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The phenology of plant invasions: a community ecology perspective

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The phenology of plant invasions: a community ecology perspective

Elizabeth M Wolkovich[1*] and Elsa E Cleland[2]

Community ecologists have long recognized the importance of phenology (the timing of periodic life-history events) in structuring communities. Phenological differences between exotic and native species may contribute to the success of invaders, yet ecology has not developed a general theory for how phenology may shape invasions. Shifts toward longer growing seasons, tracked by plant and animal species worldwide, heighten the need for this analysis. The concurrent availability of extensive citizen-science and long-term datasets has created tremendous opportunities to test the relationship between phenology and invasion. Here, we (1) extend major theories within community and invasion biology to include phenology, (2) develop a predictive framework to test these theories, and (3) outline available data resources to test predictions. By creating an integrated framework, we show how new analyses of long-term datasets could advance the fields of community ecology and invasion biology, while developing novel strategies for invasive species management. Although we focus here on terrestrial plants, our framework has clear extensions to animal communities and aquatic ecosystems as well.

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The study of plant phenology – the timing of periodic events, such as leaf budburst and flowering – has fascinated naturalists and ecologists for centuries. In the 1800s, Henry David Thoreau kept dozens of notebooks on the flowering of herbs and forbs in Concord, Massachusetts (Miller-Rushing and Primack 2008), whereas – during the early 1900s – John Muir described the phenology of pines in California's Yosemite Valley (Muir 1917). In the years since, research has shown that the timing of these events is adaptive (Volis 2007), limits species ranges (Chuine and Beaubien 2001), and plays a major role in species coexistence (Fargione and Tilman 2005). Plant phenology has received increasing attention in recent decades, because it is a major indicator of climate change (Fitter and Fitter 2002; Cleland *et al.* 2007; Sherry *et al.* 2007), promoting the development of new, geographically extensive databases (Morisette *et al.* 2009), in addition to previously available long-term records (Menzel 2005).

In a nutshell:

- Community ecology theory suggests that exotic species may succeed because they have phenologies (timings of periodic life events, such as flowering each season) distinct from those of native species or are able to adjust their phenologies to a new community or climate
- We extend four major theories within community and invasion biology to incorporate phenology, including the vacant niche and priority effects models, and the role of niche breadth and phenotypic plasticity in structuring communities
- We provide a framework for testing the role of phenology in invasive species success, identifying potential invasive species, and developing management strategies that exploit phenology

Phenology may also play an important role in the success of invasive plant species, which may increase under projected climate change and disturbance regimes (Field *et al.* 2007). Many theories that attempt to explain how certain species are able to establish and spread suggest that exotic species possess unique characteristics – when compared with those of native species in their introduced community – that give them a competitive edge (Cadotte and Lovett-Doust 2002). In particular, the phenology of a plant species may be tied to many characteristics important to plant competition; each year, leaf budburst and senescence strongly correlate with the beginning or end, respectively, of a plant's acquisition of soil and light resources and the time when these species are at greatest risk of herbivory. Likewise, the period of flowering determines when many species compete for pollinators. Phenology may therefore be an important characteristic to consider when studying how communities assemble and how new species invade.

Here, we show how differences in the phenology of native and exotic species can advance theories of community ecology and invasion biology, and how many management strategies already exploit these connections. We focus mainly on terrestrial exotic plant invasions; however, our hypotheses have clear extensions to native species whose ranges and/or abundances are expected to change under future climate regimes. Because native species whose abundances increase in either their original

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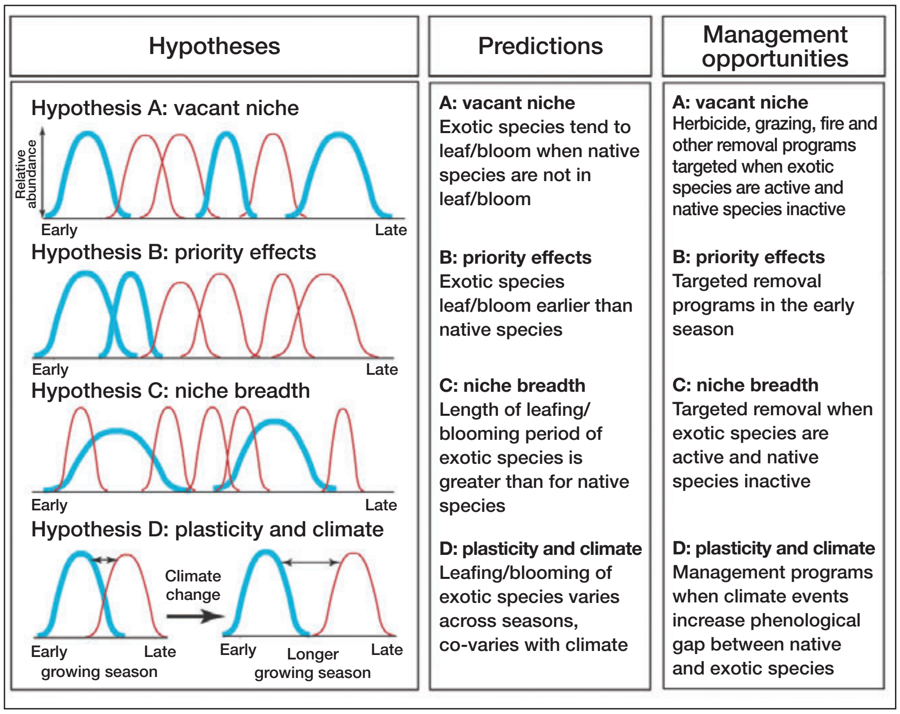

Hypotheses	Predictions	Management opportunities
Hypothesis A: vacant niche	**A: vacant niche** Exotic species tend to leaf/bloom when native species are not in leaf/bloom	**A: vacant niche** Herbicide, grazing, fire and other removal programs targeted when exotic species are active and native species inactive
Hypothesis B: priority effects	**B: priority effects** Exotic species leaf/bloom earlier than native species	**B: priority effects** Targeted removal programs in the early season
Hypothesis C: niche breadth	**C: niche breadth** Length of leafing/blooming period of exotic species is greater than for native species	**C: niche breadth** Targeted removal when exotic species are active and native species inactive
Hypothesis D: plasticity and climate	**D: plasticity and climate** Leafing/blooming of exotic species varies across seasons, co-varies with climate	**D: plasticity and climate** Management programs when climate events increase phenological gap between native and exotic species

Figure 1. *Conceptual diagrams of four hypotheses: phenological "niches" of exotic (blue line), or native (red line) species are shown as the relative abundance of individuals that are active during different times during the growing season. Exotic species may be successful because they occupy temporally vacant niches (Hypothesis A), preempt resources by being active earlier in the growing season than natives (Hypothesis B), have wider phenological niches than natives (Hypothesis C), and/or have greater phenological plasticity, which allows them to track climate change (Hypothesis D).*

or expanded range may be considered as "native invasive" species, we use the term "invasive" in its most general sense – to describe species increasing dramatically in their abundance or spread (Davis 2009). We also give examples for other ecosystems (freshwater and marine) and for animal communities. By creating an integrated framework for considering the role of phenology in controlling species invasions, we highlight how new analyses could advance ecological theory, leading to the development of novel strategies for invasive species management.

■ Extending community ecology and invasion biology theory to plant phenology

Time as a niche axis

Our hypotheses on the role of phenology in structuring plant communities focus on time as a pivotal niche axis (Figure 1). Just as with the word "space", many ecologists use "time" as a portmanteau – a single word used to mean multiple other words – for the suite of critical but limited resources available to a species at any given time (Begon *et al.* 1996). Together, space and time ("space–time") provide the common units for all species-coexistence theories (Chesson 2000). Working within the same space–time units, many coexistence theories and related research focus on the consumable resources available to multiple species (Tilman 1985), such as soil pools of nitrogen or phosphorus for plants. However, variability in space and time may also promote coexistence (Chesson 2000). For example, ant species with highly similar diets may coexist because they tend to search for food at different times of the day (Albrecht and Gotelli 2001). At a longer time scale, the storage effect model uses a temporal niche to promote coexistence via interannual variation that benefits different "long-lived" species in different years (Angert *et al.* 2009). Under this model, a species is able to coexist with other species in a community when it experiences high-abundance years, during which intraspecific competition is stronger than interspecific competition. Similarly, over a shorter time scale, species may partition time throughout a season, with certain species being more abundant at periods of the growing season when other species are less common. This idea has been suggested by previous phenological studies, which revealed that life-history events, such as flowering, were generally spaced evenly across a growing season (Veresoglou and Fitter 1984; Rathcke and Lacey 1985). A greater focus on how species may segregate through time is especially important now that anthropogenic forces have altered the start and end of growing seasons globally (Walther *et al.* 2002), but ecological theory on the expected outcomes of such alterations has lagged.

Four hypotheses for how phenology may structure communities

Hypothesis A: vacant niche

Major theories of basic ecology and invasion biology predict that invasive plants establish by obtaining resources that are not used by native plants. The "vacant niche" model (Elton 1958) predicts that exotic plants will invade communities where there is an open niche, often resulting from unused soil resources. For plant communities, the theory has been modified to include fluctuating resources; in such cases, a vacant niche can be temporally variable, occurring only for short time periods, but still highly beneficial to exotic species (Davis 2009). This could be called a temporally vacant niche. If an exotic plant species benefits from a temporally vacant (phenological) niche (Figure 1: Hypothesis A), it would tend to bloom and/or leaf earlier or later as compared with native plant species, thereby using temporally available resources (eg sunlight, pollinators, nutrients). Furthermore, if this distinct phenology is highly beneficial, as theory predicts, then invasive species would have the greatest and/or most consistent differences across years between their phenologies and those of native species.

Hypothesis B: priority effects

Another ecological model predicting species coexistence posits that species that establish earlier in the growing season should benefit by sequestering resources first, termed priority effects (Sale 1977). These "seasonal" priority effects could also be an important mechanism for facilitating the success of invasive plants (Seabloom *et al.* 2003) and would promote exotic species with earlier phenologies than native species (Figure 1: Hypothesis B). However, species exhibiting seasonal priority effects must balance the potential rewards of early access to resources with the possible risks of establishing before the growing season has fully begun – for example, they risk starting growth before the occurrence of the last frost in temperate regions or before the start of consistent rainfall events in more arid systems (Figure 2). The optimal bet-hedging strategy should depend on local climate means and on how the species maintains its abundance in years of low reproductive output; for example, species with very short-lived seed banks may be more vulnerable to risks than those species with long-lived seed banks or perennial species. However, as climate change may push systems away from their previous climate regimes (Visser 2008), local species may no longer be adapted to the best strategy for their local environment and seasonal priority effects may become a more optimal strategy in many habitats. Seasonal priority effects share some predictions with the phenological vacant niche theory, in that both predict that exotic species will have phenologies that are offset from those of native species. But while the vacant niche theory would predict exotic species' phenologies to be offset in no particular pattern compared with native species' phenologies, seasonal priority effects predict that exotic species establish consistently earlier than native species.

Evidence already indicates that many of the major invasions by plants in North America have benefited from a vacant phenological niche (Hypothesis A) or seasonal priority effects (Hypothesis B). In the eastern US, the tendency of the invasive Amur honeysuckle (*Lonicera maackii*) to stay active later in the fall season than native understory species may be one reason for its success (Resasco *et al.* 2007; Xu *et al.* 2007); in California, invasive yellow starthistle (*Centaurea solstitialis*) may benefit from similar late-season activity (Gerlach and Rice 2003). Throughout the western US, studies have revealed seasonal priority effects among many invasive grasses, including cheatgrass (*Bromus tectorum*) in Great Basin shrublands (DeFalco *et al.* 2007) and annual grasses in perennial grasslands of California (Seabloom *et al.* 2003). In aquatic systems, recent research has also highlighted the role that vacant phenological niches may play in promoting invasions. In one of the few studies of its kind, examinations of a marine intertidal community found that the phenologies of exotic species are distinct from those of native species (Byrnes and Stachowicz 2009). Additionally, one of the most widespread and harmful freshwater invasive plants, Eurasian watermilfoil (*Myriophyllum spicatum*), is believed to be especially detrimental because it shades out potential native competitors before they start to grow (Smith and Barko 1990; Madsen *et al.* 1991). However, these studies have generally been conducted at local scales and tend to focus on one or a few invasive species; the researchers did not test whether these theories hold across larger scales or can be generalized to include other exotic species.

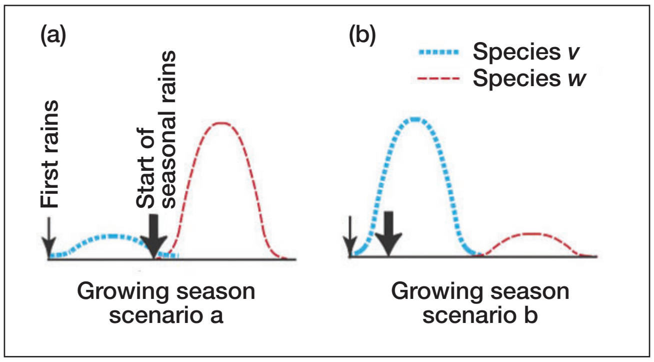

Figure 2. *Species that establish early each season may benefit from priority effects, depending on whether their cues to break dormancy reflect the actual start of the growing season. Here, we show an example of plants in an arid environment: if species* v *starts to grow immediately after the first rains, whereas species* w *waits for additional cues, then in years where the first rains occur well before the main seasonal rains (a) species* v *may have low success as compared with that of species* w*. However, (b) when the first rains are followed quickly by seasonal rains, species* v *may sequester resources before species* w *begins to grow.*

Hypothesis C: niche breadth

Recent research on the extent of niche space occupied by exotic species has attempted to work across broad geographical regions (Cadotte and Lovett-Doust 2002) to test the hypothesis that exotic species benefit by occupying greater niche space than native species (Richards *et al.* 2006). Applied in a phenological context, exotic species that have longer phenological phases (eg a more extended leafing or flowering period) than native species would effectively possess greater niche breadth (Figure 1: Hypothesis C). Such variation should benefit species by providing greater access to resources; for example, a longer leafing or flowering phase may benefit exotic species through extended access to soil nutrients or pollinators. This idea has long been hypothesized for flowering period (Kolar and Lodge 2001), and studies in California (Gerlach and Rice 2003) and across Ontario (Cadotte and Lovett-Doust 2002) have provided empirical support for this hypothesis.

Hypothesis D: plasticity and climate

High plasticity and rapid evolution of exotic species may also enhance their success (Richards *et al.* 2006), with selection pressure on invasive species to adjust their phenologies to climate being especially high given the cur-

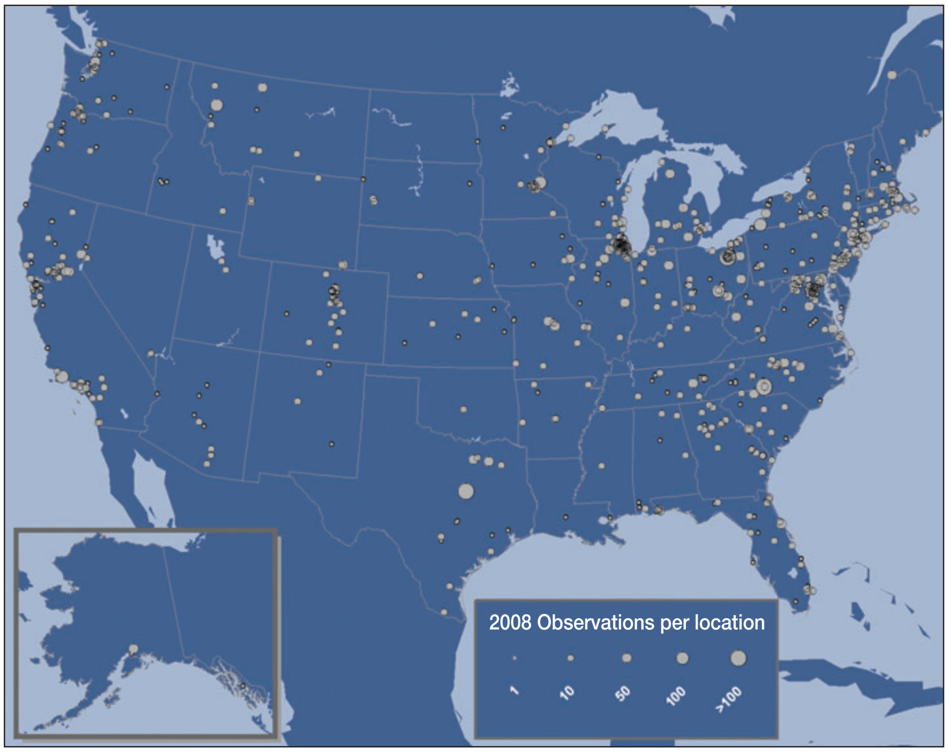

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Figure 3. *New citizen-science projects will provide tremendous amounts of spatially explicit data. Here, we show 2008 participation in Project BudBurst, which encourages submission of phenology data across the US.*

rent rate of climate change (Field *et al.* 2007). We define plasticity here as the property of organisms' genotypes to vary their phenotypes in different environments through space or time (Richards *et al.* 2006). We hypothesize that exotic species in more variable environments will benefit by responding to early precipitation or warming events, especially when native species are adapted to respond to more specific phenological cues (Levine *et al.* 2008). The mechanism for this plasticity may vary among species; while some may alter their germination strategies rapidly in introduced habitats in response to new climate patterns (Hierro *et al.* 2009), others may have simple germination cues (eg responding only to temperature or rainfall, as opposed to both) that allow them to vary dynamically with climate. Similarly, germination cues that rely solely on climate-based variables, such as temperature or rainfall, may allow species to track changes in climate through time. In contrast, other germination cues based on variables that are not expected to shift with climate change, may "fix" a species' phenology, thereby preventing a species that is sensitive to climate from effectively tracking climate. For example, species may have adapted to flower based on day length, which, prior to climate change, covaried with temperature in many regions. However, climate change will shift only temperatures, thus decoupling environmental variables such as day length from climate and possibly adversely affecting species with cues based on static variables (Visser 2008). Recent studies using Thoreau's historical dataset suggest that species exhibiting plasticity through time in their first-flowering dates alongside climate change have been the least vulnerable to extinction, and many have increased in abundance (Willis *et al.* 2008). If such plasticity is phylogenetically conserved, as Willis *et al.* suggest, it may provide a predictive framework for which species are likely to become invasive in the future (Willis *et al.* 2010).

As climate change increases variability in temperature and precipitation patterns, growing seasons will be effectively extended (Field *et al.* 2007) and more temporally vacant niches should become available for exotic species to occupy. Therefore, if exotic and invasive species have flexible phenologies, they would benefit from increased system variability that effectively results in longer growing seasons (Figure 1: Hypothesis D). Data showing that, across systems, differences between phenologies of exotic species and native species are positively related to system variability would support this, as would data indicating that differences between the phenologies of exotic and native species have increased alongside increasing climate variability over time. One such study in marine benthic communities supports this hypothesis, by showing that earlier annual warming of intertidal waters due to climate change promotes the spread of invasive species (Stachowicz *et al.* 2002). Finally, research into exploiting the unique phenologies of invasive plants – to map invasive species' cover and spread by remote sensing – has recently suggested that climate anomalies provide the best opportunity for such mapping (Huang and Geiger 2008).

■ Testing theories: current and future opportunities

Several studies have used small, local datasets to examine the role of phenology in plant invasions (Gerlach and Rice 2003; DeFalco *et al.* 2007), but there are many other sources of plant community phenology data that can be used to test these theories over large spatial and temporal scales (WebTable 1). In the US, most known community-level plant phenology data start either in the colonial period (Miller-Rushing and Primack 2008) or in the 20th century, when the use of plant phenology to document climate change catalyzed individual and organization-based research programs (some of which now span in excess of 40 years; Morisette *et al.* 2009). Today, new citizen-science programs are creating spatially extensive datasets (Figure 3). Climate-data repositories allow scientists to examine the effects of system variability and local climate trends (Hypothesis D); however, gathering the best information from such databases requires careful consideration. For example, examining how factors like rainfall and temperature influence the phenology of native versus exotic species requires an understanding of the expected germination cues of different habitats. For instance, in northern temperate forests, and many other systems not primarily limited by water, photoperiod and temperature are the primary germination- and growing-season initiation cues for plants, whereas in arid and semiarid systems, soil moisture is often a dominant germination cue (Lambers *et al.* 2008).

Large databases provide unparalleled opportunities to test the hypotheses outlined above. Although analysis can be difficult for many reasons, recent advances have made merging and analyzing multiple plant phenology datasets with climate and native/exotic status data possible (see "Opportunities and challenges" in WebTable 1). Large databases are also important for identifying variation across space, across time, or among "lifeforms" (groupings of species based on common, often structural, traits; for example, different plant lifeforms include shrubs, trees, and herbs) in which the hypothesis explains (or hypotheses explain) plant invasions. Priority effects, for example, may be most apparent in habitats such as those in the western US, where high climatic variability associated with the start of the growing season promotes invasion by species that can take advantage of early-season vacant niches. Across plant groups, priority effects may be more common among short-lived, herbaceous species that can flower and set seed before native species become active and begin to compete for key resources. Furthermore, although our hypotheses may apply most strongly to systems with distinct seasonality – as is common in temperate regions – they may also provide guidance for studying phenology in the tropics, where seasonality is generally weaker but where species may still use environmental cues to produce communities with asynchronous phenologies (Martin *et al.* 2009). We therefore suggest that future research should examine trends across multiple scales (eg predictions on local, regional, and larger spatial scales, as well as within and across different lifeforms).

Although long-term phenological observations combined with climate records provide unparalleled resources to examine trends in temporally and spatially extensive data, well-designed experiments may also provide key tests for many of the hypotheses outlined above. In particular, an examination of plasticity will require studies that use identical genotypes in different environments (Via *et al.* 1995). Additionally, basic invasion biology suggests that mechanisms that facilitate a species in becoming invasive in its introduced habitat cannot also operate in its native (or non-invasive) range, so studies that examine the phenology of invasive species in both their introduced and native ranges may advance our understanding.

■ Testing theories: consequences and extensions

Analysis of two large-scale databases

We used publicly available data from Project BudBurst (www.budburst.ucar.edu), a citizen-science organization based in the US, and the US Department of Agriculture (USDA) PLANTS database (http://plants.usda.gov; WebTable 1) to test several of our predictions, as well as to highlight some common benefits and problems associated with large-scale datasets. Specifically, we examined whether suites of exotic species showed distinct timings of leaf or flower budburst as compared with native species' timings, in order to test the vacant phenological niche hypothesis (Hypothesis A), or – for earlier phenologies – the seasonal priority effects hypothesis (Hypothesis B).

Each dataset has different benefits and drawbacks. In the Project BudBurst dataset, there are often multiple observations per species, allowing for better estimation of the mean date of a phenological event and the variation around that date. However, these data are geographically clustered, with a greater number of observations associated near areas with large or dense human populations; thus, such biased datasets would be inappropriate for many large-scale comparisons. Also, because the program is still relatively new, comparisons across years will be biased by an increasing sample size over time. We therefore used only 2008 leaf budburst/first leaf data from one state (North Carolina) – because we wanted to focus on a specific geographical area, and this state had the most observations (*n* = 497). An additional drawback to consider when using any dataset that does not exhaustively sample all species (and few do) is the actual species pool from an area versus the species included in the dataset for that area. For example, a dataset such as Project BudBurst may have preferential sampling of species early in the growing season in household yards as compared with sampling in more natural areas; if yards tend to have a higher abundance of exotic species compared to native species, observed differences between exotic and native species would be an artifact of this bias. Furthermore, if a certain plant group – shrubs, for example – is over-represented among the exotic species because of observer bias, the results could be misleading. We surveyed our list of species and found that it contained a mix of lifeforms and of cultivated and uncultivated native and exotic species, but future analyses should include a comparison of the findings with local species lists, to test for any possible biases. We used the USDA PLANTS database to assign native or exotic status for all plants for which we could gather a definite species name; however, we marked all common dandelion (*Taraxacum officinale*) observations as "native/exotic" because nativity could not be positively assigned. In contrast to the Project BudBurst data, the USDA PLANTS database has only one coarsely identified time of a phenological event per species, integrating over variation across space, yet data are available for almost all plant species in the US. Thus, to narrow the analysis, here we focused on

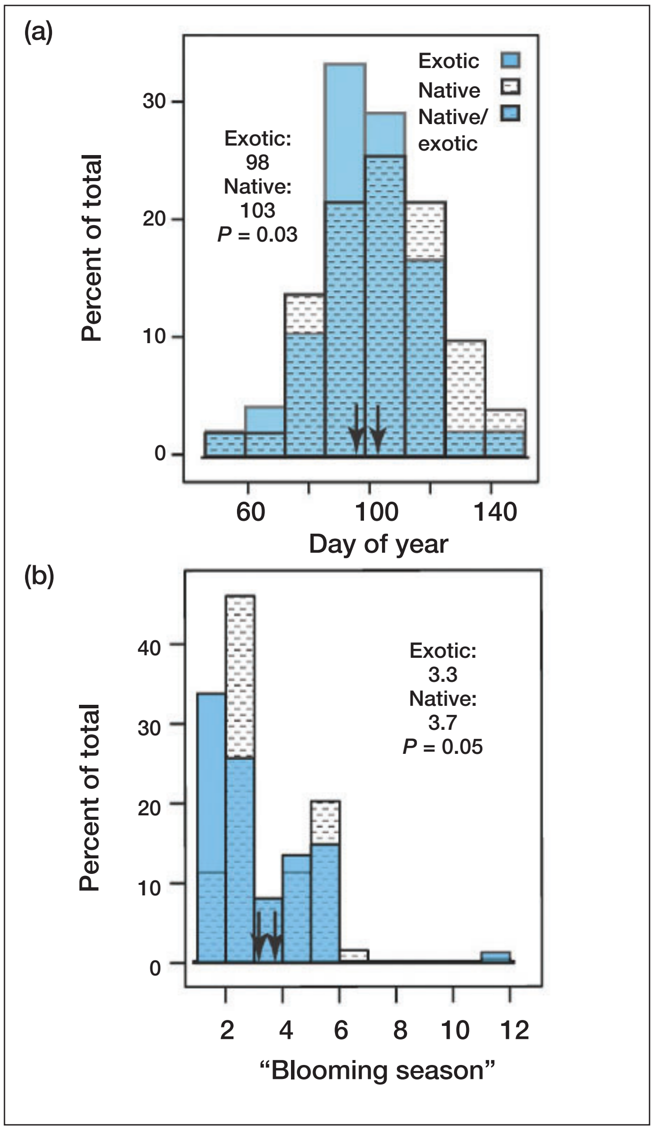

Figure 4. *Plant phenologies from Project BudBurst data (a) from North Carolina and (b) graminoids (grasses) from the USDA PLANTS database, show a consistent trend for exotic species to bloom earlier than native species. "Blooming season" is a numerical representation of USDA PLANTS seasonal periods, from early spring (1) to late fall (12). Arrows and values within the graph represent mean values for exotic versus native species.*

graminoids because they represented a phylogenetically narrow lifeform (compared with "forb/herb", "vine", "subshrub", "shrub", and "tree" options under "growth-habit").

We found that exotic species leafed (for Project BudBurst data, using a mixed-effects analysis of variance to account for multiple observations per species: $F_{2,84}$ = 3.74, $P = 0.028$) and flowered (for USDA PLANTS data, $F_{1,430}$ = 3.85, $P = 0.051$) earlier than native species (Figure 4), supporting the theory that exotic species may benefit from seasonal priority effects (Hypothesis B). These results indicate that an understanding of the role of phenology in structuring plant communities with exotic species may be a vital step in understanding how invasions succeed. Such suggestive results are further augmented by the current practices of many land managers.

Managing invasive species

Across the US, land managers already exploit differences in the phenologies of native and exotic species to decrease invasive plant cover (Table 1; Figure 1). For example, the phenology of the widespread invasive species Amur honeysuckle, which is active later in the season than native species (Resasco *et al.* 2007; Xu *et al.* 2007), is used for timing management strategies. In those parts of the Ohio River Valley invaded by honeysuckle, managers apply herbicide to forest understory soils late in the season – when only the roots of the invasive species are active. In many areas of the western US, plant phenology and the optimum timing of prescribed fire or grazing to remove exotic species have been long-standing areas of research in range management (Rinella and Hileman 2009). While much of this research has concentrated on the phenology of the invasive species, very late- or early-season treatments tend to best promote native success (Meyer and Schiffman 1999; Potts and Stephens 2009), suggesting that phenological gaps between invasive and native species may be important. Research that attempts to identify how phenological gaps may promote invasions could therefore provide information on optimum timing of management techniques and may highlight many more areas where managers could exploit the distinctive phenologies of exotic plant species. Identifying invasive species with distinct phenological niches may also lead to further opportunities to study invasive species through remote sensing (Resasco *et al.* 2007); if invasive species are green at a different time than native species, this could lead to improved collection of cover and spread data. In addition to these management opportunities, which can be used after invaders have become established, this research framework could also affect how we identify exotic (or native) species that may become invasive.

Although the vacant niche, priority effects, and niche breadth hypotheses (Figure 1; Hypotheses A–C) suggest primarily how to schedule management programs (Figure 1), the plasticity hypothesis (Hypothesis D) underlines the importance of targeted timing of management initiatives, as well as additional management opportunities. If exotic species are influenced by climate variation, managers could time removal programs (eg prescribed grazing) in years when climate anomalies – for example, unusually early rains in arid systems or unusually early, warm springs in mesic systems – will cause exotic species to be active before native species (Figure 1: Hypothesis D). Where exotic species show more variable leafing times, this may indicate a wider range of germination cues than the native species; identifying the difference in germination cues could conceivably allow managers to germinate exotics at unfavorable times of year. For example, in California grasslands, invasive grasses appear to require only one major rainfall event to germinate (Pitt and Heady 1978), whereas most native species rely on

Table 1. Many managers in the US already exploit differences in the phenology of native and invasive species

System	*Invasive species*	*Phenological difference from native species*	*Management practice*	*References*
Ohio River Valley forests	Amur honeysuckle (*Lonicera maackii*)	Active later in the season	Herbicide applied to understory forest soils late in the growing season	Resasco *et al*. (2007); Xu *et al*. (2007)
Montana and Idaho intermountain grasslands	Spotted knapweed (*Centaurea stoebe*)	Active later in the season	Herbicide applied to area in late season	Crone *et al*. (2009)
California grasslands	Yellow starthistle (*Centaurea solstitialis*)	Active later in the season	Prescribed burns in summer (dormant season for native species)	Benefield *et al*. (2001)
California grasslands	European annual grasses (*Bromus* spp, *Vulpia* spp)	Active earlier in the season	Prescribed burns or grazing early in the season	Dyer and Rice (1997)
Nebraska mixed grass prairie	Cheatgrass (*Bromus tectorum*)	Active earlier in the season	Prescribed burns or grazing early in the season	Munter (2008)

both specific temperature and rainfall cues (Levine *et al*. 2008). Based on Hypothesis D, managers in warm climates could apply small pulses of water before the rainy season, to promote exotic species germination; if soil-moisture levels are sufficiently low, the exotic species would die before seed set, thereby reducing the exotic annual seedbank.

Extending community and invasion ecology

Extending the four community assembly theories to include phenology (a) provides a framework for incorporating temporal niches into community and invasion ecology and (b) helps ecologists to understand how time may structure species interactions and communities. Although previous authors have examined the role of time in promoting species coexistence on an interannual scale (Angert *et al*. 2009), our hypotheses provide one model that considers coexistence and time on an intra-annual scale. By examining whether the most abundant species exhibit distinctive phenologies – ones that occur at specific times, are particularly long, or are more flexible – will test whether diversity in species' phenologies may be a key mechanism influencing how communities assemble. This, in turn, can provide the mechanistic groundwork for invasion biologists to predict species shifts and suggest where management based on distinct phenologies of invasive species may be most successful.

■ Conclusions

Invasion biologists have long recognized the role that phenology can play in promoting the establishment and spread of exotic species (Crawley *et al*. 1996). However, to date, studies have generally only considered flowering period as one of many plant traits that could predict invasiveness (Crawley *et al*. 1996; Cadotte and Lovett-Doust 2002) or have been conducted on small local scales. The hypotheses outlined in this paper could have broad applications in invasion biology and community ecology, as well as in the management of invasive species. Although we have focused on North America to illustrate these concepts, available data and potential applications are global.

A greater focus on time as a structuring force in communities is especially important with the advent of human-induced climate change. Ecologists have actively studied the outcomes of anthropogenic alterations of space for decades, and humans have also clearly altered timing by shifting growing seasons globally (Walther *et al*. 2002). Ecological theory is now challenged to understand and predict the outcomes of altered habitat space and time.

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WebTable 1. Current data resources provide tremendous opportunity to test the four hypotheses (outlined in the main text) across large spatial and temporal scales; here we review some of the major resource types available for North America

Data types	*Description*	*Examples*	*Spatial and temporal scales*	*Opportunities and challenges*
Individual-based plant phenology data collection programs	Data, often on flowering, are collected by researchers as part of specific projects that continue as monitoring projects; includes historically collected data that are updated by researchers and some long-term citizen-science records	Concord, Massachusetts, including Thoreau's observations (Miller-Rushing and Primack 2008); Gothic, Colorado (Miller-Rushing *et al.* 2008); Northern Great Plains, Minnesota and North Dakota (Travers and Dunnell 2009); Elevation gradient of Sky Islands in Arizona (Crimmins *et al.* 2009)	Spatially spotty but covering a range of latitudes and longitudes. Many have 20+ years of continuous data, whereas others have100+ years of sporadic data collection	Datasets often have tremendous temporal scales and generally include observations on hundreds of species. However, many datasets include wide variation in the frequency and design of data collection. For phenology data in particular, less frequent data collection often makes absolute knowledge of first bloom or leaf dates impossible. Advances in uncertainty theory (Wikle 2003) allow fitting basic models that estimate errors surrounding such dates (Dose and Menzel 2004)
Organization-based plant phenology data collection programs	Large-scale citizen-science projects that provide data protocols and websites to store data. Botanical gardens often have records of local blooming patterns	Project Budburst (www.budburst.ucar.edu); USA National Phenology Network (Betancourt *et al.* 2007, www.usanpn.org/?q=plant_phenology); Missouri Botanical Garden (www.mobot.org/MOBOT/bloom/)	Generally cover vast spatial scales, but have less comprehensive records for many locations. Many have much shorter temporal scales than individual-based datasets	Citizen-collected data often raise concerns about data quality (Silvertown 2009); however, the major organizations running citizen phenology data work to minimize such issues. Also, small targeted amounts of data collected by scientists can be designed to test the differences between scientifically collected and citizen-collected data, making possible the calculation and propagation of error surrounding citizen-collected data
Climate data	Historical and current data on climate variables, such as precipitation and temperature; additionally, "reanalysis products" provide climate data which include interpolations across space and/or time (for areas without sufficient local climate records)	NCEP/NCAR re-analysis (http://dss.ucar.edu/pub/reanalysis/); NCDC (www.ncdc.noaa.gov/oa/ncdc.html); Hadley Centre (www.metoffice.gov.uk/climatechange/science/hadleycentre/); PRISM Climate Group (www.prism.oregonstate.edu/)	Cover large spatial and temporal scales, usually at very fine intervals	Variation in which products are available is patchy, both across space and through time; this may make matching climate data (of consistent quality) to phenology records difficult. Re-analysis products may not take into account important local factors, such as slope. Making full use of products and deciding on metrics (eg of precipitation variability) may catalyze more collaborations between ecologists and climatologists

continued

WebTable 1. – *Continued*

Data types	*Description*	*Examples*	*Spatial and temporal scales*	*Opportunities and challenges*
Species information	Generally, government- or non-profit-based repositories of species information (eg lifeform, native/exotic status, range, blooming period, categorizations as invasive or harmful)	USDA PLANTS database (http://plants.usda.gov/); State native and invasive plant lists (eg California Native Plant Society; www.cnps.org/)	Generally excellent spatial coverage at the gross scale, whereas finer scale lists, such as county or state plant lists, may vary in their coverage. Temporal scale of coverage for plant lists is often short (<10 years)	Provides important information to supplement other data resources, such as native/exotic status, range in North America, and indicators of which exotic species are considered invasive (noxious weeds)

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