Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Using trait-based ecology to restore resilient ecosystems: historical conditions and the future of montane forests in western North America

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Historical reference conditions have provided empirical benchmarks for guiding ecological restoration but the relevance of historical conditions has been questioned in this era of rapid global change. Trait-based ecology offers an alternative approach for setting restoration objectives. If we understand which phenotypic traits confer high survival in a given environment, then we can restore assemblages of species with favorable trait combinations to reduce mortality risk, achieve functional outcomes, and enhance restoration success. Our objective was to compare restoration prescriptions based on historical reference conditions versus trait-based objectives in southwestern United States mixed conifer forests. To optimize survival and enhance resilience under projected increasing frequencies of fire and drought, we constructed and evaluated models based on combinations of three traits: thick bark, dense wood, and moderate leaf nitrogen concentration. Models with multiple traits accurately derived historical species abundance distributions, which is a necessary condition for the application of trait-based models under less certain future conditions. Model results indicated that trait-based restoration objectives could be achieved in two ways: by manipulating abundances of species that already coexist at a site or by adding native species from warmer climates to the local species pool. The latter approach may create no-analog communities of native species. Restoration goals based on either historical reference conditions or future projections are special cases of a more general class of desired future conditions that are derived from trait-based objectives. Functional ecology provides a general, flexible, and theory-based approach to restoring resilient ecosystems at a time of rapid environmental change.

Key words: bark thickness, climate change, community assembly, mixed conifer forests, reference conditions, wood density

Implications for Practice

- To restore resilient ecosystems, practitioners can select species with favorable trait combinations to reduce mortality risk under changing environmental conditions.
- In the western United States where drought and fire are projected to increase in frequency, restoration can include managing for species with traits such as dense wood, tough leaves, and thick bark.
- Trait-based models operationalize the process of selecting species with the appropriate trait combinations and produce ranges of relative abundances for every species, which can be rescaled to a measure of total biomass to translate the results into prescriptive site-specific treatments.
- Management plans and policies must be revised to allow for the inevitable changes in community composition under environmental change and to increase the flexibility of species selection for restoration.

Introduction

Ecologists are engaged in an important debate about how to set and achieve restoration goals in a rapidly changing world (Hobbs et al. 2009; Higgs et al. 2014; Murcia et al. 2014). Historical reference conditions have long been the gold standard on which to base restoration objectives in many ecosystems (White & Walker 1997; Landres et al. 1999). For well-studied ecosystems, historical ecosystem structure, composition, and function provide robust empirical information for defining desired future conditions (Moore et al. 1999; Swetnam et al. 1999). However, current and future environmental conditions are becoming more disparate from historical environmental conditions in this era of rapid global change (Harris et al. 2006; Choi et al. 2008; Hobbs et al. 2009) and historical reference conditions are completely unknown for many ecosystems in long-inhabited regions of the world (Thorpe & Stanley 2011).

Author contributions: All authors conceived the research and collected the data; DCL performed the analyses; all authors wrote and edited the manuscript.

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doi: 10.1111/rec.12342

Rather than restoring historical assemblages that may not survive the changing environmental conditions, a more general approach has recently emerged that emphasizes achieving functional objectives to restore resilient ecosystems (Hobbs & Cramer 2008; Seastedt et al. 2008; Jackson & Hobbs 2009). Ecosystem resilience is the ability of the ecosystem to maintain essential features of its composition, structure, and function in the presence of disturbance and environmental change (Halofsky et al. 2014; Waltz et al. 2014).

Species that were dominant in historical ecosystems were abundant because they had traits that endowed high survival rates in those conditions (Keddy 1992; Shipley 2010). As the environment changes, the trait values that optimize survival will necessarily change as well. If we understand which traits confer fitness (i.e. higher survival and reproduction) in the new environmental conditions (Aitken et al. 2008; Kimball et al. 2012), then we can manage for species with more favorable trait combinations to reduce mortality risk and enhance restoration success (Funk et al. 2008; Martínez-Garza et al. 2013; Laughlin 2014*a*; Cadotte et al. 2015; Ostertag et al. 2015). Trait-environment relationships can be indicative of which trait values confer fitness in a given environment (Laughlin & Messier 2015), but there are caveats to this approach. Rare or small species may exhibit different traits and life history strategies than dominant species yet still maintain high per capita population growth rates, and the composition of forest communities comprised of long-lived organisms may reflect responses to past climates or disturbance events. Although acknowledging that trait frequencies are not a direct proxy for fitness, understanding how trait combinations shift along environmental gradients is a first approximation to linking traits to performance (Shipley 2010).

The key advance of recent trait-based models is their ability to derive a range of abundances for each species in the regional pool that can be used as a prescription for establishing assemblages of phenotypes that are adapted to the given conditions (Laughlin 2014*a*). However, it is unknown how restoration objectives based on historical structure and composition would differ from an approach based on traits under changing environmental conditions. It is important to critically evaluate the accuracy of the models and compare restoration prescriptions that are based on history versus trait-based ecology. The objective of this article, therefore, is to compare restoration prescriptions based on detailed historical reference conditions versus those that are based on the traits of well-adapted phenotypes for the given conditions. In order for trait-based models to be useful in restoration, they need to be able to reproduce historical assemblages where the optimum trait combinations for those conditions are known. If trait-based models cannot reproduce historical assemblages when these trait values are known, then trait-based approaches will be unreliable to plan for the future because the optimum traits for future conditions are unknown, or at best, they are predicted using statistical trait-environment relationships (Frenette-Dussault et al. 2013). Furthermore, the accuracy of model output may depend on the number and importance of traits used in the model because additional traits provide more information about functional differences among species and because increasing trait dimensionality improves predictions of community composition and niche differences (Laughlin 2014*b*; Kraft et al. 2015).

We synthesized data on historical conditions (i.e. forest structure and composition) and functional traits in southwestern United States warm/dry mixed conifer forests to compare the traditional and trait-based approaches to setting restoration objectives. This ecosystem is useful for this comparison because historical reference conditions in these montane forests are well-studied and quantifiable. Prior to the late 1800s AD, warm/dry mixed conifer forests in Arizona, U.S.A. were characterized by a frequent, low-severity fire regime and were generally dominated by shade-intolerant and fire-tolerant trees (Fulé et al. 2004; Huffman et al. 2015). Since the beginning of the 1900s, fire suppression along with timber harvesting practices favoring the removal of large trees have allowed shade-tolerant and fire-intolerant species to significantly increase in abundance. This has led to important functional shifts because current forests are now dominated by species with thinner bark, lower wood density, and slightly lower leaf nitrogen (N) concentrations (Strahan et al. in review).

Two major changes have been predicted to occur in the western United States over the next century: increased wildfire frequency and increased drought severity. First, earlier spring onset and warmer temperatures are drying out fuel loads and priming forests for more frequent fires (Westerling et al. 2006). In this case, optimum traits in the past serve as a guide for restoration (Harris et al. 2006; Fulé 2008). Given that historical forests were composed of fire-tolerant species with thick bark (Fulé et al. 2004; Strahan et al. in review), species with thick bark should also be a large component of the future forest. Second, hotter droughts are also likely to occur with increasing frequency (Breshears et al. 2005; Allen et al. 2015; Millar & Stephenson 2015). In this case, reliance on the past alone limits the available options because the climate is rapidly changing. A trait-based solution is to apply ecophysiological principles to restore forests that are drought resistant. Species with traits associated with a conservative growth strategy, such as dense wood and low to moderate leaf nutrient concentrations, may be more able to resist drought-induced cavitation and tolerate resource limitation, respectively (Hacke et al. 2001; Westoby et al. 2002). Only a few trees in western mixed conifer forests have dense wood, so expanding the pool of native species may be required to achieve these functional objectives (Millar & Stephenson 2015).

We asked two main questions to investigate how trait-based models can be applied in this new era of restoration ecology. First, can trait-based models accurately derive historical species abundance distributions, and does the number and combination of traits affect the accuracy of model output? Second, how do the species abundance distributions derived from the model change when trait values are used that confer higher survival under projected future conditions, and when other native species that are adapted to warmer climates are added to the species pool?

Methods

Study System

Two mixed conifer forests in Arizona were used to define reference conditions using historical forest structure and composition. First, historical forest conditions were determined in a 1,135 ha warm/dry mixed conifer ecosystem on the Black Mesa Ranger District of the Apache-Sitgreaves National Forest in northern Arizona (2,313–2,405 m elevation range, 695 mm average annual precipitation, and 5.5 °C average annual temperature) (Huffman et al. 2015). Current overstory composition and structure were determined using 147 permanent 0.04 ha plots, arrayed on a 250-m systematic grid. Species identity and diameter at breast height (dbh; measured at 1.37 m height on stem) were recorded for live trees, and diameter at stump height (dsh; measured at 40 cm above root collar) was recorded for dead trees. Historical forest structure in 1879 was reconstructed to quantify the changes following fire exclusion. For trees that were alive during contemporary sampling, radial growth increments were measured on tree cores and a proportional reconstruction method was used to calculate historical tree diameters (Bakker 2005). For trees that were dead during contemporary sampling, a percentile-based exponential decay model was used to estimate tree death date and then tree diameter was reconstructed in 1879 using a stand reconstruction model (Bakker et al. 2008). Fire scar analysis indicated that the mean point fire interval across the site was 11.8 years, indicating that historically the fire regime was characterized by high frequency, low-severity fires. However, the frequent fire regime was abruptly halted after 1879 (Huffman et al. 2015).

Second, reference conditions were also determined in a 490 ha never-harvested mixed conifer forest (the "Northwest 3" unit) in Grand Canyon National Park (GCNP), Arizona, U.S.A. (2,427–2,549 m elevation, 650 mm annual precipitation, and 5.9°C average annual temperature). Current overstory composition and structure were determined using 30 plots of 0.1 ha arrayed on a 300-m systematic grid. We recorded species and dbh of all trees greater than 15 cm dbh on the entire plot, and on all trees between 2.5 and 15 cm on a 250-m^2 subplot (Laughlin et al. 2011*b*). Fire scar analysis indicated that the mean point fire interval across the site was 8.7 years, indicating that historically the fire regime was characterized by high frequency, low-severity fires. However, the frequent fire regime was abruptly halted after 1879 (Fulé et al. 2003). This forest was burned twice with prescribed fire in the last few decades, which restored forest structure to conditions similar to those reported as the historical range of variability in this forest type (Fulé et al. 2004; Huisinga et al. 2005; Laughlin et al. 2011*b*). Given its long-term protection from logging and Grand Canyon National Park's burn-only approach to forest management, this forest is a useful extant reference site.

Nine tree species were detected in the forest on the Black Mesa Ranger District in Arizona (Table 1). The five conifer species included *Pinus ponderosa* (ponderosa pine), *Pseudotsuga menziesii* (Douglas-fir), *Pinus strobiformis* (southwestern white pine), *Abies concolor* (white fir), and *Abies lasiocarpa* (subalpine fir). The four broadleaf angiosperms included *Populus tremuloides* (quaking aspen), *Quercus gambelii* (Gambel oak), *Acer grandidentatum* (big tooth maple), and *Robinia neomexicana* (New Mexico locust). Five tree species were detected in the Northwest 3 unit in GCNP: *Abies concolor*, *Picea engelmannii* (Engelmann spruce), *P. ponderosa*, *P. menziesii*, and *P. tremuloides* (Table 1).

Table 1. Names and four-letter codes of tree species in this study.

Species	*Common Name*	*Code*
Abies concolor (Gordon & Glendinning) Hoopes.	White fir	ABCO
Abies lasiocarpa (Hooker) Nuttall	Subalpine fire	ABLA
Acer grandidentatum Nutt.	Bigtooth maple	ACGR
Juniperus deppeana Steud.	Alligator juniper	JUDE
Juniperus scopulorum Sarg.	Rocky Mt. juniper	JUSC
Pinus edulis Engelm.	Pinyon pine	PIED
Pinus ponderosa P. & C. Lawson	Ponderosa pine	PIPO
Pinus strobiformis Engelm.	Southwestern white pine	PIST
Populus tremuloides Michx.	Quaking aspen	POTR
Pseudotsuga menziesii (Mirb.) Franco	Douglas-fir	PSME
Quercus gambelii Nutt.	Gambel oak	QUGA
Robinia neomexicana A. Gray	New Mexico locust	RONE

We measured three functional traits that influence tree performance in a semi-arid region with a frequent fire regime: bark thickness (expressed as an average percentage of stem diameter), wood density (mg/mm^3), and leaf nitrogen (N) concentration (% dry mass). Bark thickness and wood density are important traits that affect fitness along gradients of fire frequency and moisture availability, respectively, as discussed above. Low leaf nitrogen concentration corresponds with dense, long-lived leaves that are associated with a conservative growth strategy in low resource conditions (Westoby et al. 2002). All traits were measured following standardized protocols described in detail in Laughlin et al. (2011*a*). Figure 1 illustrates where each species occurs within the three-dimensional trait space by plotting their average trait values.

The Model

Trait-based models can be used to derive species abundance distributions that satisfy the selected functional trait values to meet a restoration objective (Laughlin 2014*a*). There are four main steps. Step 1: Articulate the objectives of the project. For example, a practitioner may wish to restore a plant community that is resilient to drought. Step 2: Translate the objectives into trait values that will achieve those objectives. For example, to increase resiliency to drought, select traits such as dense wood. Step 3: Define the species pool and quantify the traits of these species. This list could include all native species known to have occurred in a specific site, or could be the species that are available for seed mixes. Step 4: Set up and solve a system of linear equations.

Systems of linear equations can be used to estimate species probabilities given any set of constraints, where in this case the

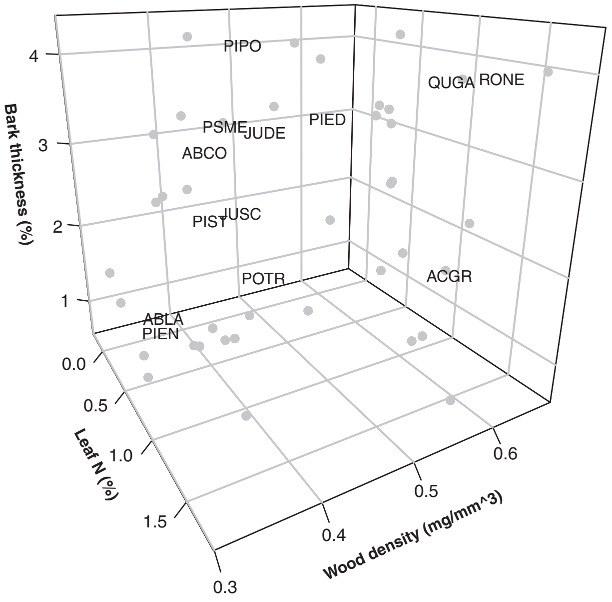

Figure 1. Species locations within a three-dimensional trait space. The species names are shortened to four-letter codes (see Table 1) and their location is defined by the species' three average trait values. The gray points are shadows cast onto each panel to illustrate bivariate scatterplots between each pair of traits.

constraints are functional traits that are proposed to optimize survival (Laughlin 2014*a*). A vector of unknown species relative abundances (p_i) can be estimated by developing a system of linear equality and inequality constraints:

$$\sum_{i=1}^{S} t_{ik} p_i = \overline{T}_k, \tag{1}$$

$$\sum_{i=1}^{S} p_i = 1, \tag{2}$$

$$p_i > 0. \tag{3}$$

Equation 1 states that the linear combination of the *k*th trait from the *i*th species (t_{ik}) and unknown species relative abundances (p_i) is equal to the constraint $\overline{T}_k$, where $\overline{T}_k$ is the *k*th trait value of an average unit of biomass or individual in a community. There are K (the number of traits) of these constraint equations, and S is the size of the species pool. The values of $\overline{T}_k$ are defined in Step 2 (above). Equation 2 constrains the abundances to sum to one so that the solutions represent relative abundances or probabilities. Equation 3 constrains the abundances to be non-negative (there are S of these inequalities). In practice, there should be fewer traits than unknown species abundances, which results in an underdetermined system of equations with many possible solutions (Lay 2006).

The range of possible solutions provides valuable information about the potential range of variability in species abundances that satisfies the trait constraints. The "limSolve" package in R (van den Meersche et al. 2009) can be used to obtain a sample from the solution set. The "xsample" function uses a Markov chain Monte Carlo (MCMC) algorithm to uniformly sample the solution set of any constrained linear problem. This application of linear algebra can be applied to the problem at hand by rewriting Equations 1 and 2 in matrix form $\mathbf{Ax} = \mathbf{b}$, where $\mathbf{A}$ is a matrix of coefficients (i.e. species mean traits), $\mathbf{x}$ is a matrix of unknown relative abundances, and $\mathbf{b}$ is a vector of constants (i.e. trait constraints) representing the right-hand side of the equations. As long as the constraints are consistent (i.e. either one or an infinite number of solutions exists), one can obtain a uniform sample from $\mathbf{x}$, which will represent the range of species abundances that meet the trait-based objectives.

This model uses species-level trait means and does not explicitly incorporate intraspecific trait variation, which can be an important source of variation related to population responses to environmental change (Jung et al. 2014). Using data collected at the individual level, interspecific variation accounted for 93% of the variation in leaf nitrogen, 77% of the variation in wood density, and 46% of the variation in relative bark thickness. Although it is possible to incorporate such variation into the modeling framework, this increases the complexity of the modeling process and these data are currently rarely available in restoration projects. Model results that use only mean values will be similar to model results that use both means and variances when the trait constraints are unimodal, as is the case here (Laughlin 2014*a*).

Data Analysis

We conducted the following analyses to answer the two main research questions. First, we asked whether trait-based models could accurately derive historical species abundance distributions. If the answer to this question is no, then trait-based models will yield unreliable forecasts of species abundances in an uncertain future. To answer this question, we used historical mixed conifer forest composition to calculate the community-weighted mean trait values and used these as constraints in the model (i.e. the $\overline{T}_k$). The historical average trait values in the Black Mesa Ranger District were the following: wood density was 0.46 mg/mm^3, bark thickness was 3.5%, and leaf nitrogen was 1.5%. The average trait values in the Grand Canyon National Park reference site were the following: wood density was 0.43 mg/mm^3, bark thickness was 3.7%, and leaf nitrogen was 1.4%. To test model accuracy, we evaluated the linear relationship between the average model-derived species abundances and the average observed historical reference site species abundances. We also analyzed whether the number of traits affected the accuracy of model output. The model-derived species abundance distributions were computed using one trait, two traits (all three pair combinations), and three traits, and we compared observed species relative abundances to model-derived species abundance distributions. To test model accuracy, we evaluated the linear correlations between each of these distributions and the observed relative abundances to determine if the number of traits improved the output of the model.

Second, we asked how the species abundance distributions change when traits that confer higher fitness under projected future conditions are used, and when other native species adapted to warmer climates are added to the species pool. The critical step when applying this model to meet future conditions is the selection of the trait constraints ($\overline{T}_k$). There are both theoretical and practical considerations for selecting these trait values. First, from a theoretical perspective, these trait constraints represent the trait values that confer the greatest survival in a given environmental condition, so physiological and ecological principles must be used to select the appropriate traits (Westoby et al. 2002; Reich et al. 2003). In many cases, we are still learning which trait values confer survival in a given environment. Restoration ecology offers an experimental testing ground to advance our understanding of how trait-environment interactions drive organism fitness. Second, from a practical perspective, it is important to select reasonable trait values that fall within the range of trait values present in the species pool, otherwise there will be no mathematical solution. For this analysis, thick bark was chosen because of the projected future increase in fire frequency, and high wood density and moderate leaf nitrogen concentration were chosen to enhance resilience under drought stress (Hacke et al. 2001; Westoby et al. 2002; Laughlin et al. 2011*a*). We fit two models. For the first model, output was obtained using the species that are currently present in the study site. For the second model, we added three other native species that occur in warmer and drier ecosystems to the species pool: *Juniperus deppeana* (alligator juniper), *Juniperus scoparium* (Rocky mountain juniper), and *Pinus edulis* (pinyon pine) (Table 1), because these species have some potential for establishing in these sites in a warmer environment (Laughlin et al. 2011*a*). To express the model-derived relative abundances in terms of basal area for each species, we multiplied the relative abundances by the targeted total basal area based on historical forest structure.

Results

Trait-Based Model Accuracy

Contemporary mixed conifer forests on the Black Mesa Ranger District are co-dominated by *Pinus ponderosa*, *Abies concolor*, *Pseudotsuga menziesii*, *Pinus strobiformis*, and *Quercus gambelii* (Fig. 2A & 2B). However, historical (1879) forests were dominated by *P. ponderosa*, with much lesser contributions toward total basal area by *P. menziesii*, *A. concolor*, and *Q. gambelii* (Fig. 2C & 2D). The model-derived species abundances (shown in Fig. 2E) using all three historical trait values were strongly correlated ($R^2 = 0.96$, Table 2) with the reconstructed historical abundances (shown in Fig. 2C). The model-derived species abundances using two traits at a time captured the dominance of *P. ponderosa* and secondary dominance by *P. menziesii*, and all exhibited strong correlations with observed abundances (Table 2). The models using either bark thickness and wood or bark thickness and leaf nitrogen rivaled the model using all three traits (Table 2). The model-derived species abundances using one trait at a time were more uniform across species, did not predict the dominance of *P. ponderosa*, and exhibited the weakest correlations with the observed abundances (Table 2), indicating that more than one trait is required to achieve accurate reproductions of historical assemblages.

Reference site mixed conifer forests in Grand Canyon National Park are currently dominated by *P. ponderosa* with lesser contributions from *A. concolor*, *P. menziesii*, *Picea engelmannii* and *Populus tremuloides* (Fig. 3A & 3B). The model-derived species abundances (shown in Fig. 3C) using all three trait values were strongly correlated ($R^2 = 0.99$, Table 2) with the observed abundances in the reference site (shown in Fig. 3B). The two-trait models that included bark thickness were each significantly correlated with observed abundances, but the model using leaf nitrogen and wood density was not significantly correlated with the observed abundances (Table 2). The bark-only model was the only one-trait model that yielded accurate abundances (Table 2), indicating that bark thickness was the most important trait for accurately reproducing the assemblage at this reference site.

Setting Trait-Based Objectives for the Future

To derive an assemblage of species that may be resilient to drought and frequent fire, bark thickness was maintained at the historical average of 3.5% (percentage of stem diameter), leaf nitrogen concentration was maintained at the historical average of 1.5%, and wood density was increased from historical levels to 0.50 mg/mm^3. This wood density value was selected because it was the intermediate value between the softwood conifers that currently dominate mixed conifer stands and the hardwood species and drought-tolerant *Pinus edulis* (Fig. 1). However, there were no solutions to this set of constraints because the system of linear equations was not consistent; in other words, no combination of species abundances could achieve this proposed set of traits. To obtain a set of solutions, a minor adjustment to leaf nitrogen was made by increasing it from 1.5 to 1.6%. The four species that had the highest abundances in the model output were, in the order of decreasing abundance, *P. menziesii*, *P. ponderosa*, *Q. gambelii*, and *Acer grandidentatum* (Fig. 4A). These four species were allocated the highest abundances by the model because the linear combination of those abundances and the species' trait values equaled the chosen trait constraints.

Three native species were added to the species pool to acknowledge the possibility that other species adapted to warmer environments may be more suited to future conditions. Using the same trait values to achieve a resilient future community as above, the six species that had the highest abundances in the model output were, in the order of decreasing abundance, *P. ponderosa*, *Q. gambelii*, *P. edulis*, *Juniperus deppeana*, *P. menziesii*, and *A. concolor* (Fig. 4C & 4D). These six species do not commonly coexist across large contemporary landscapes in the southwestern United States and in combination would represent a no-analog community.

Discussion

Strict reliance on historical reference conditions may limit our flexibility in restoring ecosystems because they do not acknowledge current and future environmental change

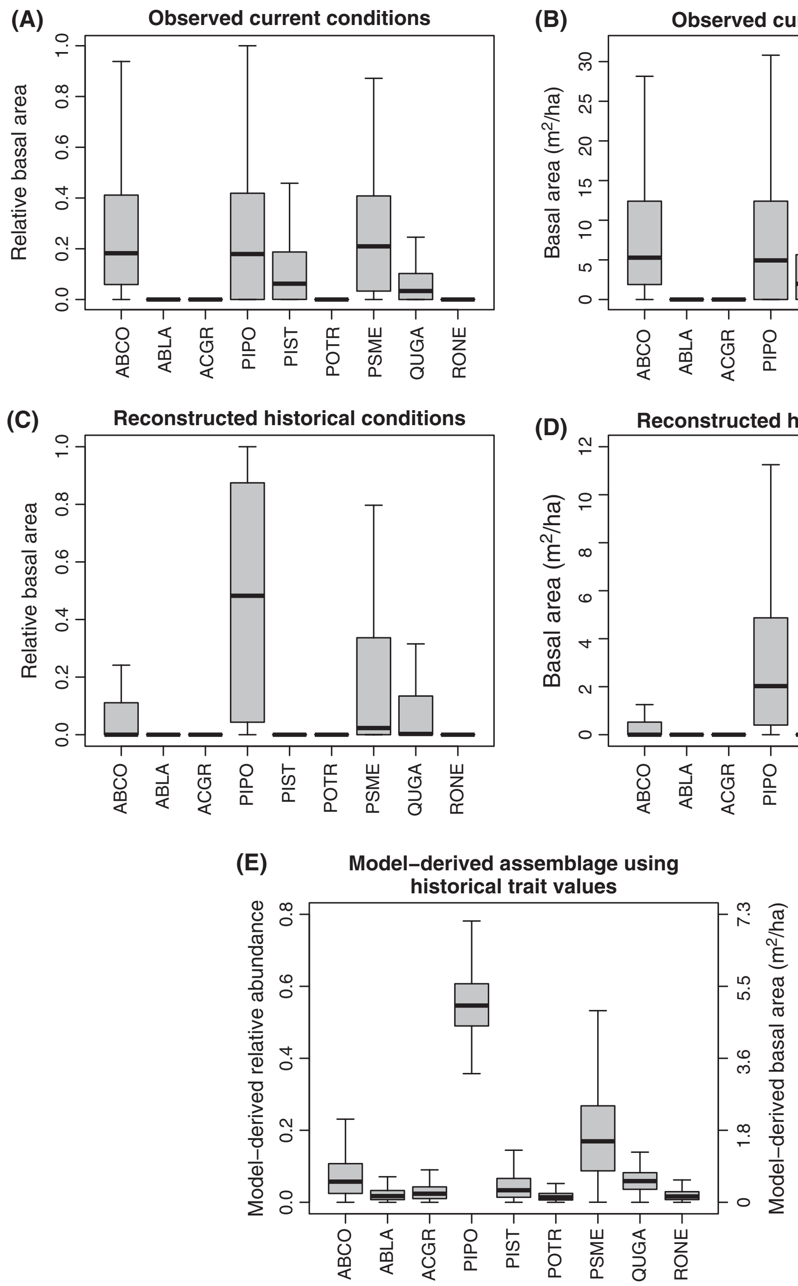

Figure 2. Current conditions of (A) relative abundance and (B) basal area (m^2/ha^1) for each species in the mixed conifer forest on the Black Mesa Ranger District, Arizona. Reconstructed (C) relative abundance and (D) basal area in the same forest in 1879 (Strahan et al. in review). (E) Trait-based model output of relative abundances and basal area using historical trait values. Relative abundances were rescaled to a total basal area of 9.1 m^2/ha. Four-letter species codes are found in Table 1.

(Harris et al. 2006; Choi et al. 2008; Higgs et al. 2014). In this article, we have shown that trait-based models can reliably reproduce historical and reference site species abundances, and that shifts in the dominance structure of extant communities may be required to maintain forest structure under a regime of increasing fire frequency and drought. Our results also indicate that no-analog assemblages of native species could be useful for maintaining forest structure into the future (Millar & Stephenson 2015).

Restoration goals based on either historical data or future projections are special cases of a more general class of desired future conditions that are derived from trait-based objectives (Fig. 5). Species occurred in historical ecosystems because they had the traits that endowed them with higher survival rates in those environmental conditions. Likewise, species that will succeed in the future will be those that express phenotypes that are the most adapted to future environmental conditions (Fig. 5). It has been predicted under a changing climate that large shifts

Table 2. Results of which trait combinations and dimensionalities yielded the most accurate species abundance distributions. NS, not significant. Accuracy was assessed by the R^2, the coefficient of determination, for the linear relationship between the observed species abundances and the model-derived species abundances. Significance of linear relationships: ***p < 0.001; **p < 0.01; *p < 0.05.

		Type of Reference Conditions	
Number of Traits	*Traits in the Model*	*Historical (Black Mesa)*	*Reference Site (Grand Canyon)*
3	Bark, wood density, leaf N	$R^2 = 0.96$***	$R^2 = 0.99$***
2	Bark, wood density	$R^2 = 0.93$***	$R^2 = 0.99$***
2	Bark, leaf N	$R^2 = 0.96$***	$R^2 = 0.96$**
2	Wood density, leaf N	$R^2 = 0.70$**	$R^2 = 0.71$ *NS*
1	Bark only	$R^2 = 0.27$ *NS*	$R^2 = 0.95$**
1	Wood density only	$R^2 = 0.51$*	$R^2 = 0.59$ *NS*
1	Leaf N only	$R^2 = 0.27$ *NS*	$R^2 = 0.23$ *NS*

in forest structure, species relative abundances (Tarancón et al. 2014), and species' environmental optimums (Laughlin et al. 2011*a*) will occur in montane forests of western North America. Incorporating these predictions into planning may enhance restoration success. In the case of western montane forests, simultaneously reducing fuel loads and managing for species with traits that promote fire and drought tolerance may be an effective restoration strategy (Churchill et al. 2013; Halofsky et al. 2014; Duveneck & Scheller 2015).

The answer to our first research question is "yes": trait-based models can accurately reproduce historical and reference site assemblages when their trait distributions are known. This result is important because it is a necessary condition for the application of such models to derive assemblages under less certain future conditions. Moreover, to achieve the best results more than one trait will often be required to select the appropriate assemblage of species. Managing for appropriate species will depend on an adequate number of traits for two reasons. Mathematically, it is easier to discriminate between species in higher trait dimensions. Ecologically, independent traits provide unique information about how a species functions, so more information about adaptations enhances our ability to select the best species (Laughlin 2014*b*). In mixed conifer forests, bark thickness was an important trait because it separated species according to fire resistance strategies. However, wood density was also important, especially under future conditions, so more than one trait was often required to select a range of species to simultaneously promote both fire and drought tolerance. The additional use of moderate leaf nitrogen concentrations further constrained the set of solutions to derive a drought tolerant assemblage. When the species pool is large, using multiple traits will be even more important (Sonnier et al. 2010), although it is still not certain what ratio of traits to species is required to optimize model accuracy.

We also asked how the species abundance distributions change when traits were selected to enhance resilience to drought and fire, and three important implications emerged. First, trait values must be logically consistent with the range of traits in the species pool. Our first choice of trait values was not possible because those constraints produced an inconsistent system of linear equations. In other words, there were no solutions and we could not derive any predicted species abundances. It is important to consider the range of multidimensional trait combinations that exist in the species pool when setting trait-based objectives. Second, adjustments to the relative dominance structure of the current species pool could meet the selected trait values. Specifically, by increasing the relative abundances of *Pseudotsuga menziesii*, *Quercus gambelii*, and *Acer grandidentatum*, we could achieve an assemblage with both relatively thick bark and dense wood. Third, no-analog assemblages of native species that do not readily coexist in contemporary landscapes would satisfy future trait-based objectives. Two native species, *Juniperus deppeana* and *Pinus edulis*, which currently occur at lower elevations that are warmer and drier, could be introduced to these forests to increase diversity and enhance community-level drought tolerance. *Juniperus deppeana* can resprout following fire, which confers long-term fire resilience if fire intervals are not too short. However, *P. edulis* is fire intolerant despite having relatively thick bark. This demonstrates that although these species may provide resilience to drought, not every species will also be tolerant to disturbances such as fire. Achieving multifunctionality is an important challenge and restoration practitioners will need to be aware of the tradeoffs that occur when trying to meet multiple restoration objectives. Careful selection of species using expert knowledge will still be needed to select species in restoration because functional traits do not always perfectly describe the ecological niches of species.

Novel assemblages composed of species that are not currently associated with one another may become increasingly common in response to rapid global change (Hobbs et al. 2009). By expanding the species pool, we detected other native species that had thick bark, dense wood, and moderate leaf nitrogen concentration to satisfy the traits that were predicted to confer maximum survival under more frequent fires and droughts. A combination of six species met the trait-based objectives: *Pinus ponderosa*, *Q. gambelii*, *P. edulis*, *J. deppeana*, *P. menziesii*, and *Abies concolor* (Figs. 1 and 4B). These species rarely occur together in close proximity at present, except perhaps along short and steep gradients from shaded canyons to rocky hillslopes. This combination of species may represent a no-analog community for the southwestern United States. We deliberately restricted our species pool to native species (Williams & Dumroese 2013), but recognize that there may be circumstances

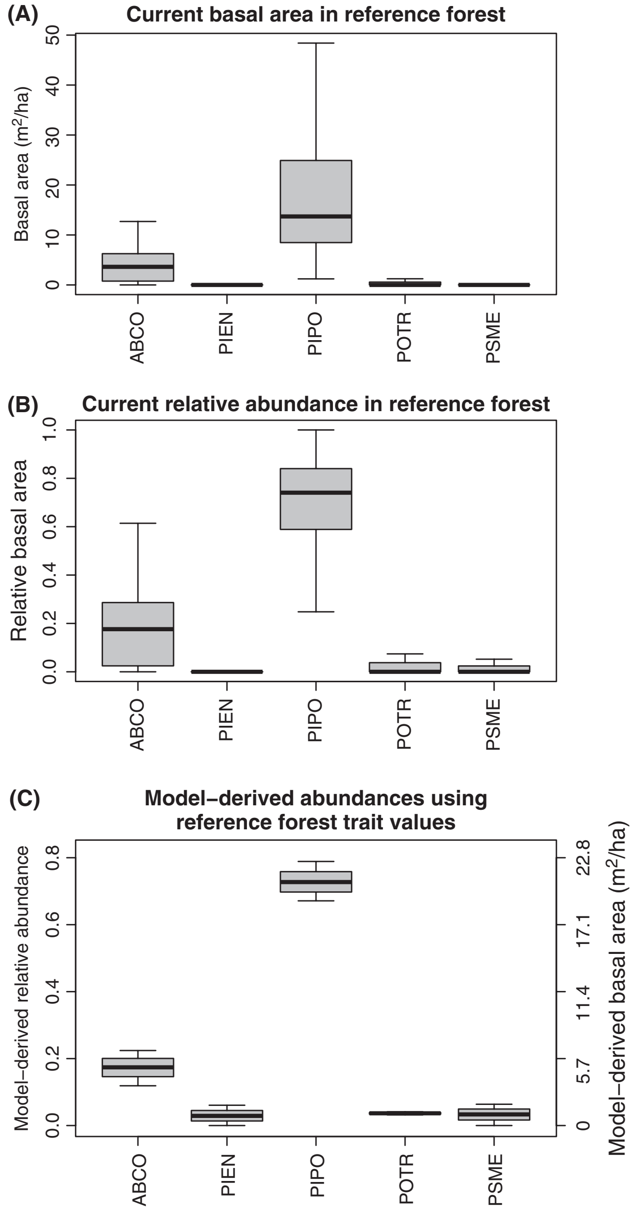

Figure 3. (A) Observed basal area and (B) observed relative abundances of species in the reference mixed conifer forest in Grand Canyon National Park, Arizona, U.S.A. (C) Trait-based model-derived relative abundances using three functional traits. Relative abundances are scaled on the right axis to a total forest basal area of 28.5 m^2/ha. Four-letter species codes are found in Table 1.

in other ecosystems where non-native species could be beneficial to maintain specific ecosystem processes (Ostertag et al. 2015).

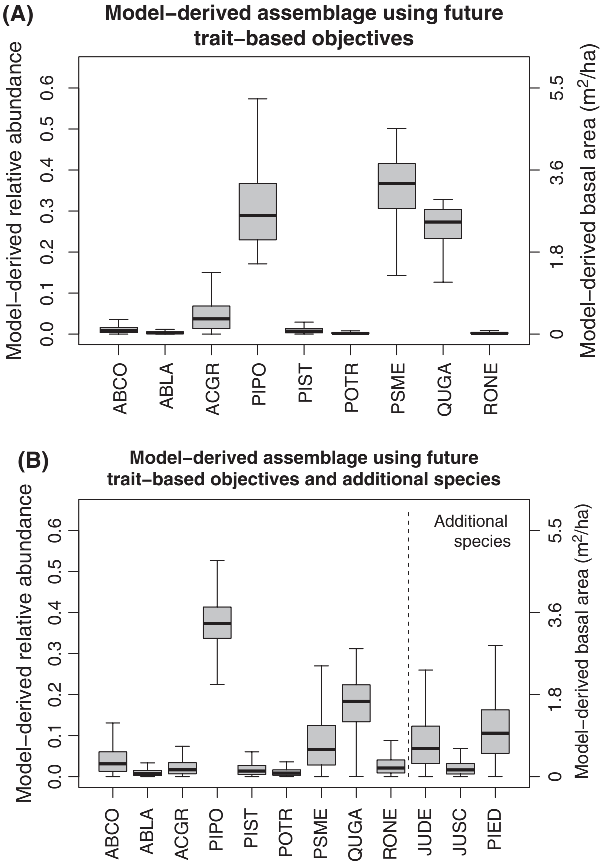

Figure 4. (A) Trait-based model output of relative abundances using future trait-based objectives. (B) Trait-based model output of relative abundances using future trait-based objectives and three additional native species. In both panels, the same results are scaled on the right axis to a total forest basal area of 9.1 m^2/ha. Four-letter species codes are found in Table 1.

The trait-based approach illustrated here yields a species abundance distribution, but an important question remains: how do you design prescriptive treatments to achieve these objectives on the ground? Restoration prescriptions that use undecomposed evidence of historical forest structure in southwestern forests are objective, empirical, and site-specific strategies for determining which trees to keep in a restoration thinning treatment (Tuten et al. 2015). In monospecific *P. ponderosa* forests, canopy composition is much less important than structural elements such as tree density and spatial arrangement. However, restoration in most other ecosystems requires some consideration of abundances for a diversity of species (Funk et al. 2008). If the restoration project is starting from a denuded site, then the results illustrated in Figures 2–4 provide a description of the relative abundances of each species that can be used to create diverse seed mixes or planting designs (Pywell et al. 2002; Bakker & Wilson 2004). However, the strategy will be much different for preventative and proactive restoration treatments in forest stands. If the treatment is to be implemented on an existing forest, then the prescription needs to reduce the importance of undesirable species and increase the importance of desirable species while simultaneously meeting structural objectives (Churchill et al. 2013). The output of the trait-based model is a relative abundance distribution that sums to one because they represent probabilities. Therefore, in the case of forests, one of the first decisions is to determine the targeted total basal area. If, for example, you desire to restore forest structure and composition by thinning the forest from 31.6 to 9.1 m^2/ha (Huffman et al. 2015), then you can multiply the model-based

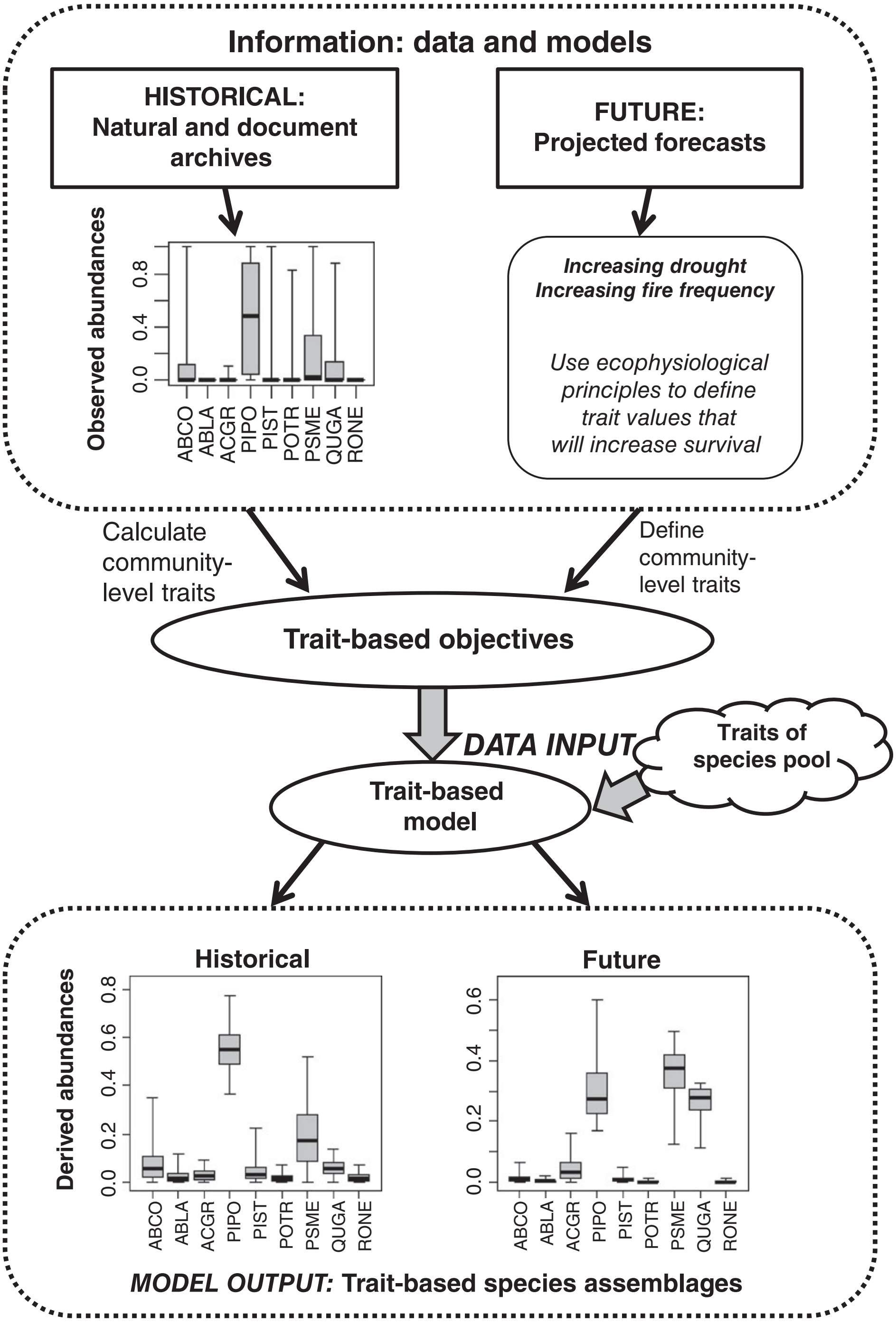

Figure 5. Ecological restoration that is based on either historical or future conditions is both special cases of a more general class of desired future conditions that are derived from trait-based objectives. Historical data or forecasting models can be used to set trait-based objectives (i.e. average trait values). For example, historical forest structure can be used to define which traits enhanced survival historically. Restoring ecosystems that are resilient to future changes can be accomplished using this same general approach: ecophysiological principles can be applied to select which trait combinations will promote fitness in the new conditions. Four-letter species codes are found in Table 1.

relative abundances by 9.1 to express the relative abundances as basal area per species (see Figs. 2E, 3C & 4B).

Spatial scale is also important to consider. The models use stand-level average trait values as input; therefore, the output must also be interpreted as a stand-level average. However, stand-level averages do not directly reflect species abundances at the forest patch scale (e.g. 0.1 ha) because of the large natural range of variability in species composition among patches in mixed species forests. In other words, a species that is uncommon at the landscape scale may dominate a small patch of forest. A common goal for restored forests is high structural and compositional heterogeneity (Peterson & Anderson 2009), and compositional heterogeneity can be important for achieving multifunctionality at a landscape scale. The trait-based prescription is useful for determining which species should dominate at a landscape scale, but fine-scale patches can still be dominated by less common species while still meeting the overall landscape-scale objectives. For example, *Populus tremuloides* was not one of the five dominant species that were predicted to dominate future mixed conifer forests (Fig. 4), but retaining or enhancing patches of *P. tremuloides* within the larger landscape would promote compositional heterogeneity and improve wildlife habitat. Alternatively, practitioners can interpret the derived relative abundances illustrated in Fig. 4B as the relative area in the landscape that is occupied by each species: *P. ponderosa* will occupy 40% of the landscape, *Q. gambelii* will occupy 20% of the landscape, and *P. tremuloides* will occupy less than 5%. Land managers will also need to balance prescriptions to achieve other restoration goals, such as habitat provisioning and pest management, which were not directly included as objectives in the model used here. Importantly, rare or less common species, such as *P. tremuloides*, with different trait combinations may be important for achieving these objectives. In these cases, the model output should be used as a general guide to define ranges of species abundances that satisfy the stated goals, but flexibility in managing species abundances will be important for achieving multiple management objectives simultaneously.

This model is a statistical translation of environmental filtering (Keddy 1992), and here we focused on the filtering effects of climate and fire frequency. However, we acknowledge that this model does not incorporate other known drivers of community assembly, such as species interactions and dispersal limitation (Fukami 2015). Indeed, species that are not currently present at a site, and are therefore dispersal limited, will need to be introduced through seed addition or direct planting. In the example presented here, *P. edulis* and *J. deppeana* do not currently occur in mixed conifer forests in Arizona, so these species may need to be introduced from off-site. Most restoration prescriptions to reduce fuels and restore historical forest structure in the western United States do not include seeding or planting seedlings of other tree species (Fulé et al. 2012; Churchill et al. 2013). However, species are and have been predicted to shift their distributions into higher elevations in the future (Lenoir et al. 2008; Laughlin et al. 2011*a*). This restoration activity would assist the migration of these species (Vitt et al. 2010; Williams & Dumroese 2013; Duveneck & Scheller 2015; Grady et al. 2015) in order to construct resilient communities to maintain forest cover and forest ecosystem services (Millar & Stephenson 2015). Introducing species from off-site would be the largest departure from current vegetation management practices and will likely cause the most discussion and debate among the land managers that oversee the restoration of these forests. Many of the current federal U.S. policies, such as the USDA Forest Service's Reforestation Policy FSM 2472.03, restrict the use of offsite species in restoration programs. Revisions and updates to such policies are needed to permit scientists and land managers to experiment with assisted migration to maintain forest structure and service provision under rapid environmental change (Williams & Dumroese 2013; Duveneck & Scheller 2015; Grady et al. 2015).

The approach used here did not explicitly incorporate trait plasticity and intraspecific variation, which will likely affect how species respond to global change (Jung et al. 2014). In our study, interspecific variation was high in leaf nitrogen (93%) and wood density (77%), but it accounted for only 46% of the variation in bark thickness. This rather high intraspecific variation in bark thickness will affect how individuals survive under changing fire frequencies and these individual-level responses will affect the persistence of populations over time. Focusing on species-level trait means will often be the most practical approach for restoration planning given the current constraints on data availability. However, incorporating intraspecific trait variation may be necessary when all traits exhibit strong environmentally induced plasticity, or when multiple trait values per trait are chosen as constraints to achieve high functional diversity (Laughlin 2014*a*).

How many traits are required to achieve high model accuracy in diverse ecosystems? There are not enough studies to rigorously answer this question, but it was recently shown that models with four to eight traits measured from multiple plant organs performed well across a range of ecosystems (Laughlin 2014*b*). After choosing the list of traits, how do you select the appropriate trait values to set restoration objectives? Although much deeper fundamental understanding of traits is required to choose exact trait values for any given situation, we recommend two approaches to improve this understanding. First, trait values can be selected according to empirical trait–environment relationships. For example, Frenette-Dussault et al. (2013) used empirical relationships between traits and an aridity index to predict how optimum trait values might change under the more arid conditions of climate change scenarios, then used these trait values to predict future community composition. Given the increasing number of studies that are quantifying trait–environment relationships at biogeographic scales (Violle et al. 2014), this approach could be applied across a range of ecosystems. Second, our imperfect understanding of how traits confer survival along environmental gradients is an opportunity for restoration ecology. Using this framework, experiments can be designed to test which trait combinations yield desirable outcomes under varying environmental conditions (Laughlin 2014*a*).

Specifying desired future conditions in terms of trait-based objectives is a general, flexible, and theory-based approach to restoring resilient ecosystems at a time of rapid global change. Trait-based models are a new tool for selecting phenotypes for restoration, but project success will still rely on an understanding of which trait values confer optimum fitness. There is an urgent need to deepen our understanding of which multidimensional trait combinations promote survival under a range of environmental conditions to enhance restoration success.

Acknowledgments

This research was supported by grants from the Royal Society of New Zealand Marsden Fund (UOW1201) and the USDA Forest Service.

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Coordinating Editor: Elise Gornish

Received: 2 November, 2015; First decision: 7 December, 2015; Revised: 4 January, 2016; Accepted: 4 January, 2016