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Review

Restoration ecology through the lens of coexistence theory

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Advances in restoration ecology are needed to guide ecological restoration in a variable and changing world. Coexistence theory provides a framework for how variability in environmental conditions and species interactions affects species success. Here, we conceptually link coexistence theory and restoration ecology. First, including low-density growth rates (LDGRs), a classic metric of coexistence, can improve abundance-based restoration goals, because abundances are sensitive to initial treatments and ongoing variability. Second, growth-rate partitioning, developed to identify coexistence mechanisms, can improve restoration practice by informing site selection and indicating necessary interventions (e.g., site amelioration or competitor removal). Finally, coexistence methods can improve restoration assessment, because initial growth rates indicate trajectories, average growth rates measure success, and growth partitioning highlights interventions needed in future.

Highlights

Ecological restoration success can depend on environmental conditions and species interactions, and initial trajectories may not reflect long-term outcomes.

Coexistence theory can help diagnose restoration outcomes early by assessing whether focal species can increase when at low density.

Partitioning the effect of the environment and competition on the low-density growth rates of focal species can help guide restoration efforts.

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Advancing restoration ecology with coexistence theory

As human influence over Earth's ecosystems increases and the amount of land available for traditional conservation dwindles, ecological restoration is gaining traction as an essential tool for biodiversity conservation [1]. Despite enthusiasm, the discipline of restoration ecology has struggled to become a predictive science capable of consistently improving restoration outcomes [2,3]. Over the history of restoration ecology, frameworks often assumed a monotonic recovery trajectory [4] or aimed for a 'carbon copy' of a past site [5], drawing largely from theories of ecological succession and community assembly [6]. At the same time, there is long-standing appreciation that restoration trajectories are often nonlinear [7,8] and outcomes can diverge due to conditions specific to the site and time period of project implementation [9,10]. Explicitly incorporating the role of variability in restoration frameworks is important to guide and assess efforts in a variable and changing world [6,9].

Within the broader field of ecology, Modern Coexistence Theory (hereafter 'coexistence theory') [11,12] has emerged as a framework to delineate the effect of environment and species interactions on whether and how species coexist, ultimately influencing community composition and diversity. Coexistence theory emphasizes the importance of spatial and temporal variability for community dynamics and provides analytical metrics to assess species success in relation to average and variable conditions. Coexistence theory has led to advances in numerous ecological subfields, such as community ecology [13–15], invasion biology [16,17], and trait-based ecology [18–20]. Here, we unify coexistence theory and restoration ecology to improve restoration goals, strategies, and assessment in an increasingly variable world (Figure 1). We concentrate on restoring biodiversity in herbaceous plant communities, because they are both a frequent focus of ecological restoration and a model system for developments in coexistence theory. However, our proposed approaches and principles are adaptable to other systems.

Coexistence theory

Coexistence theory is a framework for understanding and delineating common **coexistence mechanisms** (see Glossary) that maintain species coexistence [11]. These include classic niche partitioning as well as mechanisms that depend on environmental fluctuations. For example, coexistence theory has formalized that differences in the responses of species to environmental fluctuations can lead to temporal niche partitioning when species are able to 'store' through bad years, such as through seed banks or adult stages, a component of the commonly considered '**storage effect**' mechanism [12,21]. Similarly, temporal fluctuations in the abiotic environment or biotic interactions that lead to greater benefits in good years relative to bad years tend to promote species persistence [22–24]. A key contribution is that coexistence theory provides analytical tools to quantify both coexistence and the contributing role of environmental variability.

How can we assess whether a species will persist or go extinct over time? Persistence is commonly assessed via the **invasion criterion**, whereby species can coexist if they can each increase from low density while experiencing species interactions from the surrounding resident community [11,25]. The invasion criterion is evaluated by calculating the **low-density growth rate (LDGR)** of each focal species; a positive LDGR indicates that the focal species can persist, while a negative LDGR indicates a species cannot invade or, if present, is predicted to eventually go locally extinct [11,12]. As such, the LDGR reflects the joint influence of the intrinsic growth of the focal species in the absence of interactions, and the net impact of interactions with the resident community [12]. Long-term persistence is assessed by averaging the LDGR over periods that capture the full range of environmental variability that the species experiences [14]. The use of LDGR to assess coexistence is helpful but imperfect; as one example, it fails to capture scenarios in which the growth of a species depends on the presence of conspecifics (e.g., Allee effects) [12]. However, a focus on low-density growth generally reflects realistic field conditions, because most populations experience periods of rarity, especially within small restoration sites and/or diverse communities [26].

Does environmental variability help species persist or increase their risk of extinction? Coexistence theory addresses this question through **growth rate partitioning**, which accounts for the variation that occurs in time [27] or space [28]. Different partitionings have been developed to target different dynamics [22,27–30], but the common idea is that the LDGR is written as a sum of terms, each reflecting a mechanism by which variability alters coexistence. For example, in a partitioning developed by Ellner *et al.* [30], simulations are conducted in which variability is turned 'on' or 'off' for each component of the population model of a species (such as **intrinsic growth rate** and competition coefficients), singly and in combination, to assess the importance of variability in each parameter for the overall LDGR of the species [14,23]. This is especially helpful for restoration scenarios, because it isolates the effect of environmental variability on the intrinsic growth of a species versus the competition they experience. In a similar vein, simulations can be conducted to partition the consequence of different restoration strategies (such as modifying the environment versus the resident community) on the persistence and abundance of focal species (Box 1).

Goal setting

Restoration goals are often centered on achieving a desired community composition, and success has historically been assessed by comparing the abundance of target species in restored

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versus reference communities (Figure 1A [1]). However, after management, many species are still in flux, experiencing transient dynamics that are not indicative of long-term persistence [31,32] but rather representing successional stages [33] or restoration actions, such as planting or seeding [34]. These dynamics, paired with the short monitoring windows of many projects [3], limit our ability to link abundance patterns to long-term persistence dynamics in restoration [35].

Center goals on population viability as well as abundance

A coexistence theory approach can reconcile discrepancies between early indicators of success and long-term persistence for species [32,36]. The invasion criterion provides a clear restoration goal: a positive LDGR for each focal species, which puts the focus on long-term population persistence, while not precluding abundance-based metrics of biodiversity as additional gauges of restoration success (Table 1). This is most appropriate when the focal species has minimal effect on the resident community or when its effect is aligned with ancillary restoration goals, such as a competitive effect on an undesirable resident. For the restoration of species of conservation concern, single-population analyses can be sufficient [37,38]. This approach deviates from traditional coexistence theory in that the focus is on the LDGR of the species of interest rather than on the reciprocal LDGR of all species in the community, which greatly reduces data requirements. However, in the case of diverse communities, goals could delineate how many target species are expected to persist, with the persistence of each species quantified separately [39], so long as the primary concern is how the focal species interact with the existing resident community rather than with one another [19,40]. Finally, a coexistence theory approach can be used to develop goals for nondesired species, such as aiming for nondesirable species to have negative growth rates, leading to local elimination.

Include environmental variability within the restoration target

To date, the use of variability in setting goals has generally relied on quantifying historic ranges of variability within target ecosystems, a data-intensive exercise (e.g., [41]) that does not explicitly link community fluctuations to specific environmental variables. By contrast, a coexistence theory approach focuses on when and how the viability of a species shifts in variable environments [14,42,43], informing more quantifiable restoration goals (Table 1). For example, Usinowicz and Levine [44] mapped how LDGRs vary along a climate gradient and used this to forecast population viability under climate change, an approach that could be used to set realistic goals for current versus future climate conditions.

Implementation

Improving restoration actions are at the heart of restoration ecology, with science ideally helping to address such questions as: what sites have the most potential for restoration success [45]? Is passive restoration (i.e., simply ceasing the causes of degradation) sufficient, or is active restoration necessary [46]? If active restoration is needed, should restoration target the abiotic conditions of the site, its biotic community, or both [47]? To what degree are these outcomes influenced by temporal environmental variability [7,34]? While myriad considerations, social and ecological, inform restoration planning, coexistence theory may help predict outcomes in relation to spatiotemporal environmental variability and restoration strategies (Figure 1B).

Prioritize where and how to restore based on species–environment interactions

Environmental conditions and biotic interactions vary across landscapes [48], and the same action can have different outcomes at different locations. A demographic approach informed by coexistence theory can assist in anticipating varied outcomes. Specifically, fitting models between focal species and the resident community under relevant environmental conditions can be used to forecast the LDGR and abundance of focal species under different abiotic and biotic scenarios

Glossary

Coexistence mechanisms: mechanisms that promote the LDGR of species within a community. This includes the storage effect.

Equilibrium abundance: expected, or average, abundance that one or more species would attain in a given environment. In coexistence theory, the equilibrium of the 'resident community' (all species in the community when the focal species is absent) is used to calculate the LDGR of the focal species. When communities fluctuate, equilibria vary through time or space and their distribution is important. In many fluctuating communities, equilibria are difficult to calculate due to the number of species, their interactions, and the complexity of dynamics, such as lagged effects. In these cases, samples of undisturbed communities may provide the best available estimate of equilibrium.

Growth rate partitioning: technique to identify components of species dynamics that sum up to the LDGR. Different forms of partitioning focus on different mechanisms. Here, we focus on partitioning that separates the LDGR in the absence of fluctuations from fluctuation-dependent shifts in the LDGR that manifest through intrinsic growth rates and species interactions.

Hysteresis: historical conditions create alternate outcomes that are stable, such as when the numerically dominant species in a community depends on the historical relative abundances of species.

Intrinsic growth rate: multiplicative rate of increase (population in year 2/ population in year 1) of a species when it is at low density and other species are not present.

Invasion criterion: condition that is met when every species in a community has a positive LDGR. In such cases, the species are predicted to coexist stably.

Low-density growth rate (LDGR): also termed the 'invasion growth rate'; population growth rate when a species is at low density and other species in the community are at their non-zero equilibrium. In fluctuating environments, it is averaged through time (over the distribution of fluctuations). When the LDGR of a species is positive, it is buffered from extinction because its population is expected to grow when at low density.

(Box 1). When focal species have a high LDGR under conditions reflective of a site, especially in combination with the potential to attain a large population, the site may be conducive to restoration success. Alternatively, if focal species have low or negative LDGRs under current conditions, simulations that modify the environment or resident community can be used to determine whether additional restoration actions could produce success (Box 1).

A demographic approach to restoration planning, in which a population model is combined with field data to project population outcomes, recently gained traction [45]. For example, Larios *et al.* [49] assessed how the likelihood of success for the native perennial grass *Stipa pulchra* (purple needle grass) changed across a gradient of nitrogen (N) deposition in California (Figure 2). N deposition is spatially variable (Figure 2A) and the growth and survival of *S. pulchra* and its primary non-native competitor, the annual grass *Avena fatua* (wild oats) (Figure 2B), vary greatly in relation to N and the competitive environment (Figure 2C,D). As a consequence, the authors found that *S. pulchra* was always successful at low N (Figure 2E,F) but was outcompeted by *A. fatua* at high N (Figure 2I,J), such that sites with high levels of N deposition should be deprioritized for restoration. Modeling abundance as well as LDGRs provided further insight: even though the LDGRs of *S. pulchra* were always low but positive, its expected **equilibrium abundance** relative to *A. fatua* decreased substantially with N addition (Figure 2E–J).

Storage effect: occurs when species experience mostly interspecific competition in environmental conditions in which they do poorly, and mainly intraspecific competition in conditions in which they do well. The covariance between the environment and competition allows populations at low density to grow in good environments because they experience low competition.

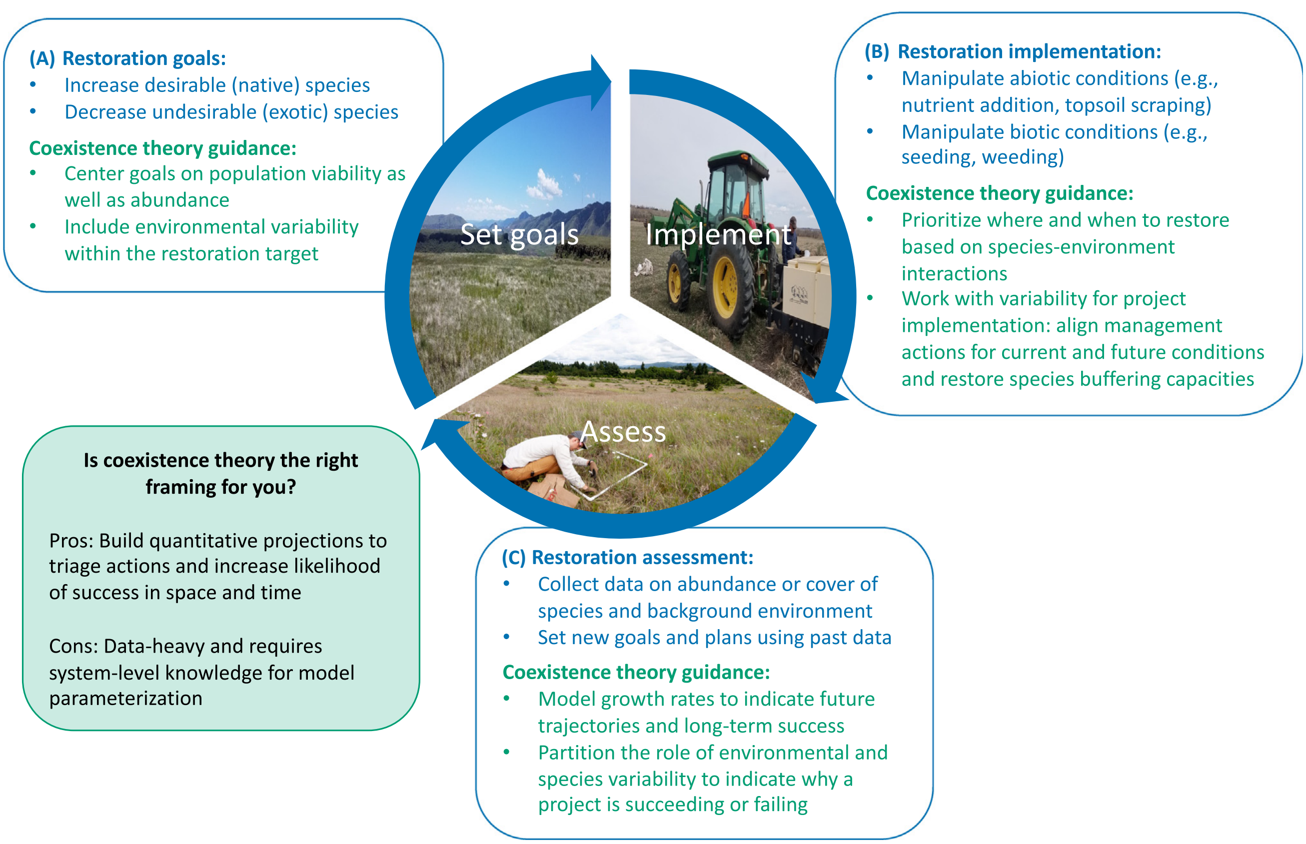

Figure 1. Integrating coexistence theory into restoration ecology provides new tools to improve (A) setting restoration goals, (B) implementing restoration projects, and (C) assessing restoration success. Photos by N. Shackelford (A), L. Hallett (B), and Lily's Lens Photography (C).

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Box 1. Applying coexistence models to restoration scenarios

Coexistence models can be used to assess restoration success and make predictions about the outcomes of different restoration interventions. To be realistic, these models should describe the performance of a species over the range of environmental and competitive conditions it experiences (Figure IA,B). Site descriptions, including long-term climate records, soil maps, vegetation monitoring, natural history, and practitioner experience, can inform the range of conditions to include. A common approach is to fit a population model for the focal species under each representative environmental condition. This can be done both experimentally, by creating different environmental conditions and manipulating the densities of focal and resident species within them, and observationally, using monitoring data that capture a sufficient range of environmental and competitive scenarios. The yield of the focal species (e.g., biomass or fecundity) should be measured, as well as the abundance of the resident community. While the functional form of the population model may vary by system, these measures allow both the intrinsic growth rate of the focal species' (λ) and the effect of neighboring species (α) to be estimated for each environmental condition (Figure IC,D).

Once models are fit, the LDGR can be calculated through a simulation in which the focal species is introduced at low density to the existing resident community. In variable environments, long-term persistence can be predicted by calculating the average LDGR using parameters associated with each environmental condition, weighted by the frequency with which they occur. Similarly, the role of variability on average LDGR can be partitioned through simulations in which each parameter (e.g., λ, α) either varies with the environment or is held constant, singly and in combination (Figure IE). The role of different restoration interventions can likewise be simulated by either altering the distribution of environmental conditions used to calculate the average LDGR of the focal species (to reflect restoration actions that ameliorate site conditions) or by reducing the density of the resident community before calculating average LDGR (to reflect restoration actions that reduce competitors) (Figure IE). Finally, the long-term abundance of the focal species can be predicted through simulations in which growth at each time step is calculated using parameters associated with either observed or targeted environmental conditions. While a benefit of the LDGR is that it only requires modeling the focal species, abundance predictions are improved by reciprocally modeling the residents, especially when the focal species substantially affects them.

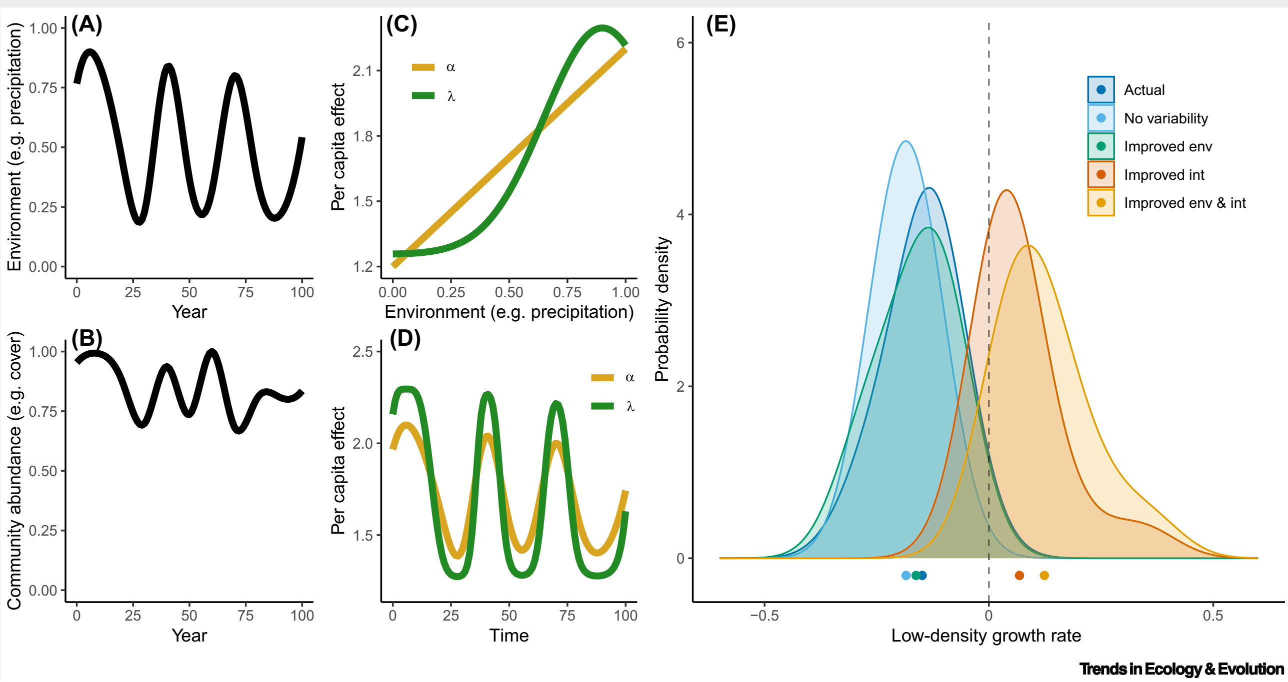

Figure I. Predicting the consequences of restoration using a coexistence theory approach requires data quantifying (A) environmental variability and (B) equilibrium abundance of the resident community across years. Experimental or sampling data for the focal species allow calculation of (C) the direct effect of environmental conditions on the intrinsic growth (λ) of the species and indirect effect via competition (α). In this example, the resident community has the largest competitive impact in wet environments that also provide ideal growth conditions for the focal species. Consequently, the positive (λ) and negative (α) effects of the environmental variability mirror each other over time (D). These measurements are used to generate restoration predictions: (E) the distribution and the mean (points below distribution) of the low-density growth rate (LDGR) of the focal species without intervention ('Actual'; dark blue) and if environmental variability were removed ('no variability'; light blue), as well as simulated restoration actions that ameliorate the environment (here, by shifting the environment up 0.25 units to reflect irrigation; 'Improved env'; green), reduce competition (here, by removing 40% of the resident abundance, to reflect competitor management; 'Improved int'; red), or both ('Improved env int'; orange). In this example, ameliorating the environment alone provides no benefit: removing competitors is necessary for focal species persistence (details and alternative scenarios provided in S1 in the supplemental information online).

Table 1. Information required to apply coexistence theory in diverse restoration situations

Restoration goal	Information	Situation	Refs
Increase plant cover/biomass	Species-level variation in cover/biomass under different environmental conditions from bare patches to full cover	After mining events, constructing roads or other actions that entirely remove plant cover	[90,91]
Increase keystone species	Variation in keystone species performance across environmental conditions when grown alone versus when grown in competition with itself or with all other species	After loss of keystone species due to fire, flooding or other strong perturbation, or following introduction of a keystone species that has dramatically altered the ecosystem	[92,93]
Remove undesired of invasive species	Variation in invasive species performance across environmental conditions when grown alone versus when grown in competition with itself or with all other species	After an invasion event due to a new introduction or to changes in environmental conditions that indirectly allows an invasion, such as human disturbance or nitrogen deposition	[34,94]
Increase functional biodiversity	Variation in the performance of each functional group separately across environmental conditions. Differences in performance should distinguish the effect of environmental conditions from the effect of the density of other functional groups (including itself)	After a perturbation event that has particularly affected some functional groups. These perturbations can include pest outbreak, nutrient deposition, or extreme events, such as heat waves	[95,96]
Increase species richness	The most data-demanding restoration goal because it should account for the performance of each individual species across independent axes of environmental conditions and species densities	Restoration goals aiming to increase or mitigate negative effects of global change drivers on biodiversity, such as climate change, invasive species, or land use intensity	[97,98]

Once candidate sites are identified, the LDGRs and predicted abundances of focal species under different scenarios can also indicate reasons for restoration success or failure. For example, the invasion criterion has been used within a context of biological invasions to understand why late-phenology invaders sometimes have a competitive advantage over earlier natives [50]. Similarly, a demographic approach can parse which life stages and management actions are most relevant for long-term persistence. For example, Bowles *et al.* [51] identified that demographic processes of seedling growth and survivorship were critical to the long-term population growth of *Asclepias meadii* (Mead's milkweed) and were enhanced when sites were annually burned. In the case of Larios *et al.* [49], a **hysteresis** effect was observed at intermediate levels of N, such that *S. pulchra* could exclude *A. fatua* when the former was already established but not when it was initially rare (Figure 2G,H). This suggests that restoration should only be attempted at these sites if the actions could feasibly produce *S. pulchra* dominance of desirable species (e.g., via removing annual grasses and planting adult *S. pulchra* plugs).

Work with variability for project implementation

Align management actions for current and future conditions

Environmental variability contributes to fluctuations in species abundance [11] and restoration outcomes [3]. Previous work on the effects of variability in restoration practice has focused on variability during the year or years of project implementation [10,52]. These so-called 'year effects' can have strong and persistent impacts on community assembly, with consequences for the success of the populations of target species, whether naturally regenerating [53] or seeded for restoration [54–56]. This work has also leaned on the complementary understanding that environmental variability may contribute to variability in species interactions [57], to identify that management outcomes may be contingent on interactions between abiotic conditions and the presence or arrival timing of other species, including invasive species [55,56,58]. For example, MacDougall *et al.* [59] found seeding in a wet year resulted in lower-than-expected native establishment if the resident non-native competitors were not also simultaneously removed, but native establishment was not impacted by non-native species in a dry year.

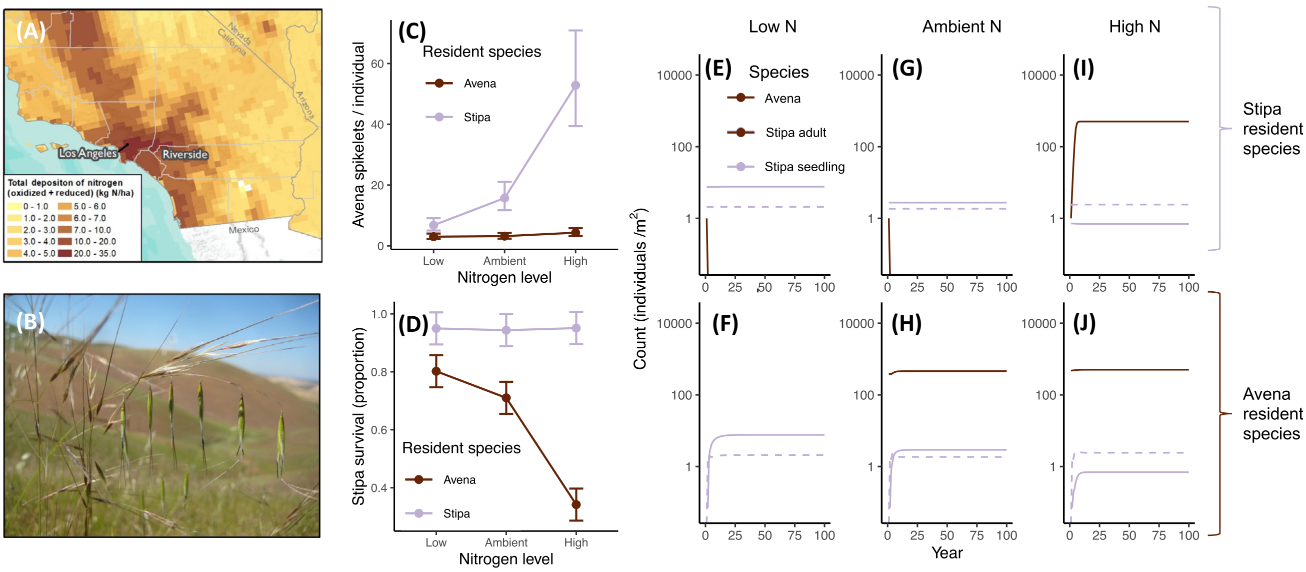

Figure 2. Applying coexistence theory to site selection for restoration of the native perennial grass *Stipa pulchra* (purple needle grass) in California. (A) Nitrogen (N) deposition levels for 2011 vary across southern California. (B) *S. pulchra* with its non-native annual grass competitor *Avena fatua* (wild oats) in the background. (C) Number of *A. fatua* spikelets produced on a focal individual when in competition with itself (an *A. fatua*-resident community) or in competition with a *S. pulchra*-resident community along an N deposition gradient. *A. fatua* per-capita seed production is particularly high when it is at low density in a *S. pulchra* community under high N. (D) The proportion of *S. pulchra* individuals that survived when in competition with itself (a *S. pulchra*-resident community) or in competition with an *A. fatua*-resident community along an N deposition gradient. *S. pulchra* survival is particularly low when it is in competition with an *A. fatua*-resident community under high N. (E–J) Simulations of population trajectories when *A. fatua* is introduced at low density to a *S. pulchra*-resident community (E,G,I) and when *S. pulchra* is introduced at low density to an *A. fatua*-resident community (F,H,J) at different levels of N. At low N, *A. fatua* cannot invade *S. pulchra* (E) but *S. pulchra* can invade *A. fatua* (F). At intermediate (ambient) levels of N, *A. fatua* can persist if established but cannot invade *S. pulchra* (G,H). At high N, *A. fatua* can always invade and reach high abundances, whereas *S. pulchra* abundances are very low when in competition with *A. fatua* (I,J). This suggests that sites with low N are good candidates for *S. pulchra* restoration, that care should be taken when restoring sites with ambient N to ensure a well-established resident *S. pulchra* population, and that restoration will likely be unsuccessful at sites with high N. Map created by Tracy Popiel with data from Environmental Protection Agency's CMAQ: The Community Multiscale Air Quality, Photo by L. Larios, data from [49].

A coexistence theory approach can help meet the challenge of identifying the strength and cause of year effects on restoration outcomes [52,60]. First, applying the invasion criterion to different monitoring years or experimental conditions can indicate the strength of year effects; a strong relationship between yearly fluctuations and LDGR would suggesting timing restoration for favorable conditions, if they can be anticipated, or repeating across multiple years if they cannot. Second, decomposing the average LDGR of focal species into the direct impacts of the environment, species interactions, and their covariance can indicate which component of the year effect to target. For example, Bakker *et al.* [54] found that wet years were directly beneficial for native species, but also increased competition from non-native species. If environmental effects on intrinsic growth are the more powerful component of this year effect, then native seed addition, especially in wet years, would likely be sufficient. By contrast, if increased competition is the more powerful component, removing non-native competitors in wet years would be essential (e.g., the scenario in Box 1).

Restore species buffering capacities

An often-implicit restoration goal is to achieve a resilient community that can buffer and adapt to existing and future conditions [61]. For many communities, the capacity to respond to changing environmental conditions is stored in seed banks or other forms of propagule banks that provide temporal safeguarding [62]. Within restoration, seed banks have often been used to gauge the type of interventions needed; for example, passive restoration may be possible in scenarios with high native seed bank diversity [63]. However, with rare exceptions [64], restoring the seed bank is not typically a focus of management actions per se.

Coexistence theory can provide some guidance on restoring buffering capacity within a system. For example, the storage effect, whereby a good year can outweigh or buffer a species through bad years [11,21], can be used to prioritize species mixes that coexist temporally over a wider range of environmental conditions [65], with a focus on restoring a seed bank as well as immediate establishment [66]. In addition to the storage effect, a second dominant coping mechanism for seed-banking species is bet hedging, where long-term success is gained through limiting dormancy breaking with specific environmental cues [67]. Both concepts demonstrate that density-dependent models can predict optimal germination strategies [68] and influence restoration outcomes [34]. Species may operate along a continuum of these two strategies, and evaluating the LDGR of species may provide better insight into the long-term persistence of a species within a system and, thus, its buffering capacity.

Assessment

Monitoring and assessment are critical aspects of restoration [1,3]. Early assessment can assist the restoration process by diagnosing initial trajectories [69] and informing adaptive management actions [70], and ongoing assessment is essential to judge restoration success [71]. Assessment also informs future projects, helping to identify which interventions should be retained, discontinued, or modified in subsequent efforts [3]. Monitoring in a way that captures gradients in environmental or competitive conditions can be particularly useful for adaptive management [72,73], because it allows practitioners and researchers to test alternative hypotheses about the role of these forces for restoration success [69] (Figure 1C).

Model growth rates to predict future trajectories and long-term success

Given its focus on population dynamics, coexistence theory offers the potential to diagnose trajectories early [34] and across changing conditions [43,60,74]. The effects of restoration activity are often transitory [69], such that an initial comparison of restored and reference communities will be misleading. Aoyama *et al.* [34] observed this effect in the construction and seeding of California vernal pools to support the rare plant *Lasthenia conjugens* (Contra Costa goldfields). Constructed and reference pools had similar *L. conjugens* abundances for nearly 10 years (Figure 3A–C), but negative LDGRs in the constructed pools early in the timeseries predicted their (ultimately observed) decline, suggesting that the abundances of the restored populations were inflated by initial seed addition. Using a demographic approach to calculate LDGR and diagnose these trajectories early would allow practitioners time to adapt or augment management actions [32,75,76].

Partition the role of environmental and species variability to investigate why a project is succeeding or failing

Over the long-term, partitioning average LDGRs can help identify the factors governing restoration success or failure. In the case of Aoyama *et al.*, growth rate partitioning revealed a strong negative effect of environmental variability on the intrinsic growth (λ) of *L. conjugens*, especially in constructed pools, but a positive effect of variability on competitive effects. This suggests that the constructed pools provided especially poor habitat in 'bad' years relative to the reference, but that removing competitors, especially in 'good' years, may substantially offset this effect (Figure 3D,E). Further partitioning indicated that pool depth was an important mediator; average LDGR was negative in deep and shallow pools, but positive in medium-depth pools (Figure 3F–H). This provides a target for future restoration efforts that is not immediately obvious from abundance patterns. Periodic inundation in deep pools likely led to an infrequent but markedly negative effect of 'bad' years on *L. conjugens* LDGR, whereas competition with non-native annual grass likely drove negative

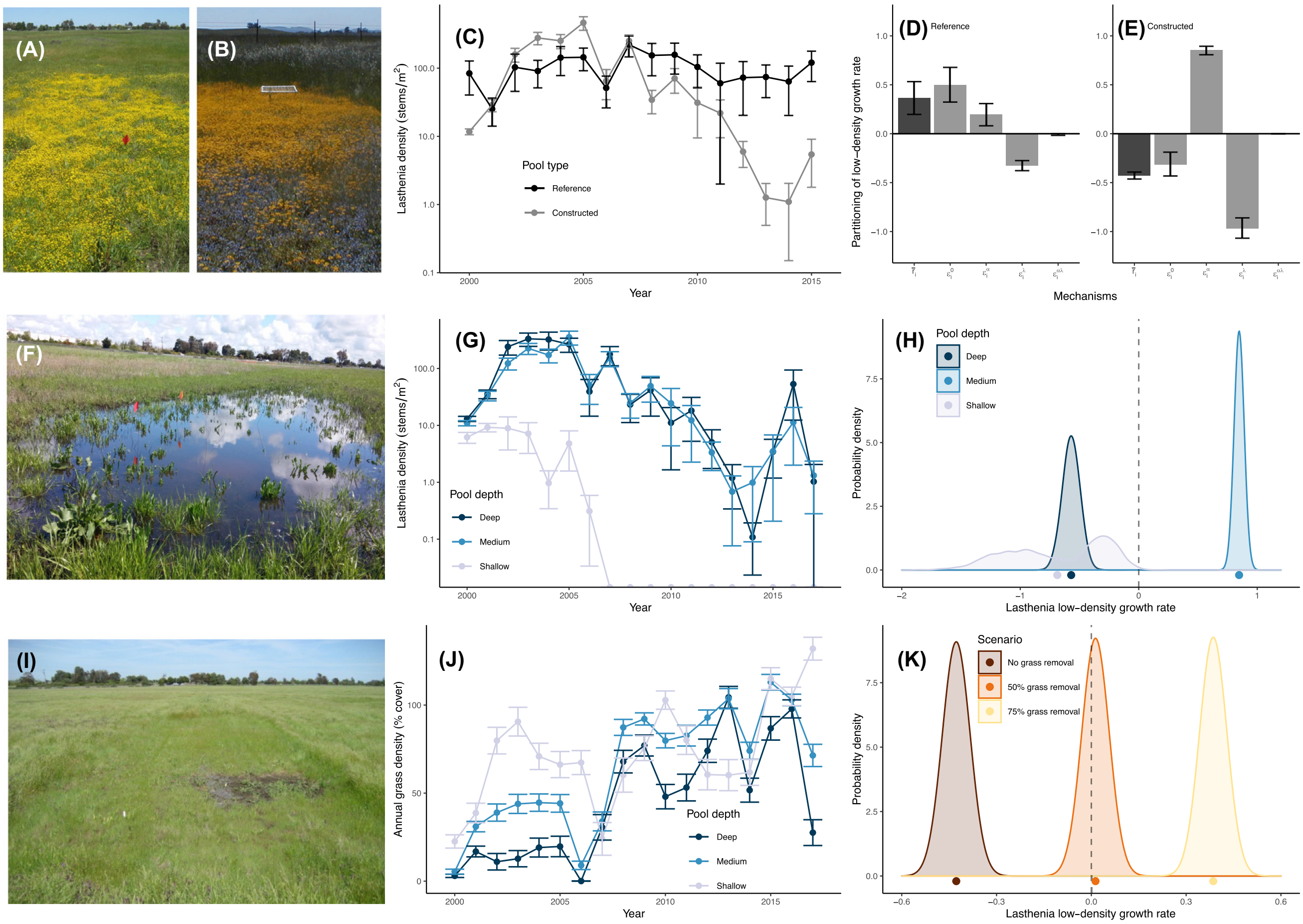

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Figure 3. Applying coexistence theory to assess and improve vernal pool restoration in California. (A) A reference vernal pool with a high abundance of the rare plant *Lasthenia conjugens*. (B) A restored, human-constructed pool shortly after restoration, also with a high abundance of *L. conjugens*. (C) The average trajectory of *L. conjugens* density in reference versus constructed pools over time. Abundances were similar for the first 10 years, after which those in the constructed pools declined. (D,E) Low-density growth rate (LDGR) partitioning for *L. conjugens* in the reference (D) versus constructed (E) pools. The reference pools had a positive average LDGR ($\bar{r}_i$), whereas the constructed pools had a negative average LDGR; in part, this was because growth under average conditions (ϵ_i^0) was positive in reference and negative in constructed pools. Environmental variability aided *L. conjugens* by providing a release from competition (ϵ_i^α), but hurt *L. conjugens* by negatively affecting its intrinsic growth rate (ϵ_i^λ). These effects were strongest in the constructed pools, contributing to the negative average LDGR. (F) Depth is an important environmental driver in vernal pools (compare the deep pool in the foreground and the shallow pool in the background). (G) *L. conjugens* density in constructed pools over time by pool depth. (H) The average LDGR of *L. conjugens* by pool type. *L. conjugens* populations were viable in the medium but not in shallow or deep pools. This indicates that medium depth should be the target for future restoration efforts. (I) Competition from non-native annual grasses is a strong driver of *L. conjugens* dynamics. (J) Non-native annual grass percentage cover in the constructed pools by depth; grass cover is higher in shallower pools. (K) The average LDGR of *L. conjugens* across constructed pools under different scenarios of non-native annual grass removal. A positive average LDGR when 50% or more grass cover is removed suggests that ongoing management, such as mowing annual grass, is an effective management option for existing pools. Adapted from [34]. Photos by A.F. (A,F,I) and Sharon Collinge (B).

LDGR in shallow pools. Simulating a 50–75% reduction in non-native grasses generated a positive LDGR for *L. conjugens* across the site, indicating that active management could sustain *L. conjugens* populations, even when restoration failed to achieve ideal pool depth (Figure 3I–K).

Extensions, limitations, and future directions

Bridging the science–practice divide is a general problem for restoration [3,6], and an acute one in the case of coexistence theory. Data requirements are a particular barrier, because these models require variation in both absolute and relative species densities in all relevant environmental conditions (Table 1). This information is not always available from monitoring data alone; for example, high-resource environments tend to have dense neighborhoods, making it difficult to estimate intrinsic growth with confidence. As such, a mixture of observational and experimental approaches is best. Furthermore, applying the models requires a relatively specialized knowledge of population modeling and, ultimately, the model outputs are only predictions; an iterative process between model development and restoration action is important for model validation. Ideally, this process would allow for model testing, such that less mechanistic and more easily generalized models could also be explored [77]. Identifying and uniting relevant collaborators is a nontrivial challenge [78], but an essential one to link these disciplines.

Species diversity poses a particular challenge to the application of coexistence theory. First, it compounds the data barrier; obtaining requisite data to apply this approach to all species in a community is unrealistic. One response is to restrict the application of coexistence theory to restoration that targets a small number of focal specie, such as high-importance native species or problematic invasives [34,49]. Another, non-mutually exclusive response is to reduce the dimensionality of the system by grouping species by functional [79] or phenomenological [57,80] characteristics. This may be particularly helpful when there is a diverse resident community. Second, coexistence theory assumes that, at any one time, there is only a single species growing from low density, but this may be incorrect in multispecies restoration. For example, including a particularly competitive species in a restoration seed mix may exclude additional restored diversity, as is evident in studies of restoration seed mixes [81–83]. Finally, higher-order interactions, in which the presence of a third species mediates the mode and strength of the interaction between two others [84], could enable or erode coexistence in ways that our approach may not readily make sense of biologically. Such complications may be particularly important when species in the restored community depend upon one another [85]. Future theoretical and empirical developments focused on multispecies interactions, including across trophic levels, are needed to expand the applicability of coexistence theory to restoration ecology, as well as to ecology writ large [86–89].

Concluding remarks

Coexistence theory provides a framework to understand the separate and interactive effects of the environment and species interactions on ecological communities. As we show here, coexistence theory can be applied in restoration ecology, an application that has long been called for [6] and may reciprocally advance coexistence theory (see Outstanding questions). Coexistence theory suggests that restoration goals should be based on the growth rates of species as well as their abundances, because the latter can be biased by initial treatments and sensitive to environmental variability. Second, coexistence theory provides a way to partition the effects of spatial and temporal variation in the environment and competition on the growth rates of focal species, helping practitioners to select sites and identify what types of intervention are effective. Third, coexistence theory provides a mechanistic way to assess restoration success, because initial growth rates can provide an early indication of trajectories and long-term average growth rates can indicate ultimate success. Integrating principles and tools from coexistence theory is an important step to making restoration ecology a predictive science in a variable world.

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Outstanding questions

How can practitioners and modelers best collaborate to effectively apply coexistence theory to restoration projects?

Can applications of coexistence theory to restoration advance our theoretical understanding of when and where environmental variability, species interactions, or their combined effect promote species persistence and coexistence?

What is the minimum amount of monitoring data necessary to apply a coexistence approach to different restoration goals?

Can a coexistence approach to restoration be generalized to more systems? Are less mechanistic models a way to do this?

How can a coexistence approach be best applied to multispecies restoration? Is the assumption that focal species have minimal competitive overlap suitable for most restoration projects?

Is it appropriate to group resident species by functional characteristics or growth strategy? Are there alternative approaches that do not require a priori assumptions about the system?

Are other interaction types, such as facilitation and higher-order interactions, central to restoration outcomes? If so, how can a coexistence approach be modified to account for them?

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Declaration of interests

No interests are declared.

Supplemental information

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