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► To cite this version:

Martin Breed, Peter Harrison, Armin Bischoff, Paula Durruty, Nick Gellie, et al.. Priority actions to improve provenance decision making. Bioscience, 2018, 68 (7), pp.510 - 516. 10.1093/biosci/biy050 . hal-01787836

HAL Id: hal-01787836

<https://univ-avignon.hal.science/hal-01787836>

Submitted on 21 Nov 2018

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Priority Actions to Improve Provenance Decision-Making

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Selecting the geographic origin—the provenance—of seed is a key decision in restoration. The last decade has seen a vigorous debate on whether to use local or nonlocal seed. The use of local seed has been the preferred approach because it is expected to maintain local adaptation and avoid deleterious population effects (e.g., maladaptation and outbreeding depression). However, the impacts of habitat fragmentation and climate change on plant populations have driven the debate on whether the local-is-best standard needs changing. This debate has largely been theoretical in nature, which hampers provenance decision-making. Here, we detail cross-sector priority actions to improve provenance decision-making, including embedding provenance trials into restoration projects; developing dynamic, evidence-based provenance policies; and establishing stronger research–practitioner collaborations to facilitate the adoption of research outcomes. We discuss how to tackle these priority actions in order to help satisfy the restoration sector’s requirement for appropriately provenanced seed.

Keywords: assisted migration, ecological restoration, local adaptation, restoration genetics

The restoration sector’s demand for seed is enormous and is rapidly increasing with the growth in the global restoration effort (Verdone and Seidl 2017). Choosing the geographic origin—the *provenance* (see the glossary in box 1 for definitions)—of seed used in restoration is an early and fundamental decision faced by restoration practitioners (Miller et al. 2017). The traditional practice has been to source seed local to the restoration site—*local provenancing*—because it is expected to maintain the evolutionary history of plant populations (e.g., local adaptation), minimize maladaptation, and limit deleterious genetic effects (e.g., outbreeding depression).

Global change has sparked a broad and robust debate on whether nonlocal seed should be used in restoration and, if so, under what circumstances (Hamilton 2001, Wilkinson 2001, Broadhurst et al. 2008, Mijnsbrugge et al. 2010, Byrne et al. 2011, Breed et al. 2013, Williams et al. 2014, Havens et al. 2015, Prober et al. 2015, Breed et al. 2016b, Christmas et al. 2016b, Bucharova 2017). There are two central tenets to this argument: habitat fragmentation and climate change. Habitat fragmentation generally increases inbreeding and reduces effective population sizes of plant populations, which can have an impact on local seed quality by reducing fitness and adaptive potential (Vranckx et al. 2011, Breed et al. 2015). Because climate is a strong and common agent of selection in plants (Davis and Shaw 2001, Petit et al. 2008), it has been argued that provenance selection should match values of climatic variables predicted into the future (Breed et al. 2013,

Williams et al. 2014, Havens et al. 2015, Prober et al. 2015, Breed et al. 2016b, Christmas et al. 2016b).

Consequently, several alternative provenancing strategies have been proposed to supplement local provenances with nonlocal provenances. These strategies generally fall into two categories: those that attempt to increase the adaptive potential of plants at a restoration site by increasing the genetic diversity of the seed mix (e.g., relaxed local, composite, and admixture provenancing) and those that recommend matching provenances with anticipated future environmental conditions of a restoration site (e.g., predictive and climate-adjusted provenancing). Although there are theoretical underpinnings to these alternative strategies, experimental field-testing in restoration contexts is limited.

In this article, we identify several knowledge gaps and practical barriers that need priority action by researchers, policymakers, and practitioners to improve provenance decision-making from an international perspective. We discuss these priority actions in light of the global restoration challenge of restoring degraded terrestrial landscapes from grassland to forest ecosystems, but we acknowledge that the success of a provenancing strategy will be context dependent (e.g., landscape heterogeneity and age; plant species biology, demography, and evolutionary history; and management priorities, scale, and resources). By highlighting these priority actions, we hope to improve support for restoration, offer guidance for policy development, bridge

Box 1. Glossary of terms.

Admixture provenancing: Supplementing local provenances with seed collections across a species' natural distribution.

Climate-adjusted provenancing: Supplementing local provenances with targeted nonlocal provenances collected along a climate gradient in line with climate-change projections.

Composite provenancing: Supplementing local provenances with seed from multiple nonlocal provenances within gene-flow distances to mimic natural gene flow among populations.

Cultivar: The selective breeding of a genotype for favorable attributes such as fast growth or high-salinity (or other extreme environment) tolerance.

Habitat suitability model: A model of the statistical relationship between species occurrences and environment that conceptually represents the predicted spatial abiotic and biotic limits of a species suitable habitat. These models are also referred to as *species distribution models* or *ecological niche models* and draw on ecological niche theory.

Heterosis: The increased fitness of the hybrid product between two divergent provenances or species compared with parental genotypes.

Local adaptation: Superior fitness of a local population over other provenances when grown in its home environment.

Local provenance: Seed from either within the restoration site (strict local provenance) or within close geographic proximity to the restoration site (relaxed local provenance). Defining a "local" provenance is a difficult task and is rarely articulated well in papers that discuss this issue, which hinders progress in the provenancing debate. Adopting a genetically informed definition of a local provenance is probably the most useful approach, and examples include spatial delineation of provenances based on significant genetic differentiation in neutral and/or adaptive genetic markers or functional traits. However, such an approach is perhaps the least attainable for practitioners because of the costs, time, and skills required.

Local provenancing: Only using a local provenance.

Outbreeding depression: The decreased fitness of the hybrid product between two divergent provenances due to disruption of locally adapted gene complexes.

Provenance: The geographic location of a seed source that is used to describe the genetic material from that location.

Provenancing: In an ecological restoration context, refers to a seed-sourcing strategy, with a focus on the geographic location of seed source(s).

Phenotypic plasticity: The nongenetic capability of one genotype to produce a variety of different phenotypes.

Predictive provenancing: Deriving a matched seed source with predicted future home-site conditions; optimally should be based on provenance trials.

Restoration: The process of reducing the damage and/or degradation of an ecosystem by resetting the trajectory of the ecological community toward that of a reference state. This definition should potentially be broadened to capture restoration of sites that do not have a reference (e.g., pollinator habitat in agricultural matrices or biodiverse urban green spaces) and to also include sites that have been degraded to such an extent that restoration to a reference state is likely an unachievable goal (e.g., some postmining sites and novel ecosystems).

Seed zones: Discrete geographic regions that have similar environments. Transfer within zones should result in few detrimental effects on mean population fitness. Optimally should be based on progeny testing of multiple provenances.

knowledge gaps from science into practice, and ultimately improve restoration outcomes now and in the future.

Strategic goals and practitioner priorities

We identify four gaps in provenance decision-making that are commonly faced by both policymakers and practitioners. These include (1) the lack of guidance when departing from a strict local provenancing strategy, (2) the need for greater evidence-based restoration practices, (3) the potential risks associated with using nonlocal provenances, focusing on outbreeding depression, and (4) the risks and benefits of using cultivars in restoration and when they may be required. Each of these are discussed below.

Improving provenance strategy choice. Local provenancing has been the preferred approach for many years. However, a strict interpretation of local provenancing may halt restoration projects if local seed supply is insufficient (Wilkinson 2001, Broadhurst et al. 2008). Local provenancing should not be so restrictive that it stops projects, even if this means that nonlocal provenances are introduced. In cases in which broader provenances are used or a change in practice is implemented, documentation and ongoing monitoring will be important in order to evaluate the impacts of such changes on restoration success. Indeed, determining whether plant failure at a restoration site is due to provenance selection can be inferred through personal

observations, but without experiments and monitoring, such evidence remains anecdotal.

Departing from a strict local provenancing strategy relies on the development of robust seed transfer guidelines, such as seed zones. Seed zones generally refer to regions that have similar environments, and transfer within zones should result in few detrimental effects on mean population fitness (Hufford and Mazer 2003). Such zones are well developed in many forestry sectors because of large commercial interest in the final crop, but they are less well developed for restoration. Ideally, seed zones should reflect the likelihood of adaptive differentiation of the focal species (Kilkenny 2015, Jørgensen et al. 2016, Bucharova et al. 2017b). Geographic distance, for example, is often used as the basis of seed transfer zones (Mortlock 2000). However, geographic distance is a theoretically poor predictor of adaptive differentiation unless it correlates with environmental distance (Leimu and Fischer 2008). Indeed, genetic differentiation among populations can occur over short distances because of microsite differences, as well as over broad scales reflecting clinal variation or more major geographic barriers to gene flow (Richardson et al. 2014). As such, seed zones should reflect this environmental heterogeneity, because this is likely a better predictor of adaptive differentiation than geographic distance (Hereford 2009). Seed zones for restoration have been defined in some countries, such as the provisional seed zones in the United States (Bower et al. 2014) and *Herkunftregionen* in Germany (Durka et al. 2017). However, there is a need to develop seed-zone boundaries more generally to better reflect ecological and/or genetic differences rather than political boundaries.

Sourcing seed across political boundaries is a prerequisite when nonlocal provenances are used, requiring the exchange of seed from outside and potentially across established supply networks (i.e., among seed collectors and/or producers). Creating a mechanism to share seed across political boundaries will further help to achieve better restoration results through greater provenance options. Indeed, stakeholders in the United States have developed a strategic framework to help alleviate provenance supply issues, with the goal of improving the availability of appropriate seed for restoration. To increase the cost-effectiveness and availability of appropriate seed, the Plant Conservation Alliance (2015) developed the National Seed Strategy for Rehabilitation and Restoration, which fosters coordination among parties involved along the seed supply chain, from wild seed collection to the application in restoration projects. Similar strategic frameworks exist elsewhere (e.g., in São Paulo state, Brazil; Chaves et al. 2015). We encourage formulation of such frameworks in other countries, because they will likely help (a) establish best-practice provenance decision-making, (b) manage and potentially mitigate the risks of poor decision-making, and (c) ultimately improve accountability of provenance-choice decisions.

Growing the evidence base for restoration. There is an increased need for evidence-based restoration to achieve optimal

outcomes. Embedding well-designed common garden experiments into restoration projects is a demonstrated way to obtain empirical evidence on the effect of provenance choice (figure 1). Despite the clear benefits of such researcher–practitioner collaborations, differences in training, terminology, objectives, and reward systems can create a lag in research uptake and a barrier to collaboration (Guerrero and Wilson 2017). For example, most restoration funders demand on-ground actions over research. There need to be better cross-sector communication of the benefits of and increased funding for embedding experiments into restoration projects. Ultimately, these experiments will help inform future restoration and should become a standard part of as many restoration projects as possible.

Monitoring embedded experiments is a key part of building the evidence-based feedback loop into restoration practice (figure 1) and should be prioritized higher by funders to improve provenance decision-making. Monitoring can efficiently be done by aligning and collaborating with researchers when, for example, student projects or contracted work can be undertaken to collect, analyze, and interpret data from such experiments (e.g., Bailey et al. 2013, Breed et al. 2013, 2016a, Gellie et al. 2016, 2018). In fact, it is often the case that researchers seek more opportunities to work with practitioners to broaden the impact of their research (Evans and Plewa 2016). Nevertheless, it is important that researchers are brought in early into the restoration process, because well-designed studies (e.g., with controls and randomized treatment replicates) are more powerful than post hoc analyses (Bucharova et al. 2017a). Furthermore, the maintenance of well-documented databases on the provenances used in the experiments (e.g., geographic location, degree of fragmentation, or number of sampled mothers in a bulked seedlot) will assist in interpreting the data generated from such experiments and help to determine the factors influencing long-term success in restoration projects. However, there are few examples of good provenance-recording frameworks that allow such monitoring and analysis to take place in the absence of research collaborations. Implementing a tracking system, such as the yellow-tag system employed in the United States (Young 1996), could improve the quality of provenance information across the provenance supply chain.

Mitigate the risk of outbreeding depression. The risks associated with mixing provenances for restoration have been thoroughly discussed (e.g., maladaptation and outbreeding depression; see Byrne et al. 2011, Weeks et al. 2011). Unlike maladaptation, which is difficult to predict, there are practical recommendations about how to predict outbreeding depression—the reduced fitness of progeny resulting from mating between two genetically dissimilar individuals (Templeton 1986, Frankham et al. 2011, Weeks et al. 2011). The risks of outbreeding depression can largely be predicted by identifying whether there are ploidy or major chromosomal polymorphisms between provenances with karyotyping or flow cytometry (Frankham et al. 2011).

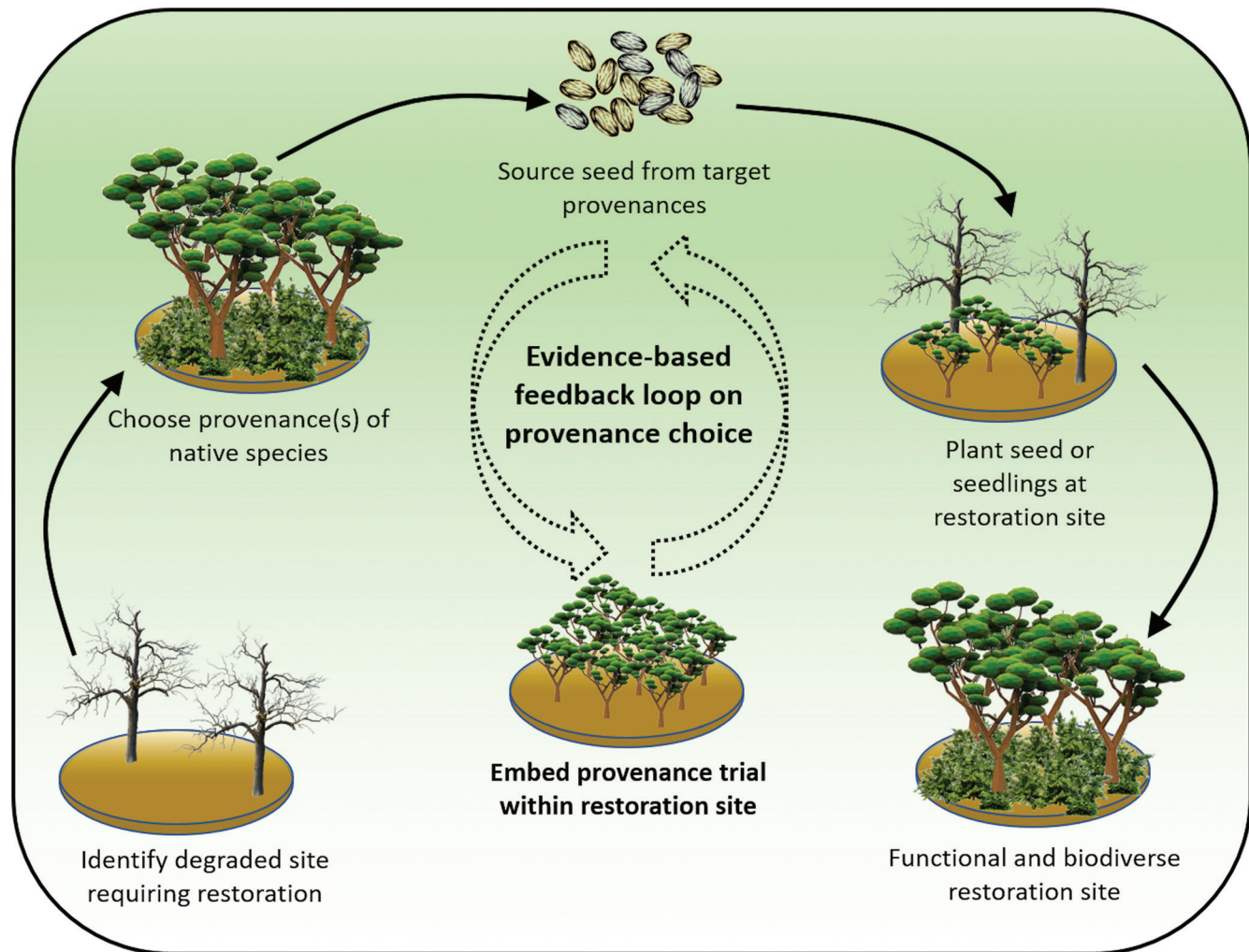


Figure 1. A schematic representation of the evidence-based feedback loop that embedded provenance trials within restoration plantings can have on improving provenance decision-making.

The frequency and phylogenetic patterns of these intraspecific ploidy polymorphisms are an active area of research. The publicly available Chromosome Counts Database (CCDB; Rice A et al. 2015) indicates that approximately 16% of plant species show ploidy polymorphisms. However, only 69 polymorphic species have been well sampled (i.e., range-wide and $n > 100$ sampling; Kolář et al. 2017). Of these 69 species, 21 were Asteraceae and 7 were Poaceae, supporting taxonomic trends identified by Kramer and colleagues (2018). Interestingly, 16% of 39 species in Kolář and colleagues (2017) showed intrapopulation polymorphisms, indicating that ploidy variation between and within populations may occur at similar rates.

Inexpensive checks for ploidy polymorphisms should be more broadly employed, especially for plant groups expected to exhibit intraspecific ploidy differences, to improve long-term restoration success by helping to mitigate the risk of outbreeding depression. For example, ploidy of species used for restoration should be initially screened in publically available databases (e.g., the CCDB). For some species, there are phenotypic correlates

with ploidy that can be the basis of rapid screening (e.g., seed mass in big sagebrush, Asteraceae; Richardson et al. 2015). Taxa in Asteraceae and Poaceae should be priority candidates for further ploidy screening when used for restoration, because of their apparent high frequency of intraspecific polyploidy.

When to use cultivars. Restoration often takes place at sites that have deviated far away from their reference state, resulting in novel environments (e.g., high salinity or nutrient levels postagriculture and novel soil postmining). It may be difficult to establish native seed, regardless of provenance, at these sites. In such cases, selectively bred cultivars may be appropriate. Indeed, the use of cultivars in restoration has gained momentum, particularly in the United States. The genetic background of cultivars can vary greatly, with some being clonal or highly inbred, whereas others are derived from polycrosses consisting of multiple pollen parents from the same or different provenances.

The use of cultivars may be problematic if they lack genetic variation or if they have traits that counteract the

restoration process (Chivers et al. 2016, Nevill et al. 2016). Furthermore, when cultivars have a narrow genetic base, they risk generating genetically uniform populations that may be less resilient to responding to environmental changes compared with those produced by wild provenances. The habitat provided by these cultivars can also have a negative impact on dependent organisms in terms of both supporting a limited set of species and disrupting ecosystem functions (Barbour et al. 2016, Mody et al. 2017). Nevertheless, the use of polycrosses may counteract some of these concerns (Chivers et al. 2016). We emphasize that cultivars should be used in a risk-assessment framework to minimize their impact on natural populations (Byrne et al. 2011, Weeks et al. 2011).

Research priorities

The push for greater evidence-based provenance decision-making has highlighted several key areas for future research. These include (a) understanding the role of phenotypic plasticity in climate resilience of provenances, (b) developing improved species habitat suitability models to guide provenance choice, (c) understanding provenance adaptation to both biotic and abiotic factors, and (d) understanding the provenance effects on dependent organisms in restoration plantings. Each of these are discussed below.

Phenotypic plasticity. The capability of one genotype to produce a variety of different phenotypes—*phenotypic plasticity*—is poorly understood for most species used in restoration. Despite this poor understanding, plasticity will likely be important in a restoration context because it can allow short-term acclimation to novel environments and thereby stabilize fitness during environmental change (Nicotra et al. 2010). Phenotypic plasticity can be quantified by growing genotypes in a variety of environments (e.g., with and without herbivores or across an environmental gradient) and determining the variation in traits produced by each genotype across environments. A broader understanding of plasticity in functional and fitness traits (e.g., water-use efficiency, specific leaf area, and relative growth rate) from theoretical, empirical, and applied-research perspectives would help provenance decision-making by understanding how trait plasticity within a particular provenance influences its potential to survive and persist under changing conditions (e.g., McLean et al. 2014). Although there is clear theoretical understanding of the potential benefits of plasticity, such as facilitating rapid evolution (Rice and Emery 2003) that increases climate resilience of restoration plantings, there is a greater need to evaluate its importance for provenance decision-making.

Habitat suitability models. A principal concern in the seed-sourcing debate is climate change, and much of our current predictive knowledge relies on habitat suitability models that incorporate climate projections (Elith and Leathwick 2009). Although habitat suitability models provide a way to select provenances for restoration plantings (Harrison et al. 2017),

they are often based on environmental layers that assume equal weighting of these factors on fitness. Extensions of these models to include both genetic information (Kilkenny 2015, Ikeda et al. 2017) and ecophysiological limits (e.g., mechanistic models; Kearney et al. 2009, Caddy-Retalic et al. 2017) provide an increased realism to their predictions. However, further research is required, with an initial focus on key species used in restoration. Predictions of plant performance based on habitat suitability models need to be empirically validated through reciprocal transplant experiments or at least an understanding of the role climate and nonclimate factors have on the study system.

Components of local adaptation. Populations are often locally adapted (Leimu and Fischer 2008, Hereford 2009, Oduor et al. 2016). Local adaptation can have both climate and many nonclimate components, including other abiotic factors such as soil and photoperiod (Savolainen et al. 2013, Christmas et al. 2016a), but biotic factors such as antagonists and mutualists are also important (Crémieux et al. 2008, Gellie et al. 2016, Potts et al. 2016, Gehring et al. 2017, Urbina et al. 2018). Some nonlocal provenances may have no history of exposure to local pests and pathogens (Potts et al. 2016), and pests and pathogens may themselves be shifting their ranges (Burke et al. 2017), potentially increasing the risk of maladaptation (Gellie et al. 2016). Little is known about the relative importance of climate compared with these other factors for most plant species, but reciprocal transplant and experimental treatments (e.g., herbivore and pathogen exclusion or exposure trials) can help tease these effects apart.

Ecological networks. The debate on seed-sourcing strategies has generally focused on mean provenance fitness. However, there are largely unappreciated extended effects of provenance choice on organisms that colonize and inhabit restoration plantings (Whitham et al. 2006, Crémieux et al. 2008, Bucharova 2017). Provenance effects have been shown to affect individual organism responses, as well as biotic communities both above- (Bucharova et al. 2016, Gosney et al. 2017) and belowground (Senior et al. 2016, Gehring et al. 2017, Urbina et al. 2018). The coevolutionary relationships between local provenances and their dependent communities (e.g., Toju and Sota 2005, Gehring et al. 2017) further emphasize the importance of considering the extended effects of using local or nonlocal provenances on ecological networks.

Conclusions

The restoration sector aims to return biodiverse, functional ecosystems at unprecedented scales (Verdone and Seidl 2017), as well as to restore valuable ecosystem services (see the Call to Action from the 2017 Society for Ecological Restoration conference at www.ser.org/general/custom.asp?page=7thWorldConference). However, the ability to meet these aspirational goals relies on supplying vast quantities of appropriately provenanced seed. Although the suitability of different provenancing strategies will no doubt

be context dependent, the debate continues. To progress the debate from largely theoretical to empirical underpinnings, we recommend here a set of priority actions that need to be adopted to improve restoration outcomes from provenance decision-making: (a) Increase testing of provenance decisions by embedding provenance experiments into restoration projects. (b) Develop policies and standards on provenance choice that are dynamic, are evidence based, are influenced by context, and incorporate risk-mitigation strategies. (c) Establish stronger research–practitioner collaborations to promote research on provenance choice and encourage the adoption of research outcomes for future restoration projects.

Acknowledgments

This article was the output of a workshop at the Society for Ecological Restoration conference in Foz do Iguaçu, Brazil, held on 28 August 2017, titled “Using Non-Local Plants in Restoration: Fallacy or Fundamental?” This work was supported by the Australian Research Council (no. DE150100542 awarded to MFB, no. DP150103414 awarded to MFB and AJL; no. LP100100620 awarded to SLK; no. ICI150100041 awarded to SLK and supported PGN; no. LP120200380 supported PAH), the National Climate Change Adaptation Research Facility funding to MFB and AJL, and the Great Basin Native Plant Project to FFK. The authors declare no conflict of interest.

Supplemental material

Supplementary data are available at *BIOSCI* online.

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