrid origin (Lind-Riehl et al. 2016). On the other hand, once we come to appreciate the history of species lineages over longer time frames, it becomes clear that it is not the individual entities themselves that are important, but rather, the evolutionary processes that generated them. This concept – that every contemporary lineage has a history and a future – was one of the revelations provided by Charles Darwin, who viewed species as continually evolving entities (Darwin 1859). In recent decades, conservation biologists have recognized the importance of intraspecific diversity as they have shifted their focus from taxonomic species to genetically and ecologically distinct groups within species, referred to as evolutionary significant units (ESUs; Crandall et al. 2000). However, making ESUs the new targets of conservation still does not acknowledge the dynamic nature of lineages over evolutionary time. The goal of preserving species, ESUs, or taxonomically defined varieties within species in perpetuity is not only likely to be futile, but is also unnatural, as it does not address the historical processes that have produced the amazing biodiversity that surrounds us. In the long run, we may be more successful in our conservation efforts if we view biological diversity as the sum of genetic diversity across all species, and focus on the preservation of evolutionary processes rather than treating taxonomic species and varieties as static entities.

Acknowledgements

The work described would not have been possible without the efforts of many undergraduate and graduate students and post docs over the past 16 years. In particular, Alisa Ramakrishnan, Trieste Musial, David Rosenthal, Rachael Workman, Caitlin Lee, Laura Taylor, Gina Marchini, Erik Hasenkopf, Nena Cole Sherlock, Caitlin Maraist, Michelle Williamson, Tina Arredondo, members of Bitty Roy's lab at the University of Oregon, and Tom Kaye and the False Brome Working Group at the Institute for Applied Ecology, have made substantial contributions to our understanding of the biology and ecology of slender false brome. Thanks to Lindsey Wise and the Oregon Biodiversity Information Center for providing the false brome occurrence data, and Elizabeth Hendrickson for generating the niche modeling distribution map. The manuscript was improved from editorial suggestions made by Alisa Ramakrishnan, Pamela Thompson, Lucianna Edenlord, and Carol Cruzan. The research in my lab was supported by grants from the USDA-CSREES 2005-35320-15317 and Portland State University.

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Figure Legends

Fig. 1. The effects of invasion by slender false brome (*Brachypodium sylvaticum*) in Oregon forests. Prior to invasion the understory is typically a rich mixture of shrubs, ferns, and herbaceous perennials (left; photo by Miguel V.). Photo on the right shows a heavily invaded region of the McDonald-Dunn Experimental Forest near Corvallis, Oregon (photo by Alisa Ramakrishnan). The inset photo is by Glenn Miller. Photos used by permission.

Fig. 2. Locations of historical herbarium collection records (red triangles) of slender false brome (*Brachypodium sylvaticum*) in Oregon from 1939 – 2003. Data were compiled by Alisa Ramakrishnan.

Fig. 3. The distribution of known locations of slender false brome (*Brachypodium sylvaticum*) in Oregon as of August, 2018 (green dots), and the potential range of this species based on niche modeling. The map was generated using data from the Oregon Biodiversity Information Center (http://imapinvasives.org/orimi/map/). The potential range of slender false brome was predicted using Maxent (https://biodiversityinformatics.amnh.org/open_source/maxent/) and was based on current climate data from the PRISM Climate Group (30 year normals for mean, minimum, and maximum temperature, and annual precipitation; http://www.prism.oregonstate.edu/). Warmer colors indicate a higher probability of future invasion by slender false brome.

Fig. 4. Comparison of leaf anatomical and hydrological traits between Oregon invasive (orange bars) and native source region plants (green bars) of slender false brome (*Brachypodium sylvaticum*). Asterisks between bars indicate statistically significant differences between each pair of means. Arrows to the right of each graph show the predicted response of each trait for drought-tolerant plants. Data are from Marchini et al. (2018b).

Fig. 5. Patterns of dispersal and colonization of sites along roads by the invasive slender false brome (*Brachypodium sylvaticum*) near Sweethome, Oregon. The size of each marker indicates the relative level of genetic diversity. The thickness of the arrows and the associated numbers indicate the number and direction of migrants. In most cases dispersal occurred over longer distances, but along one road (Wiley Creek Road) dispersal occurred more regularly over short distances creating a pattern of Isolation by distance (adjacent populations are more closely related than ones further away; map is not to scale). Data are from Ramakrishnan et al. (2010).

Fig. 6. A model for predicted changes in the rate of range expansion in an outbreeding invasive species in response to inbreeding followed by selection for the reduction (purging) of mutations (genetic load). After an initial lag period (1) range expansion begins to accelerate (2), but is slowed due to inbreeding depression in newly colonized populations at the range edge (3). Gene flow among inbred populations alleviates genetic load, after which, newly colonized populations are vigorous and range expansion becomes exponential (4).

Fig. 7. A model for an effective method for creating a successful invasive species (i.e. how to make a weed). The starting material should be a species that partly or routinely outcrosses and should be collected from several locations in the native range that represent a diversity of habitats and climatic conditions (1. Multiple Origins). Seeds from these locations should be sown together to allow plants to interbreed to generate hybrid offspring (2. Hybridization). Upon forming naturalized populations, these offspring will be subjected to selection for adaptation to the local environment over several generations. At this stage natural selection is eliminating less-fit individuals so don't fret if these populations seem to be struggling (3. Bottleneck due to selection). If adequate genetic variation was introduced at step one, then you may be rewarded with the emergence of well-adapted plants that have vigorous growth. These well-adapted invaders are likely to begin spreading as they colonizes new sites (4. Range Expansion). This range expansion may begin to stall as newly colonized populations suffer from inbreeding depression (see Fig. 6), but if you started with adequate levels of genetic variation, then selection will continue to reduce the genetic load (5. Inbreeding, Gene Flow, and Selection Reduce Mutational Load), and range expansion will become exponential (Fig. 6).

Fig. 1

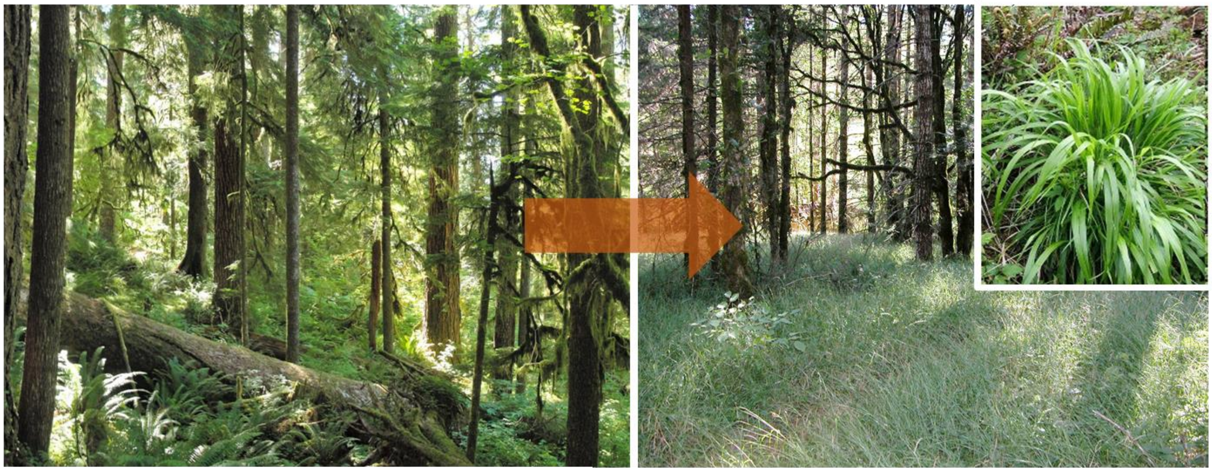
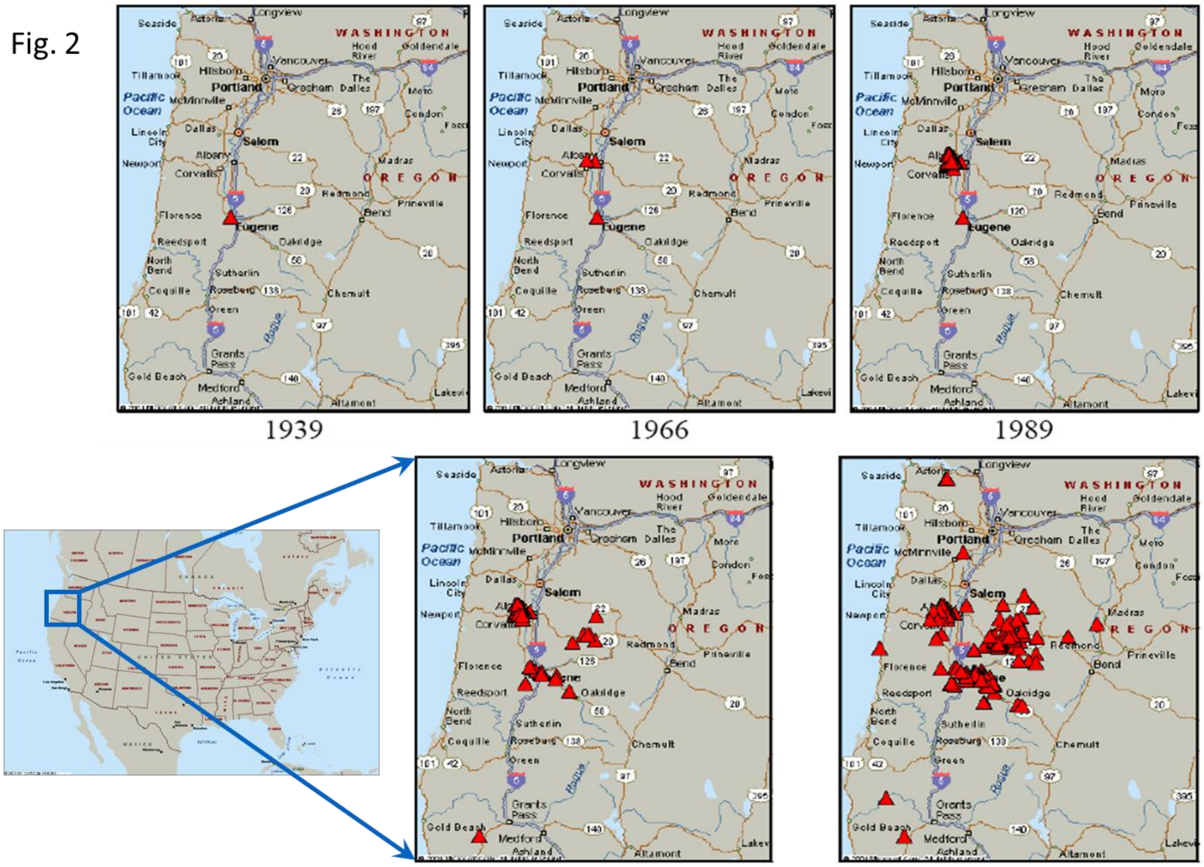


Fig. 2



1939

1966

1989

2000

2003

Fig. 3

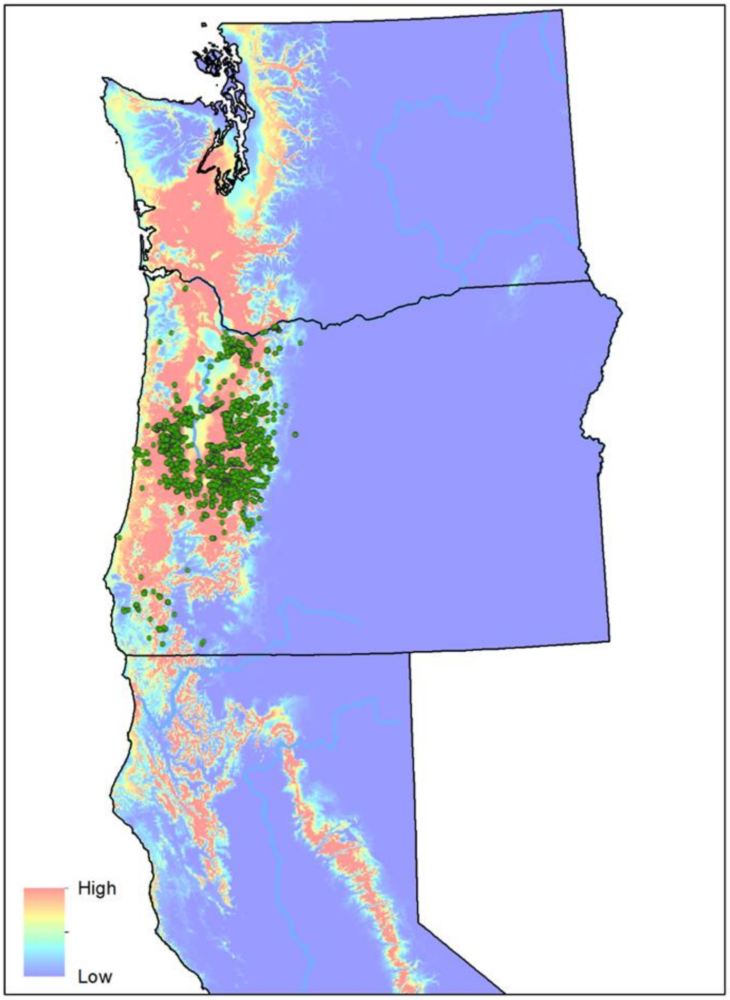


Fig. 4

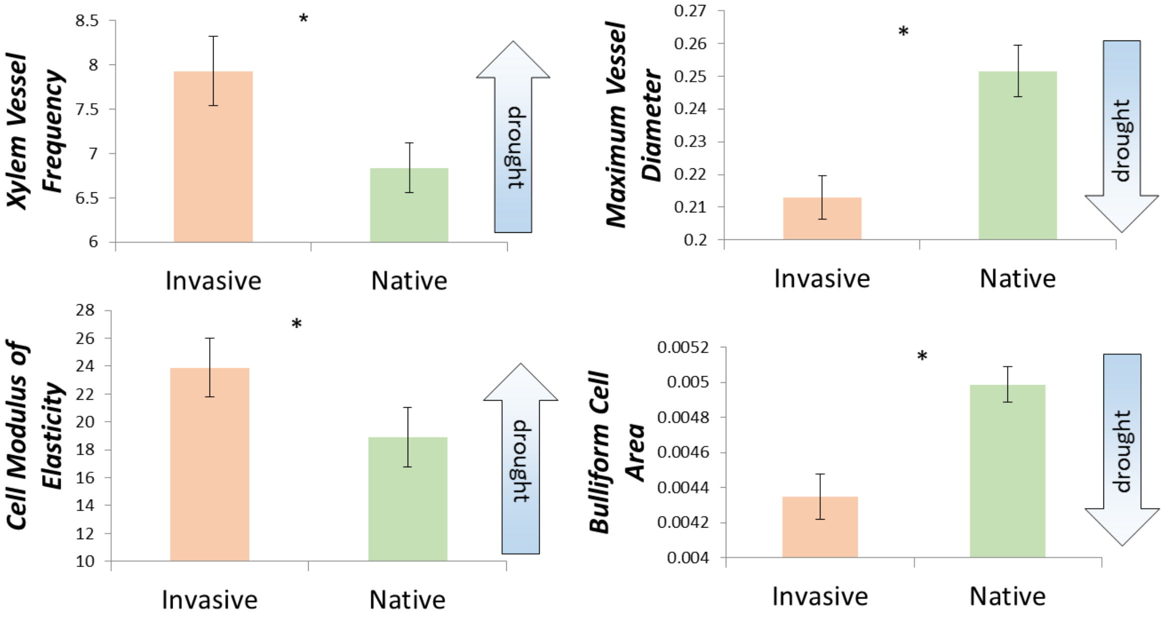
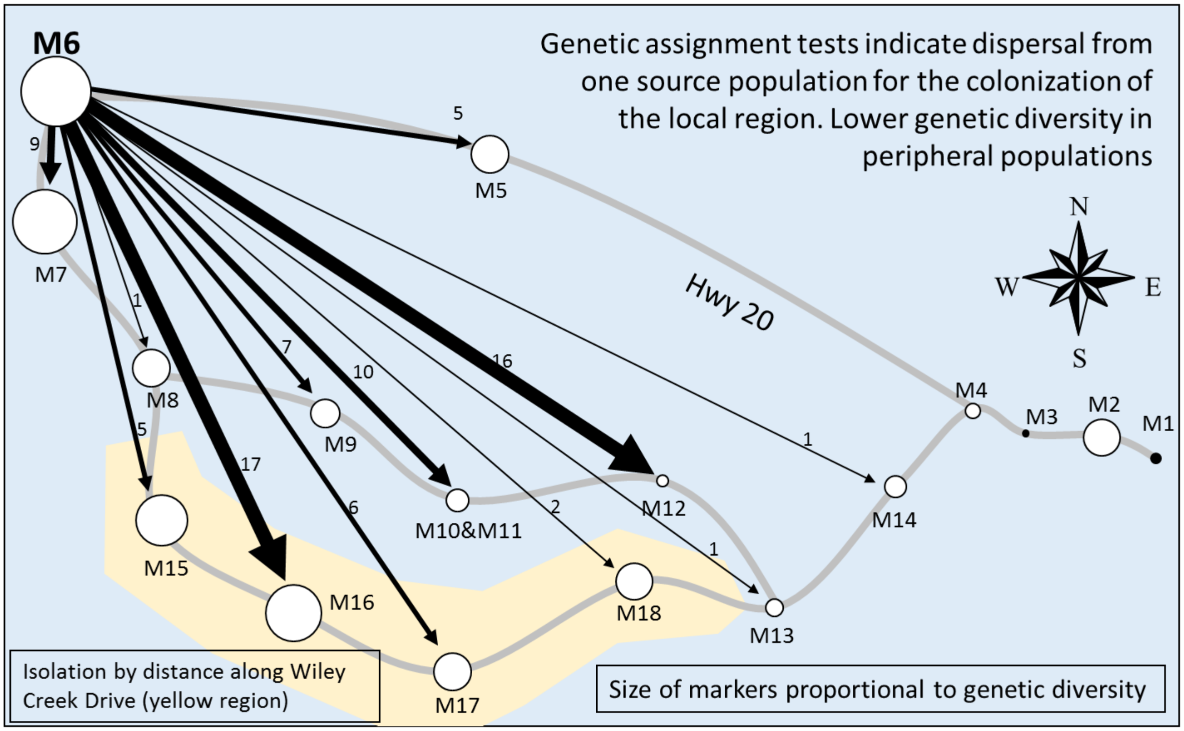

Xylem Vessel Frequency
8.5
8
7.5
7
6.5
6
*
drought
Invasive
Native
Maximum Vessel Diameter
0.27
0.26
0.25
0.24
0.23
0.22
0.21
0.2
*
drought
Invasive
Native
Cell Modulus of Elasticity
28
26
24
22
20
18
16
14
12
10
*
drought
Invasive
Native
Bulliform Cell Area
0.0052
0.005
0.0048
0.0046
0.0044
0.0042
0.004
*
drought
Invasive
Native

Fig. 5



Genetic assignment tests indicate dispersal from one source population for the colonization of the local region. Lower genetic diversity in peripheral populations

Isolation by distance along Wiley Creek Drive (yellow region)

Size of markers proportional to genetic diversity

Fig. 6

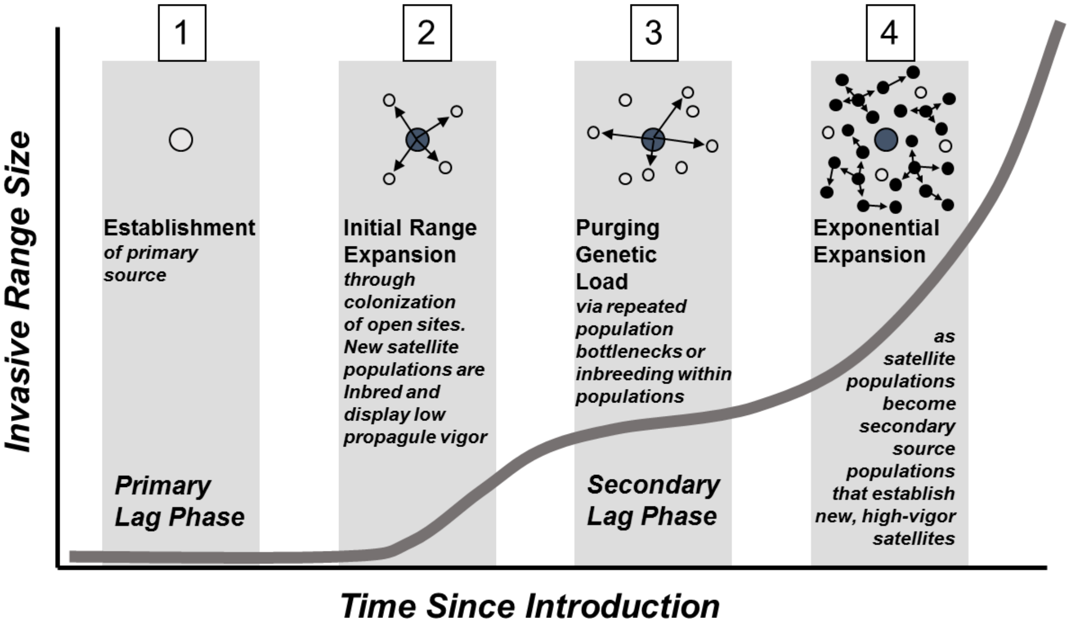
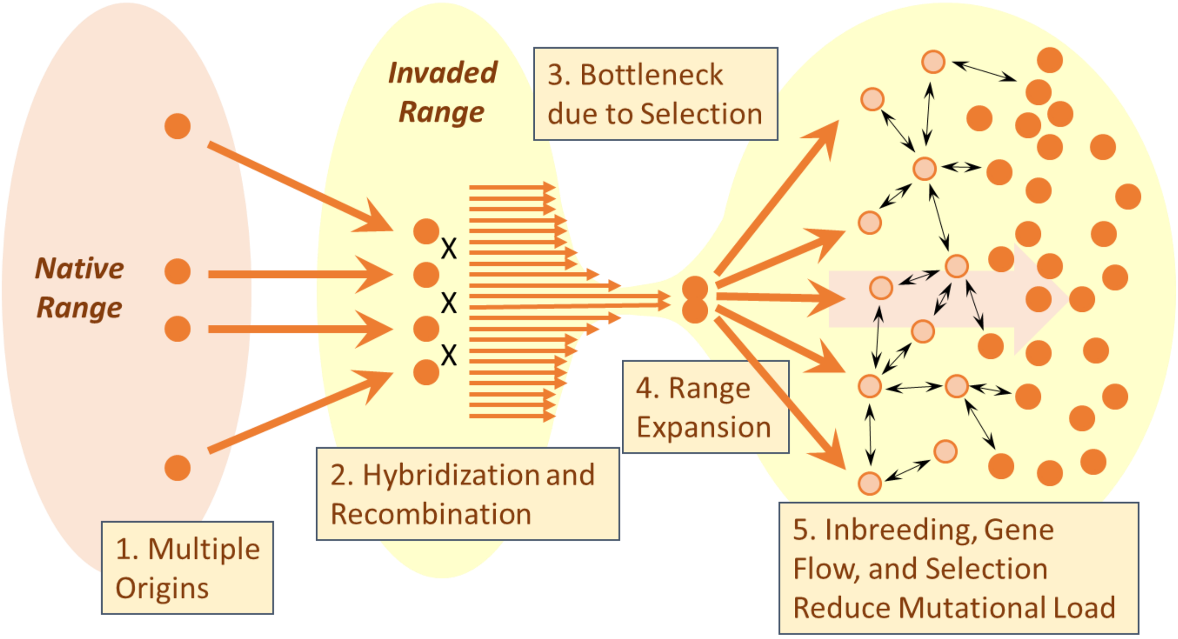

1
2
3
4
Establishment
of primary source
Initial Range Expansion
through colonization of open sites. New satellite populations are Inbred and display low propagule vigor
Purging Genetic Load
via repeated population bottlenecks or inbreeding within populations
Exponential Expansion
as satellite populations become secondary source populations that establish new, high-vigor satellites
Primary Lag Phase
Secondary Lag Phase
Invasive Range Size
Time Since Introduction

Fig. 7


Native Range
Invaded Range
X
X
X
1. Multiple Origins
2. Hybridization and Recombination
3. Bottleneck due to Selection
4. Range Expansion
5. Inbreeding, Gene Flow, and Selection Reduce Mutational Load