CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Year effects: Interannual variation as a driver of community assembly dynamics

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Abstract. Environmental conditions that vary from year to year can be strong drivers of ecological dynamics, including the composition of newly assembled communities. However, ecologists often chalk such dynamics up to "noise" in ecological experiments. Our lack of attention to such "year effects" hampers our understanding of contingencies in ecological assembly mechanisms and limits the generalizability of research findings. Here, we provide examples from published research demonstrating the importance of year effects during community assembly across study systems. We further quantify these year effects with two case studies—a grassland restoration experiment and a study of postfire conifer recruitment—finding that the effects of initiation year on community composition can dictate community as much, if not more, than the effects of experimental treatments or site. The evidence strongly suggests that year effects are pervasive and profound, and that year effects early in community assembly can drive strong and enduring divergence in community structure and function. Explicit attention to year effects in ecological research serves to illuminate basic ecological principles, allowing for better understanding of contingencies in ecology. These dynamics also have strong implications for applied ecological research, offering new insights into ecological restoration as well as future climate change.

Key words: community assembly; global change; precipitation; restoration; variation; year effects.

INTRODUCTION

Community assembly is a central process in both wild and managed ecosystems. It drives the nature of regeneration—after natural disturbances (e.g., floods, fires, tree falls), yearly in annual-dominated systems (Pitt and Heady 1978), following human land use (e.g., agriculture, Cramer et al. 2008; timber harvest, Belote et al. 2012), and during ecological restoration (Young et al. 2001, 2005, Brudvig 2011). Although the roles of

deterministic and spatially variable factors (including mean local climate, soils, propagule availability, and landscape topology) in shaping new communities have been studied in detail, much less attention has been given to the roles of factors varying from year to year (such as precipitation and temperature), hereafter known as *year effects*.

There is increasing evidence that year effects can generate considerable variability in community composition and other assembly outcomes. The most obvious source of interannual variation is weather, with strong year-to-year variability in rainfall, temperature, and associated parameters such as frost dates and drought. These conditions can drive important ecosystem dynamics, such as phenology (Forrest and James 2011) and episodic

recruitment (Brown and Wu 2005). Biotic factors can also vary from year to year (both in ways that are related to weather, as well as independent of it), potentially influencing the success of recruiting species. For example, populations of rodents often fluctuate between years (e.g., Getz and Hofmann 1999), which can impact the establishing plant community through postdispersal seed predation (Hulme and Kollmann 2005, Notman and Villegas 2005) or herbivory (Howe and Brown 1999, MacDougall and Wilson 2007, Howe 2008). These diverse factors influence the establishment, persistence, and abundance of species in the first year(s) of community development, thereby setting assembling communities on differing trajectories (Fig. 1).

There remains limited exploration, however, of how these environmental factors interact to drive the assembly of incipient communities, and how these translate into longer-term patterns of community composition. Interannual variation in assembly is rarely explored and, if anything, tends to be lumped as stochastic noise rather than specifically investigated (Johnson 2002). A review by Vaughn and Young (2010) estimated that only 5% of ecological field experiments initiated identical replicates of experiments in multiple years. However, a surprising three-fourths of the few year-replicated experiments found significantly different results based on the year of initiation.

Here, we explore what is known about the influence of year effects on assembling biotic systems. We review existing studies of the effects of interannual variation on community assembly and argue that year effects are both pervasive and important, yet currently undervalued in ecology. We also present two case studies uniquely comparing the magnitude of years effects to both treatment and site effects in manipulative field experiments. Finally, we highlight opportunities for new research that will enhance basic and applied ecological understanding and offer a window into the consequences of future climate change.

YEAR EFFECTS: THE EVIDENCE

A basic form of year effects is the observation of interannual variation in the emergence, establishment, or survival of target study species. In their 3-yr grassland restoration experiment, Bakker et al. (2003) observed strong interannual variation in the establishment and survival of native species, depending on the weather. They found that June rainfall increased establishment but decreased survivorship of a seeded native grass, likely because of increased establishment of a competitive nonnative grass. In this study, year effects resulted in fourfold variation in establishment and survivorship and were even stronger than site effects. Similarly, Werner et al. (2019) tracked the emergence and survival of seeded conifers across two initiation years, finding strong effects of year on both of these life stages. Groves and Brudvig (2019) found that emergence and survival of sown species increased both with increased precipitation, but also increased across 3 yr of study when precipitation was held constant, demonstrating that multiple weather factors can interact to produce important variation in incipient communities. Finally, seeding experiments in an oligotrophic wet meadow found that
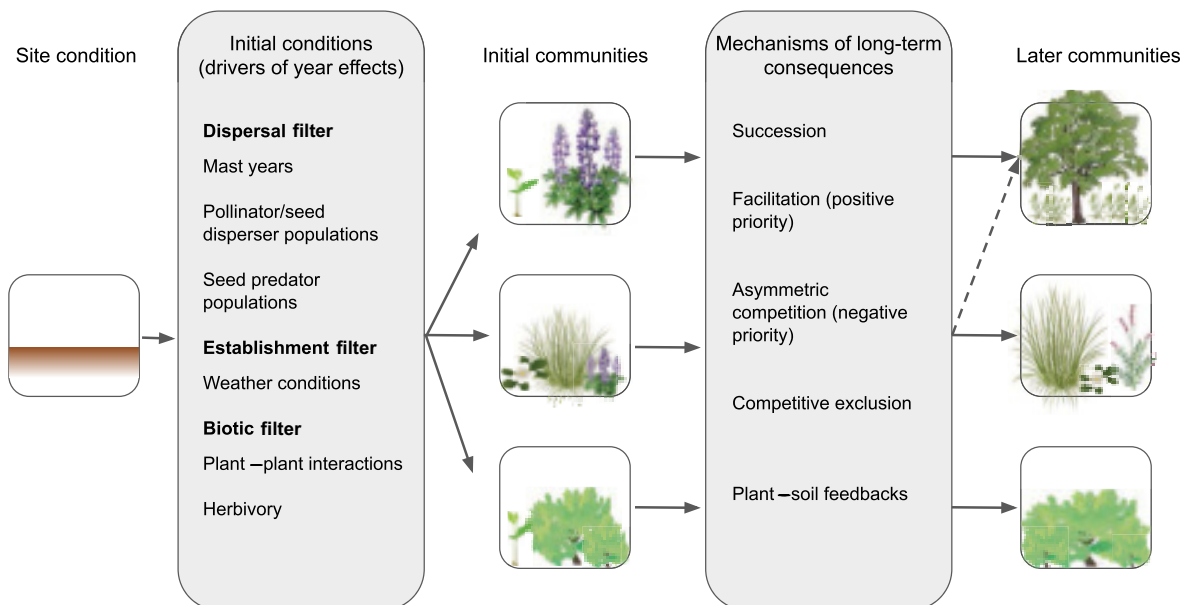

FIG. 1. Conceptual diagram of the drivers of year effects, differences in initiation communities, mechanisms of long-term effects, and consequent later communities with both convergent (e.g., succession; dotted line) and divergent trajectories (solid lines). Plant images courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

emergence and survival of seeded species differed several-fold between two initiation years, but not between season (autumn versus spring sowings; Švamberková et al. 2017), indicating that timing of propagule arrival may matter less than conditions during seedling emergence.

These species-level responses to year effects can generate community-level shifts in dominant guilds. One striking example of this is the existence of "grass years" and "forb years" in annual California grasslands. Early work on a long-term data set found temperature and rainfall to be important drivers of these annual grassland communities, with consistent precipitation in fall and spring leading to grass dominance, and milder autumn weather promoting forb dominance (Pitt and Heady 1978). Later experimental work in this system provided evidence that temperature and precipitation in the year of establishment have lasting effects on community composition (e.g., grass/forb balance) during grassland restoration (Stuble et al. 2017a, Groves et al. 2020).

In old-field succession, a study of 47 fields abandoned over three consecutive years found that the colonization of woody species, and consequent balance between woody and herbaceous guilds, differed significantly across abandonment years (Baeten et al. 2010). These differences were attributed to rainfall, with bare wet soil proving to be important for the establishment of woody species otherwise excluded by herbaceous species. Weather conditions in the year after fire also have been shown to be important drivers of success or failure of woody recruitment in mixed-conifer forests (Harvey et al. 2016, Young et al. 2019). Additionally, year effects can affect the balance between native and exotic species in newly assembled communities (MacDougall et al. 2008, Stuble et al. 2017b).

Year effects can impact cumulative metrics of community structure and function, indicating the importance of year effects at the ecosystem level. Net productivity (Tejera et al. 2019), aboveground net primary productivity, species richness and diversity (Manning and Baer 2018), and remotely sensed normalized difference vegetation index (Meng et al. 2015) have all been found to differ across multiple years of community assembly initiation. Year effects can also drive dynamics in nonplant communities. In an 11-yr observational study of native stream invertebrate community assembly, beta diversity was higher in years of low stream flow than years of high stream flow (Sarremejane et al. 2018).

In addition to their direct effects, year effects can also interact with site or treatments. In other words, abiotic and biotic treatment effects may differ (both qualitatively and quantitatively) depending on the year (Vaughn and Young 2010). During ecological restoration, seeding method (Bakker et al. 2003), herbicide use (MacDougall et al. 2008, Werner et al. 2019), priority planting (Stuble et al. 2017a), and nutrient addition (Tejera et al. 2019) have all been found to yield significantly different outcomes depending on year. For example, MacDougall et al. (2008) found that herbicide spray to reduce competition with nonnative species succeeded in promoting native dominance only in a wet year. Such differences in the strength of competitive interactions across years have been observed in seed addition experiments in both postfire coniferous forests and native grassland restorations (Thomson et al. 2018, Werner et al. 2019). Similarly, an experimental manipulation of assembly in rocky intertidal communities found that, in addition to overall differences between initiation years, the effects of predation treatments differed across years (Berlow 1997). Even weather manipulations can have variable outcomes driven by the year of experimental manipulation (Groves and Brudvig 2019, Werner et al. 2019).

Not every study initiated in multiple years finds a significant year effect. A study of the relative importance of initial conditions, historical conditions, and management treatments in prairie restorations did not find variation in precipitation in the planting year to be a significant driver of restoration outcomes (Grman et al. 2013). However, the authors note that other unconsidered interannual variation—such as solar radiation or herbivore abundance—might still be important. The potential for multiple mechanisms as drivers of year effects is echoed in the Groves and Brudvig (2019) manipulative study of prairie restoration, which did find significant effects of planting year even after holding precipitation constant.

Although studies expressly exploring year effects in community assembly generally have durations of only 1–5 yr, there is substantial evidence to indicate that the differences in structure and function observed across initiation years can have longer-term effects. Longer-term studies have observed that (at least in some systems) community composition and/or species densities seems to stabilize after just 1 or 2 yr (Bakker et al. 2003, Stuble et al. 2017a), leaving persistent community-level differences associated with year effects. The idea that these year effects may have long-term consequences is supported by the profusion of ecological literature indicating that initial community composition can have persistent effects on community dynamics (see Fig. 2; Egler 1954, Sutherland 1974, Robinson and Edgemon 1988, Drake 1990, 1991, Law and Morton 1993, Lockwood and Samuels 2004, Fukami et al. 2005, Werner et al. 2016). However, we still have limited understanding of how or when initial differences are transient or long lasting.

Year Effects: A Dearth of Attention

Despite the importance of year effects as a driver of the composition and function of assembled communities (and ultimately the outcomes of ecological experiments), the importance of year effects is rarely acknowledged and even less often explicitly tested. To get a general sense for how often researchers consider year effects, we

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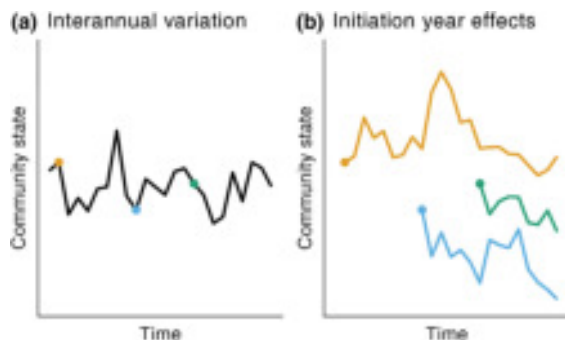**(a) Interannual variation**   **(b) Initiation year effects**

FIG. 2.   Conceptual diagrams demonstrating (a) interannual variation in a single community over time and (b) variation in three communities assembled at different time points. Although long-term studies of a single site or experiment can capture interannual variation, these dynamics are qualitatively different than initiation year effects.

conducted a review of experimental ecological studies published in *Ecology* (all issues in 2013, and one issue each from 2016, 2017, and 2018) and *Ecology Letters* (one issue each from 2016 and 2017), for a total of 68 empirical field studies. We chose the first regular issue of the year for each of these. Only 5% of articles offered a caveat about the year of sampling, and 27% had a caveat about research being carried out at a particular site. Among these issues, we also specifically examined studies that conducted field manipulations or included a condition that initiated community assembly, such as postfire regeneration or prairie restoration. Of the 14 studies that met these criteria, only 2 were initiated in multiple years. We do note that these patterns may be somewhat dependent on subfield: Vaughn and Young (2010) found that papers in agronomy journals (not reviewed here) were far more likely to consider year effects.

Although many ecologists will acknowledge that contingencies—including interannual variation in weather—matter for community assembly, year effects are often neglected in experimental design and in the reporting of research findings. The general lack of recognition of year effects is at odds with the results from manipulations of weather (and other variables known to also vary strongly from year to year) in ecological experiments that overwhelmingly demonstrate the importance of these inherently variable conditions. Explicit manipulations of these sorts of variables have repeatedly revealed that such interannually variable conditions can be strong drivers of community composition, in systems ranging from soil microbes (Rinnan et al. 2007) to plants (Lloret et al. 2009).

A general understanding of year effects as important and/or pervasive by ecologists would necessitate that authors qualify their results with caveats acknowledging that a particular study was only carried out in a single year, potentially limiting the scope of inference. A dearth of such caveats found in our review of the recent ecological literature reveals that year effects remain underrecognized.

CASE STUDIES: ON THE RELATIVE IMPORTANCE OF YEAR EFFECTS

Field methods

To quantify the relative importance of year effects on community-level metrics, we explored two empirical data sets assessing interannual variation in the outcomes of community assembly: (1) an experimental California grassland restoration study that manipulated order of species arrival during assembly across four initiation years and (2) an exploration of postfire pine establishment across an experimental precipitation manipulation across two initiation years. These experimental manipulations, implemented over multiple years and sites, allow the partitioning of variation in community structure into treatment effects, site effects, and year effects.

In the grassland restoration study, experimental plots manipulating order of species arrival were established identically across three sites in northern California and four initiation years. Specifically, we assembled communities composed of four native and four nonnative grasses from seed, adding the seeds at the same time, or adding the seed of native species either 2 weeks or 1 yr before the seed of the nonnative species (see Stuble et al. 2017*b* for more detail). Seeding was conducted (experiments independently initiated) in 2011, 2012, 2013, and 2014, with exotic grass seed added the following year for the 1-yr priority treatment. We assessed community composition in 2015, at which time we determined percent cover for each planted species. We calculated total percent cover of native grasses for each plot.

For our second case study, we examined interannual variation in *Pinus ponderosa* regeneration after fire in an empirical study which manipulated precipitation. Precipitation and interspecific competition were manipulated within plots at two sites, with seeds planted in two different years (2015 and 2016). The precipitation manipulation treatment used rainout shelters to reduce winter snowpack, and the competition treatment either removed shrubs using a cut-stump herbicide application or left shrubs present (see Werner et al. 2019 for more details). We assessed total recruitment of *P. ponderosa* seedlings in the fall of 2017.

Analyses

We estimated the relative importance of each explanatory variable (treatment effects, site effects, and year effects) in a linear model using the calc.relimp function in the relaimpo package in R to calculate the lmg metric (Grömping 2006). The lmg metric calculates the sequential R^2, averaged across orderings of explanatory variables in the model, allowing for an estimate of the proportion of variance explained by each individual predictor. For the California grassland data, we developed two general linear models that included site, year of initiation, and seeding order as fixed effects and total

percent cover of native grasses as the response variable. To understand the magnitude of year effects relative to treatment effects of differing magnitudes, we ran two models: (1) the control vs. 2-week priority treatment and (2) the control vs. 1-yr priority treatment. For the pine establishment study, we used location, drought manipulation, herbicide manipulation, and year of seedling as fixed effects and the number of living pine seedlings as the response variable.

Results

In the California grassland study, we found strong evidence for priority effects, site effects, and year effects on the composition of the assembled community (Young et al. 2017, Stuble et al. 2017*b*). Of these, year effects were the strongest, trumping the experimental impacts of both 2-week and 1-yr priority of native grasses over exotics. Year of initiation explained 76% and 62% of total explained variance in the 2-week and 1-yr priority treatment experiments, respectively (Fig. 3). In contrast, priority treatment explained 11% and 25% in the 2-week and 1-yr priority treatment experiments, respectively. Site explained 13% of total variance in both models. In general, we found that priority treatments tended to be stronger in wetter years (Stuble et al. 2017*b*).

The pine recruitment experiment showed a particularly strong effect of site, with site explaining 72% of variance in the model, possibly because of differences in slope aspect and soil depth. Although we found effects of both drought and herbicide treatments (Werner et al. 2019), the effect of initiation year was stronger than both of these manipulated conditions, with year explaining 16% of variation in pine recruitment as opposed to 11% as explained by the herbicide treatment and only 1% explained by the precipitation treatment (Fig. 4).
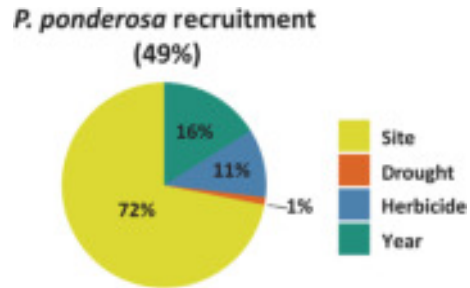

Fig. 4. Relative importance of site, drought treatment, herbicide treatment, and initiation year on recruitment of *Pinus ponderosa* seedlings. The full model explained 49% of variation in *P. ponderosa* seedling recruitment. Location was the largest driver variation in seedling recruitment, followed by year, and then the treatments.

Additionally, the herbicide treatment interacted with initiation year, such that a study of only the first initiation year would have found strong competitive effects of shrubs, whereas a study of only the second year would have observed a net neutral effect of shrubs.

IMPLICATIONS FOR RESTORATION

Ecological theories on how communities assemble can inform ecological restoration practices (Palmer et al. 1997, Young et al. 2001, 2005, Brudvig 2011, Suding 2011). Restoration, in turn, provides opportunities to test theories of how ecological communities assemble under different environmental conditions (Bradshaw 1987). Much of the evidence for year effects as drivers of restoration outcomes has been correlational, and confounded with differences in management practices (e.g., seed mix diversity/composition) and site-specific conditions (e.g., edaphic conditions).

To better predict restoration outcomes and increase our understanding of the importance of historically contingent assembly models, we need empirical evidence to determine when and how year effects influence community assembly and restoration outcomes (Brudvig et al. 2017). Understanding the importance of year effects in restoration success has at least two implications. First, a restoration failure (or success) in a given year may not be due to the failure of a particular restoration technique, but rather due to contingencies in a particular year (Groves et al. 2020). Second, if we can predict which years are more likely to lead to restoration success or failure (e.g., our increasing ability to predict El Niño events), we can time our restoration efforts accordingly to maximize the likelihood of success.

LOOKING FORWARD

Given the importance of year effects on community assembly, we provide suggestions for future research directions.

Fig. 3. Relative importance of site, priority treatment, and year of initiation in a northern California community assembly experiment. The 2-week priority experiment (left) compares native grass cover in plots in which native and exotic grasses were added at the same time to plots in which natives were added 2 weeks before the exotic grasses. The 1-yr priority experiment (right) compares plots in which native grasses were added one full year before exotics to plots in which natives and exotics were added at the same time. These models explain 56% and 60% of variation in native grass cover, respectively, and year of initiation was the largest driver of native grass cover across both treatment scenarios.

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Initiate experiments in multiple years

It is now clear that it would be beneficial if ecological field experiments were replicated over multiple years, if for no other reason than as a test for the possibility that results from a single initiation year are likely to be idiosyncratic. Unfortunately, many experiments are costly and time consuming to establish, and multiplying entire experimental designs may often be considered impractical. This may be exacerbated by the short duration of research grants, graduate careers, and academic attention spans. More generally, there will always be trade-offs between initiating studies in multiple years, in multiple sites, monitoring long term, and doing additional experiments to isolate causes of variation. We hope that this review of the ubiquity and strength of year effect will shift the balance toward temporal replication when weighing different forms of replication to implement.

Isolate causative factors underlying year effects

Though we have demonstrated that year effects can be common and impactful, the underlying drivers of such year effects are not always evident. These may include aspects of weather (e.g., patterns in precipitation, frosts, temperature) or biotic factors (e.g., variation in herbivores, granivores, weed challenge, or microbial communities). Further evidence of the mechanisms responsible for the observed affected variables could be found through both experimental and statistical approaches:

1. *Manipulate suspected drivers.* Young et al. (2015) effectively used a watering treatment to isolate rainfall as a primary cause of initiation year effects in a priority experiment. Similarly, Chang et al. (2018) found sessile invertebrate assembly in San Francisco Bay seemed to vary with salinity levels, tested this explicitly in a lab mesocosm experiment, and confirmed that this mechanism did lead to the observed patterns. In contrast, Groves and Brudvig (2019) manipulated precipitation to multiple levels and found year effects even within a precipitation level, indicating that other underlying drivers were likely involved.

2. *Multivariate analysis to tease out strongest correlates.* Including multiple types of climatic variables, such as temperature, precipitation, or cumulative variables like climatic water deficit in multivariate analyses can be useful in elucidating the drivers of year effects (Young et al. 2019). These variables can be considered on an annual level or broken down by month (as with temperature in Stuble et al. 2017b). Another approach is to use ecological and system-specific knowledge to determine which variables to consider in multivariate models (Stuble et al. 2017b). This approach requires relatively large sample sizes of years, especially if one wishes to tease apart multiple

putative causal factors (e.g., Pitt and Heady 1978, Grman et al. 2013) or incorporate spatial variation (Young et al. 2019).

3. *Syntheses of existing studies with initiation year information.* Finally, syntheses and meta-analyses may be able to utilize existing single-year studies to track patterns through time and across systems. However, this approach requires studies to include information about the conditions in the initiation year(s), which as we have shown above is currently lacking from many published papers.

Identify systems more likely to be affected by year effects

Given the high costs of temporal replication, it would be helpful to identify which situations are more or less likely to be strongly driven by year effects. For example, communities dominated by annuals or short-lived perennials can be inferred to be more responsive to interannual variation than those dominated by woody species or other longer-lived plants (but see Schäfer et al. 2019). However, the recruitment stages of many of these longer-lived species may be particularly sensitive to drivers that vary interannually, such as climate or herbivory. If the window of establishment for these communities is relatively narrow (e.g., regeneration after periodic fire or flooding events), initial year effects could have particularly long-term consequences (Harvey et al. 2016). As the catalogue of published research including temporal replication (or chronosequence data) increases through time, meta-analyses may also prove helpful.

Utilize year effects as windows into climate change

One of the challenges in climate change research is projecting the ecological effects of long-term changes in climate. Current projections include an increased frequency of extreme weather events and the emergence of nonanalog climates, patterns of temperature and rainfall that have no contemporary analogs. However, current rainfall and temperature manipulations usually fail to capture projected magnitudes in climate change, or their interactions across multiple stressors (Korell et al. 2020). We suggest that contemporary year effects can provide windows into the effects of these future climate changes.

Given that events early in community assembly (including recruitment) may have both profound and long-lasting effects on community structure, it is not unreasonable to suggest that the communities initiating in "window years" may be indicative of the community responses that will occur in the long run with climate change (Stuble et al. 2017a). This would apply both to communities recovering from natural and anthropogenic disturbances, and to restoration projects, initiated in such "window years," perhaps providing us a glimpse into future assembly dynamics. The usefulness of year effects in this context rest largely on the question: Can a single nonanalog year, or a single year of higher

temperatures (referred to here as a window year), produce ecological effects that will be functionally similar to the effects of those trends as they become multiyear norms? If not, the consequences of a single window year will be less useful in projecting the consequences of these years becoming the norm.

Finally, it is important to consider future year effects as well as current ones. Even as occasional window years create future climate conditions, it is possible that in the future that there will continue to be occasional years that recreate earlier climate norms (Serra-Diaz et al. 2016): "inverse climate window years." These years could, in turn, promote recruitment and assembly of communities similar to currently existing ones, depending on changes in associated biotic conditions and disturbance regimes.

Concluding Remarks

There is an emerging understanding that the effects of interannual variation are likely to be important drivers of community assembly, often leading to different long-term community trajectories. These year effects span systems and often interact with site factors or experimental treatments. Nonetheless, their study has lagged. Focused studies of year effects can illuminate when and how interannual variation shapes community assembly patterns, especially in conjunction with other sources of variation. Further, an improved understanding of year effects will improve our ability to effectively maintain biodiversity, promote restoration outcomes, and plan for future global change.

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CONCEPTS & SYNTHESIS