Applied evolutionary biology could aid management of invaded ecosystems

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Abstract. Invasive plant species subvert essential ecosystem services through a reduction in the abundance and genetic diversity of native plant species. A major challenge now facing land managers and policy makers is how to ensure persistence of native plants while limiting harmful impacts of invasions. Results from recent empirical studies suggest that native plants may evolve adaptations to invasive plants and that adaptive evolution in invasive plants could lessen the negative impacts of invasions. Here, we suggest ways in which knowledge of adaptive evolution in invasive and native plants could be utilized to more effectively manage invaded ecosystems.

Key words: *ecological and evolutionary theory; ecosystem health; ecosystem restoration; evolutionary application; invasive species; plant invasion; policy.*

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Background

Invasive plant species subvert essential ecosystem services (for definitions of key terminologies, see Box 1) through a reduction in the abundance and genetic diversity of native plant species (Vitousek et al. 1996, Zedler and Kercher 2004, Pimentel et al. 2005). Consequently, global demand for eradication of invasive plant species and subsequent restoration of invaded habitats has intensified in recent years (Millennium Ecosystem Assessment 2005, Suding 2011). The ultimate goal of ecological restoration is to reestablish self-sustaining ecosystems that will be resilient to current and future environmental changes without additional human input while providing vital ecosystem services (Zedler 2000, Broadhurst et al. 2008). However, when invasive plant species have established over large areas, eradicating them is rarely feasible as a management option (Rejmanek and Pitcairn 2002, Carroll 2011). A major challenge now facing land managers and policy makers is how to ensure persistence of native plants while limiting harmful impacts of invasions (Carroll 2011).

Despite the strong negative impacts that invasive plants often have on native plants, empirical studies report that some populations of native plant species can persist in invaded habitats (e.g., Callaway et al. 2005, Lesica and Atthowe 2007, Mealor and Hild 2007, Lau

Box 1. Definitions of key terminologies

Invasive plant species: Exotic plants introduced by human agency or range-expanding native plants that threaten native diversity, regional economies, and conservation efforts.

Ecosystem: A dynamic complex of plant, animal, and microbial communities and the nonliving environment, interacting as a functional unit on a given physical landscape. The size of an ecosystem could be as small as a few square meters and as large as thousands of square kilometers.

Ecosystem services: The benefits that human beings obtain from ecosystems. These include provisioning services such as food, water, wood yield in forests, and forage for livestock; regulating services such as climate regulation through carbon sequestration; cultural services such as spiritual and recreational benefits; and supporting services such as nutrient cycling that maintain life on earth.

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Table 1. Examples of studies that found adaptation of native plants to invasive plants.

Native plant species	Invasive plant species	Trait under genetic control associated with persistence of native plants in invaded habitats	Continent of study	Type of study	Reference
Sporobolus airoides	*Acroptilon repens*	higher plant height and tiller number	North America	C	Bergum et al. (2012)
Festuca idahoensis, *Pseudoroegneria spicata*, *Stipa occidentalis*, *Koeleria cristata*, *Poa sandbergii*	*Centaurea maculosa*	higher tiller number	North America	C	Callaway et al. (2005)
Impatiens noli-tangere	*Impatiens parviflora*	higher root biomass and early seedling emergence	Europe	F	Dostál et al. (2012)
S. airoides, *Hesperostipa comate*	*Cirsium arvense*	higher biomass accumulation and tiller number	North America	C	Ferrero-Serrano et al. (2011)
Lotus wrangelianus	*Medicago polymorpha*	higher seed number	North America	F	Lau (2008)
Hesperostipa comate, *S. airoides*	*A. repens*	higher relative tiller production	North America	F	Mealor and Hild (2007)
S. airoides	*Rhaponticum repens*	larger leaf area and higher number of tillers	North America	F and C	Sebade et al. (2012)
Achillea millefolium	*Holcus lanatus*	faster rate of growth and higher plant height	North America	C	Deck et al. (2013)
Agrostis capillaris, *Campanula rotundifolia;*	*Thymus pulegioides*	higher seedling biomass	Europe	C	Jensen and Ehlers (2009)
Achillea millefolium	*T. pulegioides*	higher root biomass	Europe	C	Grøndahl and Ehlers (2008)

Notes: The mean higher levels of traits under genetic control reported for remnant natives (native plant populations that have experienced selection from invasive plants) are relative to those of naïve natives (native plant populations that have not experienced selection from invasive plants). Type of study indicates whether the study was conducted in the field or controlled environment in the greenhouse (F, field; C, controlled environment).

2008, Leger 2008, Goergen et al. 2011, Dostál et al. 2012). Native plant populations persisting in invaded habitats have been termed remnant natives (Leger and Espeland 2010). Theory on microevolutionary change during biological invasions predicts that remnant natives are the result of natural selection imposed on native plants by invasive plants (Strauss et al. 2006). More specifically, the theory states that strong competition from invasive plants exerts a selection pressure on native plant populations, eliminating particular individuals (genotypes) that have low capacity to tolerate strong competition (Strauss et al. 2006, Rowe and Leger 2011). Field and controlled-environment experiments have established that remnant natives are dominated by particular individuals possessing traits under genetic control (observable characteristics such as increased root biomass and tiller production) that confer a capacity to persist in invaded habitats (Leger 2013, Leger and Baughman 2015). Table 1 provides examples of such studies. A recent meta-analysis found a general pattern of significantly higher growth performance of plant individuals from remnant natives compared to plant individuals from the same species in adjacent uninvaded habitats (naïve natives), thus supporting the idea that native plant populations may evolve adaptations to invasive plants (Oduor 2013).

Invasive plant species are themselves not static selective agents on native plants; they too can evolve adaptations to the novel environments they colonize (e.g., Godoy et al. 2010, Colautti and Barrett 2013; also see Table 2 for additional examples). Adaptive evolution in populations of invasive plant species could lessen the negative impacts of invasive plants on native plants. For instance, studies on an invasive plant *Alliaria petiolata* have shown that different populations of the species can evolve, over time and across a landscape, a gradient of decreased production of toxic allelochemicals that the species uses to suppress native plants (Lankau et al. 2009, Lankau 2012). Consequently, native plants were found to have higher growth in habitats where old populations of *A. petiolata* had evolved lower levels of toxic allelochemicals (Lankau et al. 2009, Lankau 2012). In a similar study, native plant species richness and productivity were found to be higher in grassland sites with old populations of an invasive plant *Heracleum mantegazzianum* relative to sites occupied by younger

Table 2. Examples of studies that reported occurrence of adaptive evolution in invasive plant species.

Species	Environmental condition	Reference
Prunella vulgaris	temperate evergreen rainforest	Godoy et al. (2010)
Ruellia nudiflora†	tropical forest	Ortegón-Campos et al. (2009)
Datura stramonium†	tropical forest	Fornoni et al. (2003)
Eschscholzia californica†	coastal environment	Leger and Rice (2007)
Lythrum salicaria	climatic gradient	Colautti and Barrett (2013)
Bromus madritensis	desert	Grossman and Rice (2014)
Ambrosia artemisiifolia	climatic gradient	Li et al. (2015)
Secale cereale	climatic gradient	Burger and Ellstrand (2014)
Achillea millefolium†	dry grassland	Grøndahl and Ehlers (2008)

Notes: Invasive species marked by a dagger (†) are range-expanding native species. The rest are exotic invader species.

populations (Dostál et al. 2013). Thus, adaptive evolution in invasive plant populations could attenuate the negative impacts of invasions.

In light of the emerging recognition that adaptive evolution is a continuous process in the natural environment that can influence plant species persistence, the present paper reiterates and attempts to advance previous arguments that considering evolutionary history of plant populations and processes of adaptive evolution may aid management of invaded ecosystems (e.g., Rice and Emery 2003, Leger and Espeland 2010). First, we will highlight basic processes of adaptive evolution. Then, we will describe how evolutionary theory can be applied to plant population management, with particular emphasis on maintaining genetic diversity in native populations and limiting gene flow among invasive populations (also see Table 3 for suggestions on management interventions).

Basic Processes of Adaptive Evolution

A plant population that is exposed to novel stressful environment conditions (conditions such as drought and presence of alien invaders) may avoid extinction by evolving adaptation to the novel environmental condition (Reznick and Ghalambor 2001, Bell and Collins 2008). A population evolves adaptation when particular individuals in the population have certain trait values under genetic control and are best able to survive and reproduce under the novel environmental conditions (Leger 2013, Leger and Baughman 2015). Field experiments in a variety of habitats have demonstrated that adaptation to local environmental conditions is a widespread phenomenon among different plant species in the wild (Leimu and Fischer 2008). Theoretical and empirical evidence indicates that population size is positively correlated with the capacity of a population to evolve local adaptation (Jakobsson and Dinnetz 2005, Leimu et al. 2006, Bowman et al. 2008). Large populations are more likely to evolve adaptations than small populations because large populations often have higher variation in traits under genetic control that can maintain or increase average reproductive success for the entire population under changing environmental conditions (Jakobsson and Dinnetz 2005, Leimu et al. 2006, Bowman et al. 2008). Gene flow, that is, immigration of plant propagation materials (seeds and vegetative materials) and their subsequent establishment as highly reproductive adults can also ensure persistence of a population under changing environmental conditions (Kremer et al. 2012). Gene flow has been detected among populations of tree species inhabiting contrasting climatic zones in various continents (Kremer et al. 2012). The processes influencing adaptive evolution highlighted here may be amenable to management intervention to promote or inhibit persistence of a plant population, depending on the management goal.

Table 3. Examples of how knowledge on adaptive evolution could be applied to achieve a management goal of promoting persistence of native plants while minimizing the negative impacts of invasive plants across an ecosystem.

Management goal	Intervention
Ensure persistence of native plants within an invaded ecosystem.	1) Reestablish native plant communities using propagules sourced from remnant natives that are adapted to invasive plants. 2) Establish a landscape mosaic of native plant genetic diversity across an invaded ecosystem.
Limit evolution of high levels of traits (traits such as toxic allelochemicals and higher competitive ability) that invasive plants might use to suppress native plants.	1) Limit new introductions of invasive plant materials from the native range. 2) Limit movement of invasive plant materials among different invasive populations within the introduced range.

Note: The management interventions presented here reiterate and advance existing advice to managers to prevent and control invasive plants but in the light of new and additional supporting evidence.

How Knowledge of Adaptive Evolution Could Be Applied to Management of Invaded Ecosystems

Restore heavily invaded habitats using native plant propagation materials from remnant natives

Many previous attempts to reestablish native plant dominance in invaded habitats have not been successful because of direct suppressive effects of invasive plants or the negative legacy effects of destroyed stands of invasive plants (manifested through altered chemical, physical, and biological properties of the soil; Bakker and Wilson 2004, Zedler and Kercher 2005, Ammondt et al. 2013). The large-scale nature of many restoration efforts has meant that selection of plant propagation materials for restoration has placed greater emphasis on agronomic factors (the feasibility of producing those materials in large quantities) than on the capacity of restoration propagules to tolerate altered ecological conditions of invaded habitats (Leger and Baughman 2015). Given the empirical evidence that remnant natives include individuals with adaptations making them more tolerant to invasive plants and the ecological conditions they produce (Oduor 2013), future efforts to restore native plant dominance in invaded sites should consider sourcing native plant propagation materials from remnant natives.

Apply knowledge on colonization history of an invasive plant to reestablish a landscape mosaic of native plant genetic diversity

Results from field experiments suggest that a landscape containing native plant populations with high variation in traits under genetic control is more resilient to environmental change including invasions and can provide greater ecosystem services (e.g., high nutrient cycling rates and aboveground plant biomass) than a landscape containing native plant populations with low trait variation (Weltzin et al. 2003, Hughes and Stachowicz 2004, Reusch et al. 2005, Crutsinger et al. 2006). However, strict adherence to the use of native plant materials from remnant natives in restoration may result in low variation, because remnant natives may have reduced variation in traits under genetic control as a consequence of having evolved adaptation to invasive plants (Rice and Emery 2003). Nevertheless, knowledge of colonization history of an invasive plant species across a landscape may inform efforts to reestablish a landscape mosaic of native plant genetic diversity during restoration. A single invasive plant species can colonize a large expanse of land (tens of thousands of square kilometers) by establishing different populations in a topographically and climatically heterogenous landscape (Leger 2008). Large-scale invasion often occurs in a gradual and stepwise manner, with old colonizing populations serving as sources of propagation materials that establish new colonizing populations elsewhere (Kilkenny and Galloway 2013). Field experiments have shown that a stepwise pattern of invasion can result in a landscape mosaic of invasive plant impacts, with young populations of an invasive plant species being more suppressive of native plants than old populations of the same invasive species (Lankau et al. 2009, Lankau 2012, Dostál et al. 2013). Across a landscape, habitats colonized by younger and highly suppressive populations could be restored using native plant materials sourced from remnant natives, while habitats colonized by older, less suppressive populations could be replanted with native plant materials from naïve natives. The approach to restoration suggested here could both ensure persistence of native plant populations across an invaded landscape and a sustainable provisioning of ecosystem services.

Limit gene flow among populations of invasive plant species

Limiting gene flow among different populations of an invasive plant species may prevent invasive plants from evolving adaptation to future changes in environmental conditions. Limiting gene flow may also limit the capacity of invasive plants to evolve high levels of traits such as toxic allelochemicals and high competitive ability that they might use to suppress native plants. Invasive populations of different plant species are often founded from multiple source populations within the native ranges of those species (e.g., Novak and Mack 1993, Genton et al. 2005, Lavergne and Molofsky 2007, Chun et al. 2010). Within the introduced ranges, gene flow among different populations may enhance the capacity of the species to colonize large areas (Ellstrand and Schierenbeck 2000). For instance, extensive gene flow among different populations of *Acacia pycnantha* throughout the coastal region of South Africa since the species was introduced from Australia has contributed to invasion of this plant within South Africa (Le Roux et al. 2013). Introduced from North America, *Ambrosia artemisiifolia* is one of the most problematic invasive plant species in Europe (Chun et al. 2010). Within Europe, populations of *A. artemisiifolia* inhabiting different climatic zones have high capacity to evolve adaptation to local environmental conditions as a consequence of strong gene flow (Chun et al. 2010). The highly invasive plant species *Bromus tectorum* and *Phalaris arundinacea* were introduced to their invasive range in North America from different sources in Europe, Asia, and Africa (Novak and Mack 1993, Lavergne and Molofsky 2007). Admixing of different populations as a consequence of strong gene flow has precipitated evolution of new aggressively invading genotypes within these species in North America (Novak and Mack 1993, Lavergne and Molofsky 2007). These examples suggest that limiting movement of invasive plant materials among different habitats within the introduced range may be just as important as limiting repeated introductions of exotic plant materials. Because biological invasions often start with a small number of colonists, a major focus of management efforts could be early detection and eradication of newly establishing invasive populations.

Summary

It is becoming increasingly clear that adaptive evolution is a continuous process in the natural environment that can influence plant species persistence and ecosystem processes (Carroll et al. 2014, Smith et al. 2014). Therefore, considering evolutionary history of plant populations and processes of adaptive evolution may be important for achieving a management goal of maintaining fully functional ecosystems in light of threats posed by invasive plants.

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