

REVIEW ARTICLE

State of the science and challenges of breeding landscape plants with ecological function

H Dayton Wilde¹, Kamal JK Gandhi² and Gregory Colson³

Exotic plants dominate esthetically-managed landscapes, which cover 30–40 million hectares in the United States alone. Recent ecological studies have found that landscaping with exotic plant species can reduce biodiversity on multiple trophic levels. To support biodiversity in urbanized areas, the increased use of native landscaping plants has been advocated by conservation groups and US federal and state agencies. A major challenge to scaling up the use of native species in landscaping is providing ornamental plants that are both ecologically functional and economically viable. Depending on ecological and economic constraints, accelerated breeding approaches could be applied to ornamental trait development in native plants. This review examines the impact of landscaping choices on biodiversity, the current status of breeding and selection of native ornamental plants, and the interdisciplinary research needed to scale up landscaping plants that can support native biodiversity.

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INTRODUCTION

Recent ecological studies have found that landscaping choices can affect biodiversity in urbanized areas.^{1–5} The impact of land use practices in esthetically-managed landscapes of the United States was summarized in a US Environmental Protection Agency report,⁶ which noted:

- the widespread replacement of millions of acres of native vegetation with primarily non-native ornamental plants in managed landscapes is a growing problem for the organisms that depend on native plants for food, shelter, and places to rear their young;
- many studies have documented the negative effect that non-native plants can have on the abundance and diversity of insect herbivores;
- if ornamental plants cannot serve as food for the same number and diversity of herbivores, the energy available for food webs decreases.

Non-native or exotic plants can be defined as plant species that evolved someplace other than where they have been introduced. Native plants, in contrast, share an evolutionary history with regional insects and other organisms. The observations of Erlich and Raven,⁷ with further modification,⁸ have led to an understanding of plant and insect co-evolution in which the adaptation of insects to plant defenses plays an important role. Landscaping primarily with exotic plant species would be expected to be detrimental to insect herbivores that have adapted to native plant hosts⁹ and recent studies support this hypothesis.^{1,2,10,11} Changes caused by exotic plants to the abundance and diversity of insects, and the birds that consume them, are discussed in the following section. The impact of exotic landscaping plants on other native taxa is less well studied. The spread of invasive exotic plants, however, has been linked to a decline in the diversity of reptiles, spiders and mycorrhizal fungi.^{12–15} Invasive exotic plants can affect native species through food-web dynamics or by less predictable mechanisms.¹⁶

To conserve biodiversity in urbanized areas, the increased use of native plant species in designed landscapes has been advocated by conservation groups and US federal and state agencies. This includes NGOs such as the National Wildlife Federation, the Audubon Society and the Native Conservancy and government agencies such as the EPA, the USDA and the DOT. The implementation of this goal on an effective scale faces several hurdles. There are over 32 million hectares of esthetically managed land in the United States, including urban and suburban landscapes¹⁷ and highway corridors.¹⁸ The developed area of the United States is projected to increase by nearly 80% in the first quarter of this century,¹⁹ adding millions more hectares of landscaping. The amount of land managed for esthetics is similar in scale to the land in corn cultivation (37M ha in 2014)²⁰ or in all US national and state parks (40M ha).²¹ Increasing native plant landscaping to 30%, for example, of the managed landscape would require a significant expansion of what is now a niche market.

A major challenge to scaling up the use of native species in landscaping is in providing ornamental plants that are both ecologically functional and economically viable. Similar to environmental restoration with native plants, attention should be paid to genetic diversity and local adaptability.²² Unlike environmental restoration, though, native plants must be introduced into managed landscapes through a market system in which landscaping plants that meet consumer demand are delivered profitably by the horticulture industry. Ecological function, cost-effective production and ornamental traits are qualities desired in native landscaping material that are potentially conflicting. The scale-up of landscaping plants that can support biodiversity would benefit from interdisciplinary research in genetics, ecology, and economics.

EFFECTS OF EXOTIC PLANTS ON INSECT AND BIRD ABUNDANCE AND DIVERSITY

The prevalence of exotic plants in a landscape may alter the number of ecologically important insects, as well as the composition of

¹Horticulture Department, University of Georgia, Athens, GA 30602, USA; ²Daniel B Warnell School of Forestry & Natural Resources, University of Georgia, Athens, GA 30602, USA and

³Department of Agricultural and Applied Economics, University of Georgia, Athens, GA 30602, USA

Correspondence: HD Wilde (dwilde@uga.edu)

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insect populations. In the northeastern United States, a comparison of suburban yards landscaped with native or exotic plants found that exotic plants reduced the abundance and diversity of lepidopteran insects.¹ A study of urban vegetation in Singapore determined that lepidopteran diversity correlated directly with the percentage of native plants.² Field trials confirmed the negative impact of exotic plants on specialist and generalist lepidopteran numbers¹⁰ and found a similar effect on insects of other taxa and feeding guilds.^{11,23,24} A study in which old-field plant communities were manipulated found that insect species richness was reduced on exotic plants, although insect abundance was similar on native and exotic plants.²⁵ While the effects of exotic plants on insects may differ between studies, the geographic origin of introduced plants was found to change insect community structure.

Invasive exotic plants can also alter insect populations.^{26–28} This is relevant to ornamental plants since many exotic species that have become invasive in the United States were introduced for landscaping purposes.²⁹ Field studies have found that invasive exotic plants can shift the insect population from large, specialist insects (e.g., lepidoptera) to small, generalist insects (e.g. dipteran midges), significantly reducing insect biomass.²⁶ Some invasive exotic plants, such as honeysuckle (*Lonicera maackii*), may increase insect species richness and numbers by creating a more complex vegetative structure.³⁰ Separately, honeysuckle was found to cause a decrease in caterpillar abundance that was moderated when there was higher tree diversity and more intact forest cover.³¹ Habitat fragmentation and homogeneity are common features of urban landscapes and they may mediate the effects of exotic plants on insect herbivores.

Studies have indicated that several life-history attributes of insects may be altered due to exotic plants. Insect size, egg load and attraction to mates were reduced, and developmental period was longer on exotic species.^{32,33} Native pollinators may visit abundant exotic plants more frequently, thus lowering pollination of native plants.³⁴ Lower feeding damage on exotic than on native plants has been reported, perhaps due to lower nutrient quality.^{35,36} An exotic plant with foliage that is toxic to caterpillars can be a dead-end host for a native butterfly species.³⁷ This may allow exotic plant species to escape herbivory, and persist and spread on the landscape. Overall, while exotic plants can provide certain ecological services,^{25,30,38} their ability to support native insects is limited in many ways.

Changes in insect quality and quantity can affect higher trophic levels through food web interactions. As argued by Tallamy,⁹ nearly all terrestrial birds in North America rear their young on insects, with food being a major limitation to breeding success.^{39,40} Two studies on the ecological impacts of plant origin, discussed previously with regard to insects, also examined effects on bird populations.^{1,2} In suburban Pennsylvania yards landscaped with exotic plants, a reduction in bird abundance and diversity correlated with the decrease in lepidopteran populations.¹ Both avian and lepidopteran species richness varied directly with the percentage of native shrubs and trees in urban vegetation of Singapore.² The presence of native landscaping plants was found to have a positive effect on native bird abundance and diversity in urbanized areas across different environments.^{3–5,41} Lepidoptera and birds have served as surrogate taxa in biodiversity studies because they are environmentally sensitive and relatively easy to measure.^{1,42} The corresponding changes in native lepidopteran and avian populations could be causative (fewer caterpillars make birds forage elsewhere) or correlative (exotic plants negatively affect butterflies and birds independently).

CURRENT STATUS OF THE BREEDING AND SELECTION OF NATIVE ORNAMENTAL PLANTS

A niche market has developed in the United States for native ornamental plants that provide wildlife support, as well as local adaptability. The single largest venture directed at this market is the

American Beauties™ program, a partnership between the National Wildlife Federation and two wholesale nurseries.⁴³ The program distributes native landscaping plants to independent garden centers and landscapers in the northeastern United States. Over 350 plant species are provided through this system, including native perennials, grasses, vines, trees and shrubs. In addition, Armitage⁴⁴ describes more than 400 native ornamental plants, primarily herbaceous species, that can be ordered directly from local nurseries in the United States.

Native plants for ornamental horticulture generally come from breeding, genotype selection or open-pollinated seed. Within the American Beauties™ inventory, approximately 35% of the plants are named cultivars and 65% are propagated genotypes of native species. North American plant species have been selected or bred for flowering, architecture, foliage and disease-resistance traits, although not to extent of exotic ornamentals. For example, native plant genotypes have been selected that exhibit early flowering (e.g., *Potentilla fruticosa* 'KM01')⁴⁵ or double flowers (e.g., *Cercis canadensis* 'Flame').⁴⁶ From an open-pollination breeding program, an oak leaf hydrangea genotype (*Hydrangea quercifolia* 'Snow Queen') was identified that had low, compact form and abundant, showy blooms.⁴⁷ Controlled pollination was used to develop a bee-balm genotype (*Monarda didyma* 'Sugar Lace') with a modified branching pattern and powdery mildew resistance.⁴⁸ Through the interspecific hybridization of *Baptisia australis* and *B. bracteata*, a false indigo genotype (*Baptisia* × *bicolor* 'Starlite') was produced that had early and abundant flowering.⁴⁹

Most breeding and selection of North American plant species for ornamental traits has been conducted by private sector programs, including some in Europe.^{45,48} Native perennial plants for mid-western US landscapes have been bred at the Chicago Botanic Garden using wild collected germplasm and cultivated plants from nursery sources.⁵⁰ Genera targeted in this program include *Asclepias* (milkweed), *Baptisia* (false indigo), *Echinacea* (purple coneflower), *Liatris* (blazing star) and *Penstemon* (beardtongue). Public breeding programs at US universities have developed horticultural traits in native plants of genera such as *Aronia* (chokeberry),⁵¹ *Cercis* (redbud),⁵² *Cornus* (dogwood),⁵³ *Penstemon*⁵⁴ and *Vaccinium* (blueberry).⁵⁵

ECOLOGICAL SERVICES AND ADAPTABILITY OF NATIVE ORNAMENTAL PLANTS

Many native landscaping plants available in the horticultural trade are vegetatively-propagated genotypes that have been selected or bred for ornamental characteristics. There is little information about whether native ornamental cultivars can provide the same ecological services as their parent species. One study compared two cultivars of ninebark (*Physocarpus opulifolius*) and a local genotype (Minnesota, USA) as hosts for the ninebark beetle (*Calligrapha spiraeae*), a specialist herbivore.⁵⁶ Controlled-feeding experiments found significant differences in feeding preference between the local ninebark and the purple-leaved cultivar 'Monlo', but not between the local ninebark and the yellow-leaved cultivar 'Dart's Gold'. Leaves of 'Dart's Gold' and the local ninebark had at least fourfold less anthocyanins, a potential feeding deterrent, than the purple leaves of 'Monlo'. These results indicate that while native cultivars can support specialist insects, this may vary with the ornamental trait.

Field studies comparing the effect of native plant cultivars and ecotypes on insect populations are being conducted at two botanical gardens in the United States, the Mt Cuba Center (Delaware)⁵⁷ and the State Botanical Garden of Georgia (James Affolter, pers. comm.). At the US National Arboretum, a field study is in progress that compares the impact of native and exotic ornamentals on predatory insects (e.g., parasitic hymenoptera).⁵⁸ The range over which a native cultivar can provide an ecological service, such as food-web support, has not been investigated. Scaling up the use of

native plants will likely require that they be marketed on a regional basis. The genetic diversity needed in native ornamentals to provide ecological services across a regional market needs to be examined. There are similar concerns regarding the diversity needed for native plant adaptability in ecological restoration projects.²²

For ecological restoration, environmentally defined regions can be used to estimate where native plant material is suitable.^{59–61} EPA ecoregions, for example, are geographic areas with similar geology, climate, vegetation, soils and hydrology. Ecoregions I through IV are hierarchical classifications of land areas, with environmental similarity increasing at each level. Level III ecoregions have been used to estimate seed transfer zones,^{62,63} i.e., a region within which plant material can be distributed with little risk of maladaptation.⁶⁰ Figure 1 shows, for example, a level III ecoregion that encompasses the Appalachian piedmont of the United States. Miller and colleagues⁶² found that a level III ecoregion could serve as a seed transfer zone for four of the five native plant species that they examined. Climatic data alone⁶⁰ or in combination with ecological data⁶¹ have also been used to predict regions suitable for native plant material.

For ornamentals, the regional limits of cultivar adaptability are already considered by many consumers and retailers through USDA hardiness zone ratings. Like native plant genotypes for restoration, native cultivars for landscaping could potentially be adaptable throughout a level III ecoregion or other environmentally-defined region. Research is needed on food-web support by native cultivars on a regional basis. Level III ecoregions may also be of sufficient size to be markets for native landscaping plants. The Appalachian piedmont ecoregion, for example, contains several expanding metropolitan areas in the southeast United States, including Atlanta, Charlotte and Raleigh-Durham (Figure 1).

SCALING UP THE USE OF NATIVE ORNAMENTALS

Native plants make up approximately 13% of the total sales of the nursery industry in the United States.⁶⁴ To understand the issues limiting the use of native plants in landscaping, surveys have been conducted of nursery retailers,^{43,65} landscape architects^{66,67} and Master Gardeners.⁶⁸ Three general factors that were consistently considered important in survey responses were (i) the availability of native plants; (ii) consumer preferences; and (iii) knowledge about native plants. With regard to native plant education, botanical

gardens and citizen science can be effective vehicles for increasing public awareness of the cultivation and ecological value of native plants.^{69–71}

Increasing the availability of native ornamentals would be accomplished most efficiently through existing supply chains. The major routes to market for ornamental plants in the United States, based on sales from nurseries, were through landscape firms (31%), garden centers (22%), re-wholesalers (21%) and mass merchandisers (9%).^{64,72} The plants distributed through these channels are primarily cultivars of exotic species. Scaling up native ornamentals through established distribution procedures would most likely require propagated selections of a limited number of genotypes. An economic assessment is needed of the number of different genotypes of native ornamental species that can be delivered profitably by the horticulture industry for a regional market. An alternative or complement to mainstream supply chains would be the distribution of local ecotypes by smaller nurseries specializing in native plants. It is likely that both specialty and mainstream outlets will be needed to scale up the availability of native ornamentals to consumers.

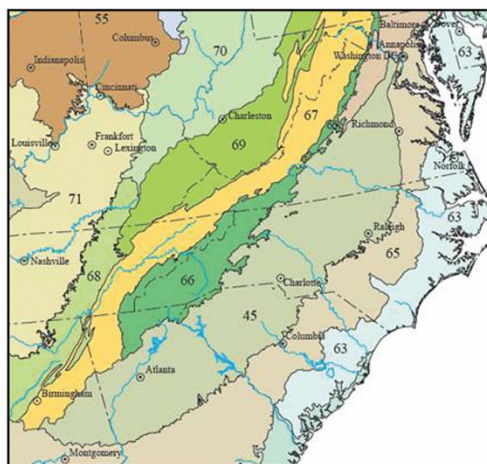
Native landscaping plants need to meet consumer preferences regarding ornamental qualities and compete with exotic alternatives in the marketplace. Native plants can often be more expensive than exotic plants, perhaps as a result of their small scale of production.⁷³ The cost of native ornamentals, however, was identified in surveys as one of the least important factors limiting their adoption.^{43,65–68} Interestingly, consumers were found to be willing to pay more for well-designed yards that included native plants instead of lawns.⁷⁴ This was determined by a contingent choice survey in which consumers in Michigan were presented with hypothetical options that varied in purchase and maintenance costs.⁷⁴ Complementing this approach, non-hypothetical auctions were conducted in Minnesota where consumers bid on native and exotic ornamental plants.^{75,76} In experimental auctions, consumers were willing to pay a \$0.35 premium for plants labeled as non-invasive and native.⁷⁵ Purchasing patterns indicated that approximately 50% of consumers considered that plants labeled as 'native' or 'non-invasive' were worth a cost premium.⁷⁶ Environmental qualities of native ornamentals could therefore be considered value-added traits that may be signaled to consumers via information and labeling strategies.

Ecology

What is the genetic diversity needed in a native plant species to provide ecological services regionally?

Economics

What is the number of genotypes that can be provided profitably for regional markets?



Genetics

Is there sufficient regional genetic diversity for breeding ornamental traits?

Figure 1. EPA level III ecoregions in the eastern United States. Different shades and numbers indicate different ecoregions, with #45 designating the Appalachian Piedmont. Ecoregions could be useful for studying interrelated questions of genetics, ecology, and economics posed by scaling up native plants.

Half of consumers in the same study purchased ornamentals based on plant traits, not plant origin or invasive potential.⁷⁶ Traits of ornamental plants that are popular with consumers include extended flowering, novel floral morphology (e.g., double flowers), compactness, and disease-resistance. 'Knockout' roses, 'Encore' azaleas and 'Endless Summer' hydrangeas are examples of top-selling exotic cultivars in the United States that have one or more of these characteristics. Some of the native ornamental species that are currently available have been selected for traits such as double flowers,⁴⁶ reduced stature⁴⁷ and foliage color.⁵⁶ Further development of native ornamentals with flowering, architecture or drought-tolerance⁷⁷ traits may be a strategy to increase native plant use among a large segment of the consumer market.

ACCELERATED BREEDING OF ORNAMENTAL TRAITS IN NATIVE PLANTS

Molecular breeding could be used to accelerate the development of native plants species with ornamental traits. Molecular markers have been used with ornamental plants primarily to identify cultivars, conduct pedigree analysis and study germplasm variability.⁷⁸ Markers have also been developed in a few cases for breeding traits such as disease resistance in roses⁷⁹ and flowering time in chrysanthemum.⁸⁰ For native ornamental plants, marker-assisted selection has the potential to accelerate cultivar development, particularly for woody species. Woody plants are an important target because (i) they have the highest wholesale value in the US ornamental plant market,⁸¹ and (ii) the hosts for the greatest diversity of lepidopteran species are native woody species.⁸²

Molecular markers have been generated for a limited number of ornamental species that are native to North America. This may be due in part to the current cost of marker development relative to the market size of a native species. Amplified fragment length polymorphism (AFLP) and simple sequence repeat (SSR) markers were developed to identify cultivars and lines of flowering dogwood (*Cornus florida*).^{83,84} The genetic diversity and population structure of *C. florida* were assessed using SSR markers.⁸⁵ A genetic linkage map of *C. florida* was constructed⁸⁶ and potential quantitative trait loci for red foliage were identified.⁸⁷ SSR markers were examined in redbud (*Cercis canadensis*) in order to determine pedigree and the applicability of molecular markers to breeding.^{88,89} AFLP analysis was used to determine the genetic diversity and degree of introgression among several deciduous azalea species (*Rhododendron* sp.).⁹⁰ In another woody ornamental, chokecherry (*Prunus virginiana*), a major quantitative trait loci for disease resistance was identified using AFLP and SSR markers.⁹¹ Saturated linkage maps⁹² and a genome sequence database⁹³ have been developed for other *Prunus* species and other Rosaceae members that could be used in ornamental trait development. Among herbaceous North American species, genetic diversity has been examined in *Coreopsis leavenworthii* with AFLP markers⁹⁴ and in *Helianthus annuus* with both anonymous SSRs⁹⁵ and gene-specific EST-SSRs.⁹⁶

To take advantage of the genetic variation present in native plant populations, reverse genetic approaches could be employed that have been used for forestry⁹⁷ and agricultural^{98,99} species. Strategies such as EcoTILLING or BRDA (breeding with rare defective alleles) use genetic screening to identify defective alleles of genes known to play major roles in the control of qualitative traits. Allelic variation has been detected in coding sequences by several screening methods, including DNA nuclease assays, high-resolution melting analysis and next-generation sequencing.⁹⁹ The genetic screening of 100–800 accessions from germplasm collections has identified defective variants of genes leading to targeted traits. Examples include improved lignin quality in black poplar (*Populus nigra*),⁹⁷ virus resistance in pepper (*Capsicum* sp.)¹⁰⁰ and improved oil quality in rapeseed (*Brassica napus*).¹⁰¹

There are several ornamental traits controlled by recessive genes that could be targeted in native plants. Many of the novel flowering and architecture phenotypes that have been obtained by traditional breeding are due to defective alleles of single genes.¹⁰² For example, floral timing has been modified in several plant species by selecting for natural *TERMINAL FLOWER1* (*TFL1*) mutations. *TFL1* represses the transition from vegetative to reproductive growth in the shoot meristem. In perennial plants such as rose (*Rosa hybrida*) and woodland strawberry (*Fragaria vesca*), *TFL1* mutations cause continuous flowering.¹⁰³ In annual crop plants, such as tomato and soybean, determinate varieties were developed through selection for defective alleles of *TFL1* orthologs.^{104,105} Floral structure has been modified by selecting for mutations of *AGAMOUS* (*AG*), a transcription factor that regulates floral organ identity. A consequence of the loss of *AG* function is the homeotic conversion of stamens to petals to produce 'double flowers'. Natural mutations of *AG* orthologs are responsible for double flowers in varieties of ornamental cherry, morning glory and anemone.^{106–108}

Novel architectural traits, such as reduced stature and increased branching, have been obtained from the loss of function of particular genes. Plant stature has been altered by selection for mutations in genes for gibberellic acid biosynthesis or signaling. Natural and induced mutations in *GIBBERELLIN 20-OXIDASE* (*GA20ox*) of rice led to semi-dwarf varieties that played a critical role in the Green Revolution.¹⁰⁹ Semi-dwarf phenotypes have been induced in crop species such as apple and tomato through the knockdown of *GA20ox* expression^{110,111} and in hybrid poplar through the overexpression of *GA INSENSITIVE* (*GAI*).¹¹² Plant branching patterns can be altered by changes in the expression of *BRANCHED1* (*BRC1*) or *TEOSINTE BRANCHED1* (*TB1*), two closely related transcription factors that repress axillary bud growth. Reduced branching due to *TB1* overexpression was critical to maize domestication;¹¹³ conversely, the knockout of *BRC1* expression in Arabidopsis and tomato causes increased branching.^{114,115} Similar to *TFL1*, *AG* and *GA20ox* mutations in different plant species, the loss of function of *BRC1* resulted in the same phenotype in diverse plants. The discovery of natural mutations in candidate genes like these could lead to ornamental traits in native plant species.

Research in model species may be useful for the identification of other genes that play major roles in ornamental traits. For example, peach (*Prunus persica*) is a model Rosaceae species¹¹⁶ that could be used to study flowering genes in woody plants. Peach has complete, autogamous flowers that are produced after a relatively short juvenile period (2–3 years) and a small, sequenced, diploid genome (227 Mb). Although gene transfer in peach is not practical, flowers can be fertilized with mutagenized pollen to generate M1 mutants;^{117,118} non-chimeric M1 populations would allow early screening for mutations in targeted genes by TILLING or next-generation sequencing. In addition to the known flowering genes that have been characterized in peach,^{119–125} floral morphology traits have been identified.^{126,127} Peach flowers can be large and showy or small with curved petals (non-showy), with the 'showy' flower phenotype (*sh/sh*) segregating as a recessive, monogenic trait. *Sh* has been mapped to peach linkage group 1.¹²⁸ Knowledge of the peach *Sh* sequence and function could potentially be applied through EcoTILLING to obtain novel floral morphology in native ornamental *Prunus* species (e.g., *P. virginiana*, *P. serotina*, *P. americana*).

Other strategies that could be used to develop ornamental traits in native plants include interspecific hybridization and polyploidization.¹²⁹ Interspecific hybridization can occur naturally, an example being hybrid azaleas produced by the North American species *Rhododendron prunifolium* and *R. arborescens*. Spatial, temporal, or biological barriers, however, usually prevent interspecific hybridization. Pre- and post-fertilization barriers can be overcome by a range of methods, including pollination techniques, ovule and embryo rescue, and polyploidization.¹²⁹ Controlled crosses with

stored pollen were used to hybridize the North American natives *Franklinia alatamaha* and *Gordonia lasianthus* for woody ornamental development.¹³⁰ Polyploidization has been induced in order to restore fertility in interspecific crosses, e.g., native azalea hybrids.¹³¹ Ornamental traits have also been developed directly through polyploidization, such as increased flower size in the North American species *Phlox subulata*.¹³² Genetic transformation or genome editing may be a more direct means to obtain certain traits, but such approaches are rarely economically viable for ornamental plants.⁸¹

During ornamental trait development in native plant species, the trait and the source material should be chosen to maintain ecological and adaptive functions. A purple foliage trait, for example, could reduce food-web support. For environmental restoration, local provenances are usually the best adapted material, although exceptions to the 'local is best' guideline may increase with climate change.^{133,134} The success of molecular markers for detecting the adaptive potential of native plant species has been mixed. For example, AFLP markers did not to reveal population differentiation related to local adaptation for three herbaceous perennial species native to Minnesota,¹³⁵ whereas AFLP markers could delineate local seed collection zones for a native Australian tree species.¹³⁷ Next-generation sequencing technology is being examined as a means to measure adaptive variation for restoration ecology, as well as the effect of outbreeding on local gene pools.¹³⁶ Whether there is sufficient regional genetic diversity in native species for breeding new traits needs to be determined. Ideally, ecological services provided by new ornamental cultivars of native species (e.g., native herbivore support) would be examined at a regional level.

CONCLUSIONS

It has been argued that the origin of a plant species has no bearing on whether it poses an ecological risk,^{38,138,139} although this is not a conclusion shared by many conservation biologists.¹⁴⁹ Exotic plants have a complex effect on biodiversity in urban areas.¹⁴⁰ Because new species are introduced into urban landscapes more rapidly than native species disappear, local biodiversity can remain high.^{141,142} The reduction of native shrub and tree cover, however, can alter the composition of native populations; ground-foraging bird species, for example, are favored over birds that are canopy foragers.⁴¹ Urbanization also tends to select for the same synanthropic species in different cities.^{142,143} Consequently, while diversity may remain high within a locality (α -diversity), the diversity between localities (β -diversity) is reduced.² The result of this trend is biotic homogenization.^{141,142} To maintain native biodiversity in urban landscapes, the cultivation of native plant species has been recommended.^{5,143–146}

The extent to which native species need to be incorporated in esthetically managed landscapes to provide ecological services is not known. Small-scale additions of native ornamental plants in New York city community gardens did not increase beneficial insect richness.¹⁴⁷ In contrast, landscaping with native shrubs and ground cover was found to increase the abundance and diversity of butterflies and birds in residential yards in Pennsylvania.¹ Suburbs of Canberra had significantly higher bird species richness when native trees made up more than 30% of the streetscape vegetation.⁴ This was assumed to be due to the increased foraging resources provided by native trees. To manage biodiversity in urban environments, residential landscapes should be considered as patches of interconnected habitat that can link other green spaces (e.g., parks, remnant forests).¹⁴⁸ A proposal has been made to replace half the landscaping devoted to grass lawn in the United States with native plants,¹⁴⁹ which would be equivalent to about 25% of the esthetically managed landscape.

To scale up native plants in landscaping to the 30% range will require that current constraints to their use be addressed.

Stakeholder surveys have found that the availability of native plants is a major limitation to increasing their use in landscaping.^{43,65–68} If native ornamentals were made more available through mainstream supply chains, it would likely be as a few selected genotypes of each species. This raises several interrelated questions, such as: what is the genetic diversity needed in a native plant species to provide ecological services regionally? What is the number of genotypes that can be provided profitably for regional markets? Is there sufficient genetic diversity within regionally appropriate germplasm for breeding ornamental traits?

Ecological objectives, including improved adaptation and sustainability, are receiving greater consideration in plant breeding.¹⁵⁰ The development of native plants with ornamental traits could be accelerated using molecular breeding approaches, although the current market size of native landscaping plants may be insufficient to justify their cost. However, as ornamental shrubs and trees alone have an annual wholesale value of approximately \$3 billion in the United States,⁸¹ molecular breeding would be feasible if native species made up a larger part of that market. Tools from restoration ecology can be applied to address the genetic appropriateness of native plant material. Environmentally defined regions such as ecoregions or seed transfer zones may be useful as a platform for integrating economic, ecological and genetic research on native ornamental plants (Figure 1). An interdisciplinary approach could help resolve competing demands for ecological function, cost-effective production and consumer appeal in native landscaping plants.

COMPETING INTERESTS

The authors declare no conflict of interest.

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