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INVITED REVIEW

Toward a comprehensive understanding of the phenological responses of non-native plants to climate warming: a review

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• **Background** Plants often shift their phenology in response to climate warming, with potentially important ecological consequences. Relative differences in the abilities of native and non-native plants to track warming temperatures by adjusting their phenologies could have cascading consequences for ecosystems. Our general understanding of non-native species leads us to believe these species may be more phenologically sensitive than native species, but evidence for this has been mixed, likely due, in part, to the myriad of diverse ecological contexts in which non-natives have been studied.
• **Scope** Here, we review the current state of knowledge on non-native plant phenological responses to climate warming. From observational and experimental studies, we synthesize: (1) the ways in which non-native plant phenology shifts with increased temperature, (2) the relative differences between natives and non-natives in phenological timing and sensitivity to warming, (3) the contingencies driving variable non-native phenological responses to warming, and (4) the ecological consequences of warming-induced phenological shifts in non-natives.
• **Conclusions** Early-season phenophases tend to advance with warming, sometimes (but not always) more so in non-native species relative to native species. Late-season phenophases, on the other hand, tend to be more variable: advancing, delaying, or remaining unchanged. Similarly, relative differences in phenological sensitivity between native and non-native plants were less consistent for late-season phenophases. However, our ability for inference is limited by the scope of studies done to date, which best represent temperate ecosystems in the Northern Hemisphere. We found phenological shifts in non-native species to be driven by various factors, including their evolutionary histories and the environmental context of the invaded system. Shifts in non-native phenologies result in varied ecological consequences, from shifting demographics of the non-native species themselves to changes in ecosystem level processes such as carbon cycling. Additional study addressing key gaps is vital to improving understanding of non-native phenological responses to warming.

Key words: Climate change, native species, non-native species, phenology, plants, species invasions, warming.

INTRODUCTION

Today's ecosystems face two serious, concurrent challenges: warming climates and the presence of non-native species. Both global change drivers threaten biodiversity and the ability of ecosystems to provide critical services (IPCC, 2013; IPBES, 2019). When combined, the impacts of warming and species invasions can be amplified, creating even greater ecological and conservation challenges (Walther *et al.*, 2009; Mainka and Howard, 2010; Hulme, 2017; Robinson *et al.*, 2020). One mechanism by which warming may intensify the impacts of

species invasions is through phenological shifts – changes in the timing of life history events (Wolkovich *et al.*, 2013; Kharouba *et al.*, 2018). Climate warming is well known to trigger phenological shifts across many plant and animal species (Cleland *et al.*, 2007; Parmesan and Hanley, 2015; Stuble *et al.*, 2021). In plants, these shifts are partly driven by sensitivity to temperature and other changing climate factors, such as precipitation (Zhou *et al.*, 2023). However, plant species vary in their phenological sensitivity – how much they advance or delay their life cycle events in response to the same climate cues (Thackeray *et al.*, 2016). Variable phenological sensitivity to warming

between native and non-native species could facilitate species invasions, making it a critical area for research (Wolkovich *et al.*, 2013; Wolkovich and Cleland, 2014).

Plants rely on temperature and other environmental cues to time key phenological events, such as germination, leaf emergence, reproduction, and fall (autumn) senescence. The ability of plants to shift phenology in accordance with environmental cues (phenological sensitivity) may depend on many factors, including (but not limited to) genetic variation, life-cycle duration, growth habit, rooting depth, resource storage, water-use efficiency, interactions with pests or pathogens, and phenotypic plasticity (Cleland *et al.*, 2007; Forrest and Miller-Rushing, 2010; Wolkovich *et al.*, 2012). Innate variation in sensitivity among species within a community may have ecological consequences. In temperate ecosystems, plants face a risk–reward trade-off between initiating phenological events too early or too late. Early spring or late fall frosts can damage leaf tissue, reduce reproductive output and waste critical carbon and nutrient resources (Gu *et al.*, 2008). However, early emergence or late senescence may offer competitive advantages. Early-emerging plants can access more resources compared with later-emerging species (Cleland *et al.*, 2012), while late-senescing plants may continue to accumulate carbon reserves longer than early-senescing ones (Fridley, 2012).

When species within a community vary in phenological sensitivities, climate warming can cause phenological mismatches. Phenological mismatch describes situations in which the phenological timing of a species becomes out of sync with key resources (Visser and Gienapp, 2019) or with other organisms, such as mutualists (Hegland *et al.*, 2009) or competitors (Nakazawa and Doi, 2012; Heberling *et al.*, 2019; Miller *et al.*, 2023). Plant species with higher phenological sensitivity may be better able to adjust to rapidly changing temperatures, thus maintaining or even increasing in abundance, driving shifts in community composition and ultimately the ecosystem functions these communities support (Cleland *et al.*, 2012; Fridley, 2012; Dawson-Glass *et al.*, 2025).

As a result of mechanisms including phenological mismatch, shifted growing seasons, and environmental risk exposure, species' phenological responses to climate change will play a role in determining 'winners' and 'losers' under future climate conditions (Cleland *et al.*, 2012; Miller *et al.*, 2023). One key area of concern is whether there will be predictable differences in the phenological responses of species that evolved within a given geographic region (native species) versus species that have been introduced by humans to new geographic regions (non-native species) (Box 1). The ability to predict how individual species might respond to climate change is key to our ability to support native species at risk for declines, and/or to mitigate the impacts of non-native species likely to increase, allowing effective targeting of conservation actions to lessen the impact of non-natives (Wolkovich and Cleland, 2014).

Research on phenological differences between native and non-native species has been an active area of ecological study, in part because phenological traits can help predict when introduced non-native species are likely to become invasive (Hulme, 2011*a*; Wolkovich and Cleland, 2014). Non-native species with phenologies that are distinct from the native species within the recipient community may prove successful due, at least

in part, to their ability to exploit 'empty phenological niches'. For example, in eastern North American old-field ecosystems, European herbs represent a large proportion of non-native species, and these invaders exhibit earlier leaf and reproductive phenologies than native herbs (Zettlemoyer *et al.*, 2019; Reeb *et al.*, 2020). Similarly, in eastern North American forests, non-native invasive woody shrubs retain their leaves later into the fall compared with both non-invasive non-native plants as well as native woody shrubs (Fridley, 2012). However, reviews and large-scale studies seeking evidence of consistent phenological differences between native and non-native species tend to present mixed results depending on the region, types of plant species, or phenophase of study (Hulme, 2011*a*; Fridley, 2012; Zohner and Renner, 2017; Gallinat *et al.*, 2018; Stuble *et al.*, 2021; Zettlemoyer *et al.*, 2022; Park *et al.*, 2024).

While ecologists have sought to identify broad trends to describe phenological sensitivities to warming in non-native species relative to natives, elucidation of unifying themes has proven difficult. Invasion ecologists, like ecologists in general (Schmitz, 2010), seek to find general rules of ecological communities, a task that has proven time and time again to be exceedingly difficult (Lawton, 1999). That said, our basic knowledge of individual systems is rich and informative (Simberloff and Losos, 2004), enhancing our understanding of the natural world, even if unifying rules have proven challenging. The mixed results of previous syntheses exploring phenological sensitivities in non-native plants are likely driven, at least in part, by contingencies associated with both the environment and the species themselves. Indeed, unique interactions between species and environments can influence how non-native species respond to warming through phenological shifts. Understanding these interactions will help us move toward a better understanding of the factors that drive responses by specific species in specific ecosystems (Parmesan and Hanley, 2015).

Here, we review the phenological responses of non-native plants to climate warming, summarizing the current state of knowledge, highlighting key drivers that may obscure general phenological patterns, and identifying where future research is needed. We review observational and experimental studies that address four distinct questions. First, are non-native species consistently advancing or delaying their phenology as a result of climate warming? Second, are non-native species advancing their phenology in response to warming at relatively faster rates than resident native species (i.e. do non-native plants have greater phenological sensitivities?)? Third, what intrinsic (e.g. functional group) and extrinsic (e.g. habitat type) factors drive contingencies in the responses of non-native plants to warming? And fourth, what are the documented impacts of warming-induced phenological shifts on the structure and function of native ecosystems? Finally, we highlight critical research gaps that could inform our understanding of the impacts of warming-induced phenology on invaded ecosystems.

LITERATURE REVIEW AND NON-NATIVE PHENOLOGICAL RESPONSES

Literature reviewed here was identified via a Web of Science Core Collection search using the terms 'TS=(phenology) AND TS=(climate change OR warming)' from January 1945 to

## BOX 1. PREDICTING THE OUTCOMES OF PHENOLOGICAL RESPONSES IN NATIVE AND NON-NATIVE SPECIES

When native and non-native plants occupy distinct phenological niches within invaded habitats, differences in their sensitivity to warming may drive predictable outcomes. The timing of a non-native plant's phenology relative to native plants likely influences the intensity of competitive interactions. Plants with overlapping phenological niches are more likely to directly compete for limited resources, while those with distinct phenological niches may experience reduced competition. Additionally, plants with earlier phenologies may exert priority effects, limiting the growth or reproduction of later species by depleting resources. Based on these assumptions, it may be possible to predict how existing differences in native and non-native phenology could interact with their varying phenological sensitivities to climate change, leading to different competitive outcomes under warming. Here, we depict three different historical (or baseline) phenological relationships and the ways in which warming may restructure each. Note that this illustration represents early-season phenophases. However, the reverse of the above-depicted relationships could be applied to illustrate how shifts affect late-season phenophases.
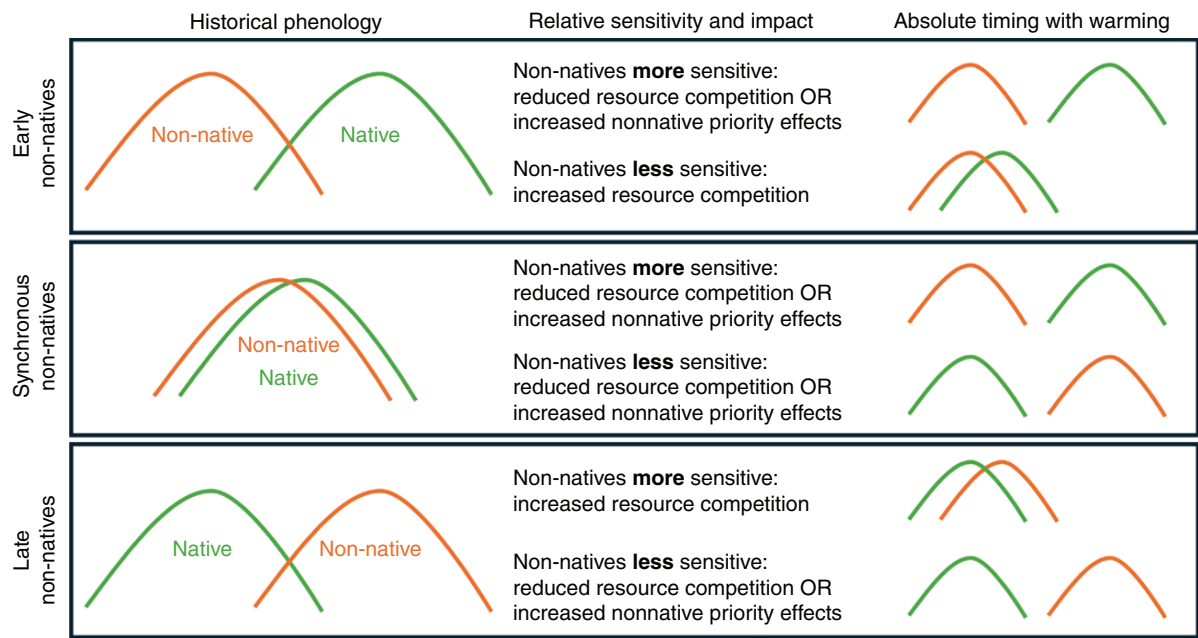
November 2022, returning 11 734 records. Note this search recovered publications that were available online in November 2022, which could have had a publication date later than 2022. We then screened the abstracts of these publications using the metagear package (abstract_screener function; Lajeunesse, 2016). We only retained papers that included phenological measurements of one or more non-native species and included a warming component. These criteria were purposely broad to encompass a large range of study types and systems. From our initial search, we recovered 172 papers that were potentially relevant to this review. Papers that were excluded during our initial screening included studies focused on animal phenology; those that did not include non-native species; or those that were a review or meta-analysis. We then reviewed the full texts of the 172 potentially relevant papers. At this stage, we excluded studies that, upon further review, did not meet the above criteria or studied non-native species only in their native range. To include additional relevant citations in our literature search, we also evaluated the literature cited in several highly cited reviews of non-native plant phenology, including Zettlemoyer *et al.* (2022), Gioria *et al.* (2018) and Gioria and Pyšek (2017). We

recovered <15 studies that were either missing or not retained from our initial search. Ultimately, we reviewed 54 articles that explored a phenological response of at least one non-native species to warming. Note that our literature search only included primary literature publications written in the English language. While we recognize that not including a broader suite of potentially relevant literature may exclude some relevant findings, the goal of our search was not to compile an exhaustive review of the published literature on non-native phenological responses to warming, but rather to gain a comprehensive understanding of major findings within the field and highlight key research gaps.

Of the 54 studies retained from our primary literature search, 12 studies (22 %) investigated a single non-native species, 2 studies (4 %) investigated multiple non-native species, and 40 studies (74 %) investigated both non-native and native species responses to warming (Table 1). Study locations spanned the globe but were primarily located in North America (52%; Fig. 1), followed by Europe (26 %), and often focused on temperate forests and woodland/shrubland systems (Fig. 2). Nearly two-thirds of studies measured phenological shifts in flowering

TABLE 1. *Details of the 54 studies that assess the phenological responses of non-native species to warming. Each study was assigned a study number from 1 to 54. Study type is classified as either observational (O) or experimental (E) and the type of warming used in the experiment is identified. The non-native and native species names (when applicable), or the number of species if more than three, were included in the study, as well as the phenophase studied, are listed for each study. Studies that include the same non-native species in both their introduced and native ranges are designated with an asterisk. 'Non-native phenological response to warming' describes whether the non-natives in each study shifted phenology to be earlier (←), later (→) or did not shift (×) in response to warming/warmed conditions. 'Non-native phenological response to warming relative to natives: absolute timing' describes whether non-natives were earlier (←), later (→) or similar (=) in their phenological timing under warming/warmed conditions relative to natives. Lastly, 'Non-native phenological response to warming relative to natives: sensitivity' describes whether non-native species experienced shifts in phenology that were of greater (+), lesser (−) or similar (=) magnitude relative to native species. In some cases, neither non-natives nor natives shifted their phenology in response to warming/warmed conditions (×). In some cases, phenological responses were inconsistent across factors in the study, including if the study had multiple sites, multiple 'sub-phenophases' (i.e. had multiple measurements of flowering at different life stages), or different levels of warming treatment. When studies reported variable responses because of these different experimental factors, or if responses changed through time, the directions/magnitudes of all responses are displayed, and the cause of the variability is recorded. When a study found responses differed by phenophase, the phenophases and their respective responses are recorded in separate rows. When all phenophases within a study responded similarly, responses are listed together in a single row. For studies that did not include native species, the final two columns are left intentionally blank.*

Study	Study number	Study type	Type of warming	Non-native species (or number of species if >3)	Native species	Phenophase studied	Non-native phenological response to warming	Non-native phenological response to warming relative to natives: absolute timing	Non−native phenological response to warming relative to natives: sensitivity
Fotiou *et al.*, 2011	1	O	Aspect	*Parietaria judaica*	None	Flowering	←/→ flowering season		
Trtikova *et al.*, 2010	2	E	Elevational gradient	*Erigeron annuus*	None	Flowering, fruiting	←		
Amouzgar *et al.*, 2023	3	O	Elevational gradient	*Pteridium aquilinum*	None	Leaf-out	←		
March-Salas and Pertierra, 2020	4	O	Elevational gradient	*Cerastium fontanum*, *Poa annua*	None	Leaf-out, flowering, fruiting	←/× species		
Osaki *et al.*, 2022	5	O	Elevational gradient	*Bidens pilosa* var. *pilosa*	None	Germination, leaf-out, flowering	←		
Hsu and Kao, 2014	6	E	Growth chambers	*Bidens pilosa* var. *radiata*, *Bidens bipinnata*	None	Germination	←/× species		
Chuine *et al.*, 2012	7	E	Infrared heaters	*Setaria parviflora*	None	Leaf-out, flowering, fruiting	←		
Howell *et al.*, 2020	8	E	Infrared heaters	*Bromus tectorum*	None	Flowering, senescence Germination	← ×		
Peng *et al.*, 2018	9	E	Infrared heaters	*Solidago canadensis*	None	Flowering, fruiting, senescence	→		
Dech and Nosko, 2004	10	O	Interannual temperature	*Lythrum salicaria*	None	Flowering Senescence	← ×		
Fitchett and Raik, 2021	11	O	Interannual temperature	*Jacaranda mimosifolia*	None	Flowering	←		
Montague *et al.*, 2008	12	O	Latitudinal gradient	*Lythrum salicaria*	None	Flowering	→		
Morais and Freitas, 2015	13	O	Latitudinal gradient and elevational gradient	*Acacia longifolia*	None	Leaf-out, flowering, Fruiting	←		
Keller and Shea, 2022	14	E	Open-top chambers	*Carduus nutans*	None	Flowering	←		

Table 1. *Continued*

Study	Study number	Study type	Type of warming	Non-native species (or number of species if >3)	Native species	Phenophase studied	Non-native phenological response to warming	Non-native phenological response to warming relative to natives: absolute timing	Non–native phenological response to warming relative to natives: sensitivity
Zhang *et al.*, 2012	15	E	Open top chambers	*Carduus acanthoides, Carduus nutans*	None	Flowering, senescence	←		
Alexander, 2010	16	E	Elevational gradient	*Lactuca serriola**	*Lactuca serriola**	Flowering	←/→ sub–phenophase	←	+
Erfmeier and Bruelheide, 2005	17	E	Growth chambers	*Rhododendron ponticum**	*Rhododendron ponticum**	Germination	←	←	+
Eyster and Wolkovich, 2021	18	E	Growth chambers	7*	7*	Germination	←/→ warming treatment	←/→ warming treatment	Not compared
Hirsch *et al.*, 2012	19	E	Growth chambers	*Ulmus pumila**	*Ulmus pumila**	Germination	←	←	Not compared
Leiblein-Wild *et al.*, 2014	20	E	Growth chambers	*Ambrosia artemisiifolia**	*Ambrosia artemisiifolia**	Germination	←	←	+
Udo *et al.*, 2017	21	E	Growth chambers	*Ulex europaeus**	*Ulex europaeus**	Germination	←/→ warming treatment	←/= warming treatment	Not compared
Peng *et al.*, 2019	22	E	Infrared heaters	*Solidago canadensis**	*Solidago canadensis**	Flowering, senescence Fruiting	→ ×	→ →	– ×
Zhou *et al.*, 2022	23	E	Infrared heaters	*Solidago canadensis**	*Solidago canadensis**	Flowering, fruiting	←	←	Not compared
Hulme, 2011b	24	O	Interannual temperature	19*	19*	Flowering	←	←	=
Fisichelli *et al.*, 2014	25	E	Growth chambers	4	9	Germination, leaf-out	←	Not compared	=
Wainwright and Cleland, 2013	26	E	Growth chambers	12	12	Germination	←	←	+
Wang *et al.*, 2022	27	E	Growth chambers	*Carya illinoinensis*	*Torreya grandis*	Senescence	→	Not compared	Not compared
Zettlemoyer and Lau, 2021	28	E	Growth chambers	11	13	Germination	←/→ warming treatment	=	=
Zettlemoyer *et al.*, 2019	29	E	Infrared heaters	27	25	Flowering, fruiting	←	←	+
Fridley, 2012	30	E	Interannual temperature	30	43	Leaf-out Senescence	← ×	= →	= ×
Fridley and Craddock, 2015	31	E	Interannual temperature	25	29	Leaf-out	←	=	=
Bertin, 2015	32	O	Interannual temperature	29	251	Flowering	←	Not compared	=
Bloom *et al.*, 2022	33	O	Interannual temperature	*Carduus nutans, Taraxacum officinale, Tragopogon dubius*	48	Flowering	←	Not compared	–
Calinger *et al.*, 2013	34	O	Interannual temperature	21	120	Flowering	←	Not compared	+

TABLE 1. *Continued*

Study	Study number	Study type	Type of warming	Non-native species (or number of species if >3)	Native species	Phenophase studied	Non-native phenological response to warming	Non-native phenological response to warming relative to natives: absolute timing	Non-native phenological response to warming relative to natives: sensitivity
Chen *et al.*, 2019	35	O	Interannual temperature	*Aesculus hippocastanum*	*Betula pendula, Fagus sylvatica, Quercus robur*	Leaf-out	←/→ time period	Not compared	+
						Senescence	←/→ time period	Not compared	–
Davis *et al.*, 2010	36	O	Interannual temperature	135	530	Flowering	←/→ site	←/→ site	+/– site
Du *et al.*, 2017	37	O	Interannual temperature	9	43	Flowering	←	Not compared	+
						Leaf-out	←	Not compared	=
Everingham *et al.*, 2023	38	O	Interannual temperature	8	29	Flowering	←/→/× species	Not compared	=
Gallinat *et al.*, 2018	39	O	Interannual temperature	18	37	Fruiting	→/× species	→	+
Gallinat *et al.*, 2020	40	O	Interannual temperature	10	15	Fruiting	×	→/= sub-phenophase	Not compared
Hulme, 2011a	41	O	Interannual temperature	76	271	Flowering	←	Not compared	+
Mantoani *et al.*, 2020	42	O	Interannual temperature	*Gunnera tinctoria*	*Juncus effusus*	Flowering	×	←	–
						Fruiting	×	→	×
						Leaf-out	←	→	–
						Senescence	×	→	×
Morecroft *et al.*, 2008	43	O	Interannual temperature	*Acer pseudoplatanus*	*Fraxinus excelsior, Quercus robur*	Leaf-out	←	←	=
Mulder and Spellman, 2019	44	O	Interannual temperature	12	29	Flowering, fruiting	←	→	=
						Leaf-out	←/→ sub-phenophase	=/→ sub-phenophase	+/= sub-phenophase
						Senescence	→	→	+
Polgar *et al.*, 2014	45	O	Interannual temperature	12	38	Leaf-out	←	=	=
Reeb *et al.*, 2020	46	O	Interannual temperature	5	6	Flowering	←	←	=
						Fruiting	←/→ season of warming	←	+/– season of warming
Von Holle *et al.*, 2010	47	O	Interannual temperature	29	41	Flowering	←/× site	=	×
Willis *et al.*, 2010	48	O	Interannual temperature	171	385	Flowering	←	←	+
Wolkovich *et al.*, 2013	49	O	Interannual temperature	13–183	93–319	Flowering	←/→ site	←/→ site	+/– site
Maynard-Bean *et al.*, 2020	50	O	Latitudinal gradient and interannual temperature	6	8	Leaf-out	←	←	=
						Senescence	×	→	×
Cao *et al.*, 2018	51	E	Open-top chambers	*Bidens frodosa, Solidago canadensis*	*Pterocypsela laciniata*	Flowering	←	Not compared	+/= sub-phenophase
Giejsztowt *et al.*, 2020	52	E	Open-top chambers	*Calluna vulgaris*	*Dracophyllum subulatum*	Flowering	←	←	+/= sub-phenophase

TABLE 1. *Continued*

Study	Study number	Study type	Type of warming	Non-native species (or number of species if >3)	Native species	Phenophase studied	Non-native phenological response to warming	Non-native phenological response to warming relative to natives: absolute timing	Non–native phenological response to warming relative to natives: sensitivity
Welshofer *et al.*, 2018	53	E	Open-top chambers	22	16	Flowering	←/→ site	←/→ site	=
						Fruiting	×	=	×
						Leaf-out	←/× site	←/= site	=/× site
Shustack *et al.*, 2009	54	O	Urban heat	*Lonicera maackii*	*Acer negundo, Aesculus glabra*	Leaf-out	×	=	×

7.5 7.10 7.15 7.65 7.70 7.75

(63 %; Fig. 1), nearly one-third measured the timing of leaf-out (31 %), and one-quarter measured timing of fruiting (26 %). Studies of late-season phenophases were comparatively less common, with only 19 % of studies measuring the timing of leaf senescence. Studies on germination phenology were also relatively rare (20 % of studies), and were largely comparisons of germination timing of a single species in its native and introduced range (45 % of germination studies).

Most studies of non-native plants found early-season phenophases, like leaf-out and flowering, advanced with warming, which is in line with findings from native plant phenology studies (Stuble *et al.*, 2021; Table 1, Fig. 1). Some phenophases, like fruiting or seed maturation, can occur throughout a growing season, depending on individual species' biology. For plant species with early-season fruiting or seed maturation, we found that these phenophases also tended to advance with warming. If a plant species' fruiting or seed maturation was toward the end of the growing season (i.e. in and around autumn in seasonal systems), however, warming sometimes caused a delay in the timing of that phenophase (Peng *et al.*, 2018). Senescence (Fig. 1) responded variably to warming across non-native species (Table 1). Germination phenology has been understudied relative to other phenophases and these studies found a mix of advanced phenology and no phenological responses to warming (Table 1).

One question of critical importance is whether non-native plants will be more responsive to warming temperatures relative to native plants (Hulme, 2011a; Wolkovich *et al.*, 2013; Zohner and Renner, 2017; Zettlemoyer *et al.*, 2022). If non-natives are consistently more sensitive than natives to warming climates, then it may signal that warming climates in invaded ecosystems promote increases in abundance of non-native species and decreases in abundance of native species. However, to date evidence on this generalizable trend is mixed (Hulme, 2011a; Wolkovich *et al.*, 2013; Zohner and Renner, 2017; Zettlemoyer *et al.*, 2022), including in half of the 40 studies that measured relative sensitivities to warming between native and non-native plants (Table 1). In 19 studies, non-natives had similar phenological sensitivity to natives, including in 6 studies where neither natives nor non-natives shifted phenology with warming. In only one-quarter of studies were non-natives more phenologically sensitive than natives, and this was most common when the studies focused on early-season phenophases. Approximately 10 % of studies found that natives were more phenologically sensitive than non-natives, while another 10 % of studies found that sensitivity differences varied by factors such as duration of warming, amount of warming, or the specifics of the phenophase measurement (Table 1).

DRIVERS OF NON-NATIVE PHENOLOGICAL RESPONSES TO WARMING

It is unlikely that a generalizable trend in phenological sensitivity exists for non-native plants across all species, ecosystems and invasion scenarios. Just as the search for broad patterns in phenotypic plasticity among invaders failed to yield consistent results (Palacio-López and Gianoli, 2011; Davidson *et al.*, 2023), more studies on non-native phenology are unlikely to provide clear answers. This complexity is typical of ecological systems, and instead of pursuing universal trends, ecologists should focus on formulating hypotheses around the specific conditions or drivers that might lead to predictable patterns (Simberloff and Losos, 2004; Schmitz, 2010). The phenological sensitivity of non-native plants to warming is governed by a range of intrinsic and extrinsic conditions (Godoy *et al.*, 2009; Calinger *et al.*, 2013; Wolkovich *et al.*, 2013; Chmura *et al.*, 2019). These factors drive which species are likely to be most responsive to warming temperatures, and where, and may dictate the relative sensitivities of native and non-native species to warming. In the following sections we discuss how patterns of phenological sensitivity may systematically vary across factors inherent to the plants themselves (i.e. intrinsic factors): traits, seasonality, phylogeny, place of origin, local adaptation, as well as factors inherent to the invaded ecosystem (i.e. extrinsic factors): habitat type, patterns of warming, and concurrent climate change factors. By offering this theoretical framework, we hope future studies on the responses of invaded plant communities to climate warming will be able to test more specific hypotheses, which could lead to greater generalizability and enhanced predictability of future impacts of non-native plants in warming ecosystems.

Life history and growth form

Phenological sensitivity may be linked to plant species' life history strategies or growth form. For example, longer-lived plants,
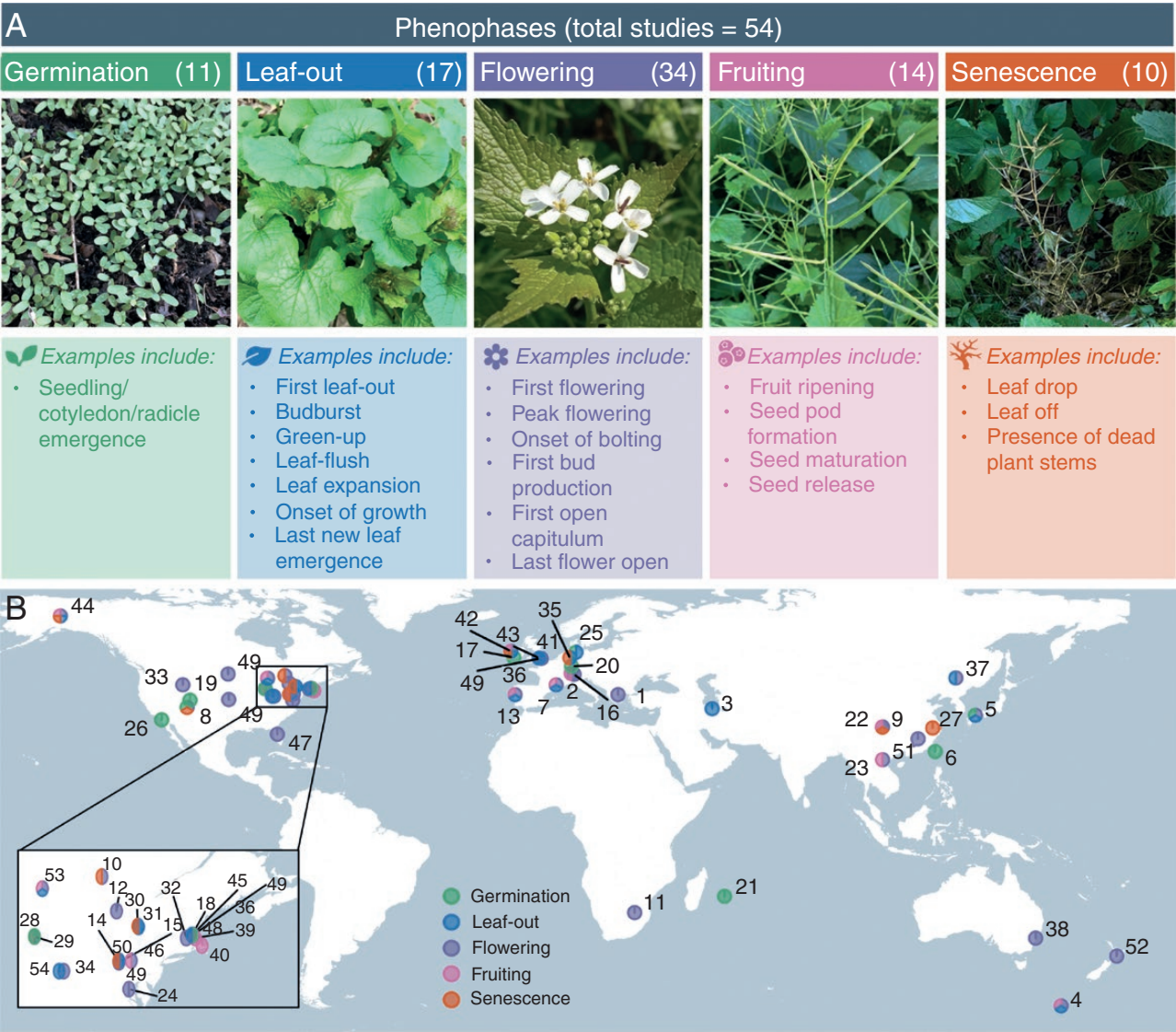
FIG. 1. (A) We define coarse phenophase categories and the individual phenophases represented within each category. Each phenophase category is illustrated with a photograph of *Alliaria petiolata* (garlic mustard), a forest herb native to Eurasia and a common invasive in North America. The number of studies including a measurement of a given phenological metric is shown in parentheses next to the phenophase (because some studies measure multiple phenophases these numbers do not sum to 54). Images of *A. petiolata* were derived from iNaturalist (observation numbers 5455046, 67834875, 84966724, 111919724, 226539016) (iNaturalist, 2017, 2021a, b, 2022, 2024). (B) Map of the location of each study included in our review, with points coloured by phenophase(s) explored. Points are labelled with a study number that corresponds to Table 1. If a study had multiple locations or represented the range of a non-native population, the mapped location of the study was approximated as a central study location. In two instances, a single central point did not accurately capture study location, because these studies occurred in multiple regions (Davis *et al.*, 2010 – study number 36; Wolkovich *et al.*, 2013 - study number 49). For these studies, we display multiple study locations.

including shrubs, trees and perennial herbs, invest a higher proportion of their carbon resources into long-lived storage tissues than short-lived annual plants. Plants that invest more in long-term carbon storage may be expected to be more conservative and less sensitive to warming (Wolkovich *et al.*, 2014). This could be because a single year of poorly timed phenology will have less dire long-term consequences for longer-lived species relative to annual species Additionally, if phenological sensitivity is a heritable trait, species with longer generation times will be slower to evolve to changing climate conditions. Over 13 000 plant taxa are now considered non-native around the globe and of the top 200 most globally widespread and successful non-native plants, 45 % are annual herbs (Pyšek *et al.*, 2017). As such, comparisons of phenological sensitivity between native and non-native species may sometimes find that non-native species are more sensitive to warming owing, in part, to a higher relative proportion of annual life history strategies in non-natives.

However, differences in the relative phenological sensitivity of non-natives compared with natives is sometimes present even when accounting for life history strategy. In a herbarium study of the flowering phenology of 141 species common to a variety of ecosystems in Ohio, USA, native and non-native annual herbs were significantly more sensitive to climate warming than

9.5

9.65

9.10

9.70
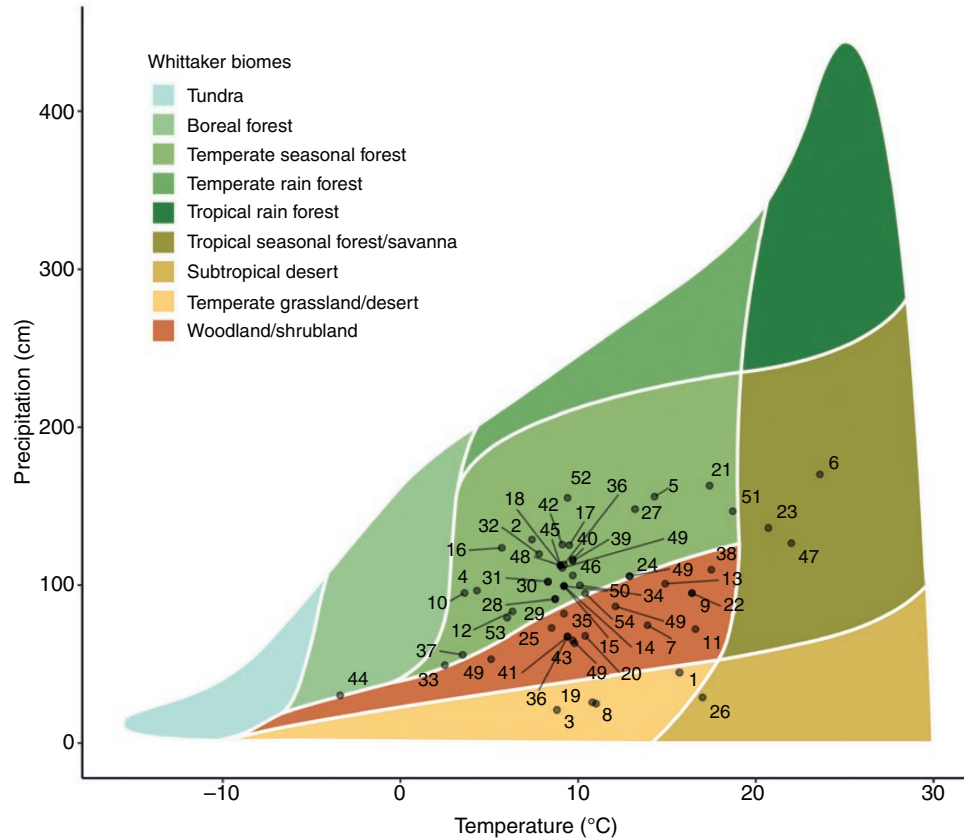
9.15

9.75

9.20

9.80

9.25

9.85

Fig. 2. Most studies on non-native plant phenology responses to warming occurred in temperate seasonal forest or woodland/shrubland ecosystems. Studies are plotted within Whittaker biomes (Ștefan and Levin, 2018) based on the mean annual temperature and precipitation of each study location (derived from Fick and Hijmans, 2017) and labelled by study number in Table 1.

9.30

9.90

perennial herbs (Calinger *et al.*, 2013). Yet, when considering only the annual herbs, non-natives exhibited more sensitivity, advancing their flowering by ~4 d per degree warming compared with the 1 d per degree warming of native annual herbs (Calinger *et al.*, 2013). Similarly, in a study of the responses of 347 native and non-native plants common to the British Isles, (Hulme, 2011*a*) found that annual herbs advanced flowering ~2 d per degree warming more than perennial herbs and 4 d per degree warming more than woody plants. Among non-native species introduced to the Isles after 1500, shorter-statured species of annual herbs common to fertile arable land exhibited the greatest sensitivity to climate warming.

Variation in traits (both seen and unseen) can be captured in phylogeny. Closely related species often display similar traits, and ultimately phenological patterns, when evolutionary pressures constrain phenology (Gao *et al.*, 2022). As such, the ability of species to adjust phenology in association with warming can, in some cases, be understood and predicted by considering these relationships. Among the studies reviewed (Table 1), the timing of leaf-out (Fridley and Craddock, 2015; Du *et al.*, 2017), flowering (Davis *et al.*, 2010; Wolkovich *et al.*, 2013) and fruiting (Gallinat *et al.*, 2018) all show strong phylogenetic signals. For example, a strong phylogenetic signal was found in the phenological sensitivities of flowering time across two distinct regions (Concord, USA, and Chinnor, UK) (Davis *et al.*, 2010). The strength of this phylogenetic signal in

geographically isolated species suggests critical phylogenetic conservation of phenological responses to warming. That said, other studies have failed to find a significant phylogenetic signal in phenological sensitivity among native and non-native species (Calinger *et al.*, 2013; Wolkovich *et al.*, 2013; Everingham *et al.*, 2023). Additionally, when accounting for phylogeny, the differences been natives and non-natives in fruiting time (Gallinat *et al.*, 2018), climate tracking (Willis *et al.*, 2010) and flowering/fruiting time shifts (Zettlemoyer *et al.*, 2019) can persist, suggesting that there are forces driving differences in phenological sensitivity beyond what can be explained by phylogeny alone.

Insomuch as many non-natives have been intentionally moved around the globe by humans for horticultural purposes (Reichard and White, 2001; Lehan *et al.*, 2013), there may be selection for certain phenological traits. For example, ornamental species with longer or unique flowering times that fall outside the window of native flowering times may be preferentially cultivated and introduced (Mack, 2005). Having unique phenological traits could, in turn, foster success in non-native species by allowing them to fill vacant phenological niches (Wolkovich and Cleland, 2014). Whether human preference for certain phenological traits has led to greater phenological sensitivity has yet to be explored in depth, but it is possible that the traits that have made non-native horticultural species attractive to humans may also benefit them in a warmer future. This is

9.35

9.95

9.40

9.100

9.45

9.105

9.50

9.110

9.55

9.115

9.59
9.60

9.120

likely a useful line of inquiry that could inform weed risk assessments seeking to prevent the introduction of potentially invasive species.

Seasonality of phenophase

In general, early-season phenological events tend to be more sensitive to warming than late-season phenological events (Fotiou *et al.*, 2011; Chen *et al.*, 2019; Chmura *et al.*, 2019; Stuble *et al.*, 2021). Even within a phenophase, species with earlier phenological timing seem to be more sensitive than species with later phenological timing. For example, earlier-flowering species are often more responsive to warming relative to later-flowering species (Hulme, 2011*a*; Calinger *et al.*, 2013; Wolkovich *et al.*, 2013; Bloom *et al.*, 2022). Similarly, woody plants with earlier leaf emergence tend to be more sensitive to warming spring temperatures than woody plants with later leaf emergence (Polgar *et al.*, 2014). One possible explanation for the apparently lower sensitivity of late-season phenology to warming is that the flexibility of later-season phenophases is constrained by phenophases occurring earlier in the year (Ettinger *et al.*, 2018; Mulder and Spellman, 2019).

In ecosystems where non-natives tend to occupy earlier phenological niches relative to native species, it may be likely that non-natives also show increased sensitivity to warming relative to natives. In many ecosystems, non-native species tend to germinate (Wainwright and Cleland, 2013), leaf-out (Morecroft *et al.*, 2008; Polgar *et al.*, 2014; Mantoani *et al.*, 2020; Maynard-Bean *et al.*, 2020), flower (Visser and Gienapp, 2019; Zettlemoyer *et al.*, 2019; Mantoani *et al.*, 2020; Reeb *et al.*, 2020) and fruit (Zettlemoyer *et al.*, 2019; Reeb *et al.*, 2020) earlier than natives. In a subset of these cases, these non-natives with earlier phenologies also demonstrated greater phenological sensitivity to warming (Wainwright and Cleland, 2013; Zettlemoyer *et al.*, 2019; Giejsztowt *et al.*, 2020; Reeb *et al.*, 2020). But it was not always the case that non-natives were more phenologically sensitive, even when their inherent phenology was earlier (Morecroft *et al.*, 2008; Polgar *et al.*, 2014; Giejsztowt *et al.*, 2020; Mantoani *et al.*, 2020; Maynard-Bean *et al.*, 2020; Reeb *et al.*, 2020). Indeed, while non-natives were broadly more phenologically sensitive than natives in an Ohio herbarium study, when considering only spring-flowering species (rather than those flowering later in the year), Calinger *et al.* (2013) failed to find differences in the phenological sensitivity between the two groups.

Place of origin

A species' phenological sensitivity is influenced by the climate conditions experienced in the native range during the course of evolution. In temperate climates, the reliability of spring warming temperature cues is highly variable among continental regions (Zohner *et al.*, 2017). For example, in eastern North America, temperatures fluctuate widely in the spring. As such, the onset of spring can be highly unpredictable from warming temperature cues alone. Plants that evolved in eastern North America, therefore, may have weakened sensitivity to spring warming temperatures because spring warming is a consistently unreliable phenological cue in the region. In

other temperate regions, including continental Europe and eastern Asia, spring temperatures are less variable (Zohner *et al.*, 2017). As such, we might expect plants that evolved in these regions to have a heightened sensitivity to spring warming because it is a more reliable phenological cue.

There is compelling evidence that, for woody plants, the continent of origin is predictive of phenological timing and sensitivity. For example, when grown in a European common garden, tree species that evolved in Europe, eastern North America and eastern Asia demonstrated different phenological timing under common climate conditions (Zohner and Renner, 2017). North American trees had shorter growing seasons owing to both delayed leaf emergence and early leaf senescence relative to European and eastern Asian species (Zohner and Renner, 2017). Indeed, warming experiments support that shrubs native to eastern North American forests are less sensitive to warming and require longer winter chilling periods than shrubs native to Europe and East Asia (Polgar *et al.*, 2014). These differences might also explain why many non-native shrubs common to eastern North American (and native to Europe and eastern Asia) forests have significantly earlier spring leaf phenology than native shrubs in the same forests (Maynard-Bean *et al.*, 2020; but see Donnelly *et al.*, 2024). However, as many non-native species tend to occupy early phenological niches, advancing phenology could increase the risk of frost damage or reduced pollination (Wilsey *et al.*, 2011; Kudo and Ida, 2013; Vitasse and Basler, 2013). The trade-offs made by species in the face of such risks seem to be influenced by climate conditions in their region of origin, with North American natives generally proving more conservative in their phenological sensitivity relative to European species, potentially driven by the milder and more predictable climate conditions in Europe (Davis *et al.*, 2010; Reeb *et al.*, 2020). Ultimately, findings suggest that adaptations to conditions within the native range can drive phenological sensitivity in the invaded range.

Consideration of the geographic origins of non-native plants could enhance the predictability of their phenological responses to warming within their invaded ranges. Hulme (2011*b*) demonstrated that shifts in the timing of flowering over 30 years across 19 non-native species co-occurring in Washington DC, USA, could be predicted based on shifts in flowering within their native range of Oxfordshire, England. This finding supports the notion that phenological responses can be conserved over large geographic distances (Hulme, 2011*b*). Similarly, plants invading regions with climate conditions like those of their native ranges exhibit similar phenology to natives within the invaded system. For example, the flowering phenology of non-natives originating in European Mediterranean climates and growing in Mediterranean climates of California, USA, the Cape region, South Africa, and the Spanish Mediterranean shared the same flowering phenology as the respective native communities, while those from other, non-Mediterranean climates flowered earlier or later than the natives (Godoy *et al.*, 2009).

Local adaptation and plasticity

Phenotypic plasticity may enhance the success of non-native species in their introduced ranges, allowing them to adjust

phenology under various environmental conditions (Wolkovich and Cleland, 2011). However, local adaptation of non-native populations within their introduced ranges may also be the cause of some phenological shifts. Disentangling these effects can inform how responsive non-native phenologies may be to warming conditions. While phenotypic plasticity may be important in the success of some non-natives (Cleland *et al.*, 2012; Wolkovich and Cleland, 2014), there is evidence that local adaptation may drive variation in phenology across the invaded ranges of some species (Weber and Schmid, 1998; Montague *et al.*, 2008). Further, the effects of local adaptation and plasticity likely interact. Phenological plasticity may differ across a species' introduced range (Trtikova *et al.*, 2010) or between the native and introduced range (Alexander, 2010).

Phenological adaptation can occur within a generation, providing evidence that non-native plants can rapidly evolve to track the climate of their invaded range. In a field experiment subjecting the forb *Ambrosia artemisiifolia* to simulated warming, Sun *et al.* (2020) found that when the offspring of parents subjected to warming were grown under common conditions, they flowered significantly later than both the parental plants and the offspring of the control plants. Importantly, the authors identified associated genetic changes, providing compelling evidence that the phenological changes observed in the warming treatment were the result of selection. Similar results were seen in Zhou *et al.* (2022), where maternal warming effects on phenology were stronger in introduced, Chinese populations of *Solidago canadensis* than native, North American populations. Interestingly, the impacts of maternal warming can sometimes differ from those of direct warming. For example, Zettlemoyer and Lau (2021) found that maternal warming delayed germination in offspring while directly warming offspring tended to advance germination. In a direct exploration of the influence of rapid local adaptation versus phenotypic plasticity, Eyster and Wolkovich (2021) compared the germination phenology of seven species in their native (Europe) and introduced (North America) ranges under a variety of growth chamber conditions. They found that native and introduced populations had similar germination timing, indicating germination phenology in both populations was broadly tolerant. However, specific conditions representing cold winters and warm springs caused phenological responses to diverge between populations, suggesting local adaptation to conditions typically seen in the North American, introduced range (Eyster and Wolkovich, 2021).

The responsiveness of non-native phenology to warming may also shift over time. Hulme (2011*a*) found invasion history to be a key predictor of phenological shifts over 30 years of warming in England. Specifically, more recently introduced species (i.e. those introduced after the 1500s) experienced the largest phenological responses to warming temperatures, while species introduced before the 1500s (as well as natives) did not experience significant phenological shifts over that period. Conversely, in a North American study, Zettlemoyer *et al.* (2019) found that non-native species that had colonized earlier were more phenologically plastic than recent colonizers, speculating that more time in the introduced range allowed for evolution facilitating their ability to shift phenological cues to match novel environmental conditions. While the Hulme (2011*a*) study was dominated by woody species, Zettlemoyer

et al. (2019) focused on grasses and forbs, potentially driving important differences in how these communities responded to changing conditions over long time periods.

Habitat type

Non-native species are likely variably responsive to warming temperatures in different habitat types, as environmental conditions can differ substantially across habitats. Further, non-natives have occupied habitats unevenly around the globe, with non-native species generally more abundant in temperate forest and grassland systems followed by the tropics (Hejda *et al.*, 2015; Pyšek *et al.*, 2017). These patterns of invasion could further confound our understanding of how non-native species respond to warming. A cross-continental comparative study found non-native species to be more phenologically responsive to warming than were native species within temperate mesic sites, with less difference between groups in drier grassland sites (Wolkovich *et al.*, 2013). Such findings suggest that temperature may be the predominant climate driver for mesic sites where water scarcity is not an issue, while precipitation may be a stronger driver in drier habitats.

Most studies of non-native plant responses to warming have focused on temperate seasonal forests, woodland/shrubland and temperate grassland/desert biomes in the Northern Hemisphere (Figs 1 and 2), with few studies conducted in boreal forests, tundras, temperate rainforests and tropical rainforests (Fig. 2). This has left us with a relatively poor understanding of how non-native phenology may be responding to warming trends in these understudied regions. However, it is likely that the considerable variation in climatic and other environmental conditions across biomes influences our understanding of the ability of non-natives to shift phenology in response to warming. Evidence suggests that flowering phenology, broadly, advances to a greater degree in response to warming in the Northern Hemisphere compared with the Southern Hemisphere (Everingham *et al.*, 2023). Additionally, non-native plants in subtropical and tropical regions can differ in the direction of phenological responses to warming compared with what has been observed in other ecosystems (Von Holle *et al.*, 2010). Given the high degree of spatial variability exhibited by plant phenological responses to warming, our understanding of phenological shifts likely reflects inherent bias in the geographic distribution of studies available for review.

Season and type of warming

Climate change can warm temperatures variably across seasons (EEA, 2012; US EPA., 2021), likely resulting in inconsistent plant phenology responses to warming depending on the season(s) with which a plant's life cycle aligns. For example, in temperate ecosystems, climate change often disproportionately warms winter temperatures relative to other seasons (EEA, 2012; US EPA., 2021). Plant phenology is cued by conditions preceding the life history event, though how far in advance can vary widely by both species and phenophase. In the Northern Hemisphere, the timing of leaf-out (Morecroft *et al.*, 2008; Polgar *et al.*, 2014; Du *et al.*, 2017; Amouzgar *et al.*,

2023), flowering (Willis *et al.*, 2010; Davis *et al.*, 2010; Hulme, 2011*a*, *b*; Calinger *et al.*, 2013; Bertin, 2015; Du *et al.*, 2017; Mulder and Spellman, 2019; Reeb *et al.*, 2020; Bloom *et al.*, 2022; Osaki *et al.*, 2022) and fruiting (Gallinat *et al.*, 2018) of non-native plants tends to be particularly sensitive to temperatures between December and May. Non-native and native species can differ in phenological sensitivity to different warming factors (Reeb *et al.*, 2020), indicating the timing of warming may be important to determining non-native phenological responses. That said, phenology cues can also be complex and sometimes counterintuitive. For example, warmer autumn temperatures increased bud dormancy in *Carya illinoinensis*, a non-native tree species in China, ultimately delaying leaf-out phenology the following spring (Wang *et al.*, 2022).

Long-term shifts in phenology may be, at least in part, driven by the relative importance of seasonal temperatures rather than large-scale trends in warming, per se. Everingham *et al.* (2023) found many non-native and native plants in their Australian herbarium study had not significantly shifted phenology since the 1800s, despite regional temperature increases across the study period. However, these species did respond to changes in temperature in the 3 months immediately preceding flowering. In a long-term field experiment, Howell *et al.* (2020) showed that an increase in interannual temperature variation had much larger effects on the timing of germination, flowering and senescence phenology in the non-native grass *Bromus tectorum* than did consistent simulated warming.

Further complicating our understanding of plant phenology in response to warming, cold winter temperatures can be an important force in advancing spring phenology in some plant species (Primack *et al.*, 2015). If non-native species require less winter chilling (i.e. the amount of cold weather needed before a plant can break dormancy) than native species, then warming winters will disproportionately slow native spring phenology relative to non-native spring phenology. This is true for eastern North American woody plants, where warmer winter temperatures delayed native plant leaf-out to a greater degree than non-native plants (Polgar *et al.*, 2014). Winter temperatures may also shape how germination phenology responds to spring warming. For example, in a study of eight North American non-native grasses and forbs native to Europe, germination was delayed by cold winters (i.e. long stratification period), even when followed by warm springs (Eyster and Wolkovich, 2021). Mild winters, on the other hand, advanced germination in the species (Eyster and Wolkovich, 2021). A reduction in the accumulation of chilling days driven by warming may also play an important role in modulating temperature sensitivity. For example, Chen *et al.* (2019) found that temperature sensitivity in leafing phenology has declined over the last 70 years for four tree species. The declines in temperature sensitivity were largely a result of chilling accumulation becoming more variable with warming.

Given the importance of warming during specific temporal windows, it may not be surprising that temperature variability within a year can also influence phenology. For example, while March-Salas and Pertierra (2020) found increased temperature variability significantly delayed reproductive phenology in two non-native grasses, *Poa annua* and *Cerastium fontanum*, only *P. annua* responded to increases in mean annual temperature

(with an advance in reproductive phenology). Similarly, Von Holle *et al.*, (2010) found that, while increases in maximum temperatures over historical time have caused non-native plants in Florida to flower slightly earlier, the range of minimum temperatures experienced throughout the year was the main determinant of flowering time. These studies suggest, in many cases, that phenological responses will be more complex than species simply responding to consistently increasing temperatures. Rather, many species will display more nuanced responses to temperature patterns throughout a region.

Other global change factors

In addition to rising temperatures, other environmental factors are changing concurrently as a result of global climate change, and these parameters have the potential to modify how phenology responds to warming. Plant phenology can respond to anthropogenic-driven shifts in the environment including changes in precipitation (Peñuelas *et al.*, 2004; Zeppel *et al.*, 2014) and increases in nutrient deposition (Wang and Tang, 2019). These environmental changes will undoubtedly interact with one another to impact plant phenology, adding further complexity to our ability to predict non-native phenological responses to global change.

Though this review focuses specifically on the impacts of warming on non-native plant phenology, several papers included in this review explore the interactions between warming and other global change drivers. Precipitation was the global change driver most commonly studied in tandem with warming (Chuine *et al.*, 2012; Hirsch *et al.*, 2012; Wainwright and Cleland, 2013; Wolkovich *et al.*, 2013; Morais and Freitas, 2015; Mulder and Spellman, 2019; Howell *et al.*, 2020; Mantoani *et al.*, 2020; Reeb *et al.*, 2020; Fitchett and Raik, 2021; Everingham *et al.*, 2023) and was shown, in some cases, to interact with warming to drive changes in non-native phenology (Chuine *et al.*, 2012), though not always (Wainwright and Cleland, 2013; Howell *et al.*, 2020). Importantly, non-natives and natives can differ in their phenological sensitivity to precipitation even in cases where they had similar sensitivities to warming (Hirsch *et al.*, 2012; Reeb *et al.*, 2020). Other factors also seem to interact with warming to drive phenology in non-native plants, including nitrogen deposition (Peng *et al.*, 2018, 2019; Zhou *et al.*, 2022) and the timing of snowmelt (Mulder and Spellman, 2019). Additional study of how warming will interact with other global change drivers will illuminate how non-natives may shift phenology in a future marked by multiple co-occurring anthropogenic changes, and may simultaneously provide insights into phenological sensitivity across different habitats.

WHY IT MATTERS

Phenology can drive vital parameters that influence plant growth and survival, including growing season length, seasonal resource acquisition and use, and interactions with co-occurring species (Iler *et al.*, 2021). As such, a plant's ability to track shifting temperatures via shifting phenology is often (though not always; see Iler *et al.*, 2019) advantageous,

and variability across species can lead to shifting community composition (CaraDonna *et al.*, 2014) and ecosystem function (Tang *et al.*, 2016; Piao *et al.*, 2019). Further, consistent differences in phenological sensitivity between native and non-native plants can exacerbate the impacts of non-native plants on native ecosystems (Zettlemoyer *et al.*, 2019). Such impacts can scale from populations to ecosystem functioning (Mooney *et al.*, 2009).

Individuals and populations

Advancing early-season or delaying late-season phenophases can extend the growing season for individual plants or populations (Fridley, 2012; Zhang *et al.*, 2012; Mulder and Spellman, 2019; Howell *et al.*, 2020). Extended growing seasons may increase annual carbon gains and promote growth and reproduction. For example, warming-induced advances in the vegetative and reproductive phenology of the non-native C_4 grass *Setaria parviflora* increased the grass's biomass and fecundity in invaded grasslands in the Mediterranean Basin (Chuine *et al.*, 2012). Similarly, the advanced germination and flowering phenology of the non-native forb *Bidens pilosa* in its invaded range in western Japan led to longer growing seasons and increased reproduction under warmed conditions (Osaki *et al.*, 2022). In some instances, plants may shift relative timing of phenophases to capitalize on growth. For instance, purple loosestrife (*Lythrum salicaria*), a late-summer-flowering perennial forb from Europe and Asia, delays flowering in warmer conditions enabling the plant to grow longer, leading to increased carbohydrate resources and greater flower and seed production later in the season (Colautti *et al.*, 2017). That said, nutrient limitations can slow vegetative growth even under more favourable growing conditions (Norby *et al.*, 2010). Alternatively, more rapid photosynthetic rates induced by higher concentrations of CO_2 may limit a plant's leaf longevity (Zani *et al.*, 2020), ultimately limiting growing season length.

For non-native species that advance (rather than delay) flowering in response to warmed conditions, warming may open entirely new flowering periods/seasons for non-native plants, ultimately enhancing their fitness (Osaki *et al.*, 2022). Similarly, the timing of fruiting/seeding can also foster improved access to resources, growth and reproduction for non-natives. Indeed, a field experiment that manipulated the seed release phenology of the non-native perennial herb *Carduus nutans* found that seeds released earlier produced larger plants in the following growing season (Keller and Shea, 2022). Such mechanisms have the potential to alter population viability variably across species, even as a species adapts in response to climate change.

Phenology is a key adaptive trait with the potential to shape species' abundances and ultimately distributions (Chuine, 2010), drawing a clear linkage between phenology and the invasion potential of non-native species. Willis *et al.* (2010), for example, found that non-natives (and particularly those classified as invasive) have been better than natives at shifting flowering times earlier to track warming temperatures over the past 100 years. Importantly, the non-natives best able to shift their flowering phenology also showed marked increases in abundance since 1900 relative to the native species. Similarly,

phenotypic sensitivity in flowering also corresponded to a high rate of successful invasion (Davis *et al.*, 2010). This suggests that climate change shapes the success of invaders and that strong historical filters likely favour the establishment of species with higher levels of phenological sensitivity. However, there is also evidence to suggest that other factors, such as the timing of introduction, may be even more important than phenotypic sensitivity in explaining successful invasions. For example, while non-natives showed both strong phenological sensitivities to warming and general increases in their distributions, the two were not linked (Hulme, 2011*a*). Instead, a non-native's date of introduction into the British Isles was a stronger predictor of their change in distribution across 30 years.

Communities

The capacity of non-native plants to shift phenologies in response to warming may not only enhance their own performance, but also influence their impacts on the native communities they invade. Differences in phenological sensitivity can play important roles in structuring competitive dynamics among species, and ultimately community composition and ecosystem function (Polgar and Primack, 2011; Rudolf, 2019). This might be particularly true when warming advances early-season phenophases, such as germination or leaf-out, which can promote carbon capture through extending the growing season (e.g. leaf longevity; Kikuzawa, 1995) or enable resource acquisition (such as soil resources like water and nutrients; Nord and Lynch, 2009) through factors like priority effects (Wolkovich and Cleland, 2014; Buonaiuto and Wolkovich, 2023; Zou *et al.*, 2023). Wainwright and Cleland (2013) found that non-natives advanced germination timing more than natives under warming, allowing them to achieve greater densities than natives, though, in this case, only when combined with increased watering. Earlier-bolting populations of the non-native forb *Lactuca serriola* experienced greater negative impacts (via competition) across five native California grassland species relative to later-flowering *L. serriola* (Alexander and Levine, 2019). We might also expect that increased growing seasons of non-native shrubs and other taller-statured plants (Maynard-Bean and Kaye, 2021) could potentially influence community dynamics by shading out natives.

Phenological shifts in non-native species can also drive large and unintuitive impacts on the reproductive success of co-occurring native species via shifts in interactions across trophic levels. For example, Cao *et al.* (2018) found that warming-induced advances in flowering extended the flowering season for two annual non-natives while simultaneously shortening the flowering season for a native annual, resulting in greater floral synchrony among the non-natives but not the native species. Zettlemoyer *et al.* (2019) also reported increased synchrony among non-natives, but not natives, under elevated temperatures. However, this increased flowering synchrony was driven by a shift in the flowering season (proportionate shifts in both the beginning and ending of flowering) rather than an extended flowering period. Regardless, floral duration and synchrony have substantial implications for key reproductive services like pollination and should thus be a focus of future research. Waters *et al.* (2020) demonstrated that advances in the

flowering of two non-native prairie species (forb *Hypochaeris radicata* and shrub *Cytisus scoparius*) drove shifts in pollinator visitation rates and ultimately seed set, though it did so variably across seven co-occurring native species. These observed changes were most likely mediated by changes in available floral resources in the community modifying pollinator foraging behaviour (Waters *et al.*, 2020). Similarly, Giejsztowt *et al.* (2020) showed that the flowering phenology of a non-native forb, *Calluna vulgaris*, was more sensitive to warming than that of a co-occurring native shrub, *Dracophyllum subulatum*. As a result, *C. vulgaris* and *D. subulatum* experienced a greater overlap in flowering. A complementary experiment revealed that this increase in floral overlap reduced reproduction of the native species via increased competition for pollinators (Giejsztowt *et al.*, 2020).

Shifts in seed set can drive demographic shifts, particularly within plant species that are particularly sensitive to reproductive rate (which is not always the case; see Iler *et al.*, 2019). Phenological changes with warming may also alter non-native species interactions with seed dispersers, with implications for reproduction and non-native spread alike. However, Gallinat *et al.* (2020) found that, despite non-natives fruiting later and comprising a large proportion of available fruits in late autumn, birds still primarily consumed native species' fruits, even if they were less abundant or no longer ripe (Gallinat *et al.*, 2020). These findings suggest that non-native fruits may become a more important food source for birds into the winter season as native fruit abundance diminishes, but indicate that autumn native seed dispersal dynamics may be robust to changes in non-native fall phenology (Gallinat *et al.*, 2020).

Phenological sensitivity and risk

While phenological sensitivity may confer benefits to non-native plants, there may also be risks associated with high phenological sensitivity. For example, advances in germination associated with increased temperatures could result in the arrival of vulnerable seedlings before the onset of reliable rains, leading to increased seedling mortality (Wainwright and Cleland, 2013). Similarly, early leaf-out could put plants at increased risk for damage associated with the possible occurrence of late frost events (Hufkens *et al.*, 2012; Fisichelli *et al.*, 2014). Frost can also make advances in flowering risky for some species. Whether frost risk associated with early flowering will increase (Augspurger, 2013; Liu *et al.*, 2018) or decrease (Zohner *et al.*, 2020; Park *et al.*, 2021) under ongoing climate change has not yet been resolved, and is likely geographically variable. A study exploring North American shifts in last frost dates relative to flowering dates from 1920 to 2015 found that for 66 % of species last frost date has advanced more than flowering date, resulting in a lower frost exposure risk for flowers (Park *et al.*, 2021).

Ecosystems

Phenological shifts in non-native plants have the potential to drive ecosystem-level dynamics, particularly in systems in which non-natives are abundant. For example, Fridley (2012) found that the delay of senescence of non-native trees, shrubs and lianas in a forest system allowed these species to capture a significant portion of their carbon after the native canopy dropped its leaves. This constitutes a notable change in seasonal patterns of forest productivity. Similarly, the extended growing seasons of non-native shrubs (driven by earlier leaf emergence and delayed senescence) have been demonstrated to reshape the physical environment on the forest floor, altering light levels and resultant temperatures on the forest floor (Maynard-Bean and Kaye, 2021). How these phenological changes in non-natives translate into other ecosystem-level impacts such as nutrient cycling and food web dynamics has yet to be explored in depth.

CONCLUSIONS AND FUTURE DIRECTIONS

Nonnative phenological responses, and comparisons with native species

Many individual studies have demonstrated that non-native species are shifting phenology with warming, but evidence that non-natives are generally more phenologically sensitive to warming than natives has been mixed, with many studies showing no differences between natives and non-natives. Further, larger studies encompassing many species note highly variable responses among species (e.g. Hulme, 2011a; Calinger *et al.*, 2013), and syntheses seeking to draw quantitative conclusions have found weak evidence for global differences in phenological sensitivity between native and non-native species (e.g. Zettlemoyer *et al.*, 2022). Most studies included in this review found some evidence that non-native plants track warming temperatures through shifts in phenology, and further, that in some cases non-native species shift their phenology to a greater extent than co-occurring natives (Fig. 3). However, there are also many examples of native and non-native species with similar phenological sensitivities. It is important to note that most research has largely focused on flowering phenology, followed by leaf-out phenology. The phenology of senescence, fruiting and germination, while critical to the fitness of individual plants and to the overall functioning of ecosystems, has been comparatively understudied. This represents a critical gap in our understanding, particularly because the literature that does exist reports that late-season phenophases (such as senescence) tend to respond less uniformly to warming than do early-season phenophases, making it even more difficult to elucidate patterns and predict future trends (Gallint *et al.*, 2015; Parmesan and Hanley, 2015).

Key intrinsic and extrinsic drivers

Nuanced differences among species and environments across studies likely obscure broad trends. The lack of a broad set of governing rules here is not unique to the study of phenological sensitivity, nor invasion ecology writ large, but rather is common to ecology, broadly. Our present understanding of warming-induced phenological shifts among non-natives is heavily biased towards studies of fast-growing herbaceous (often annual) species in temperate systems within the Northern Hemisphere. As such, our knowledge of such dynamics in tropical, subtropical, tundra, boreal and Southern Hemisphere

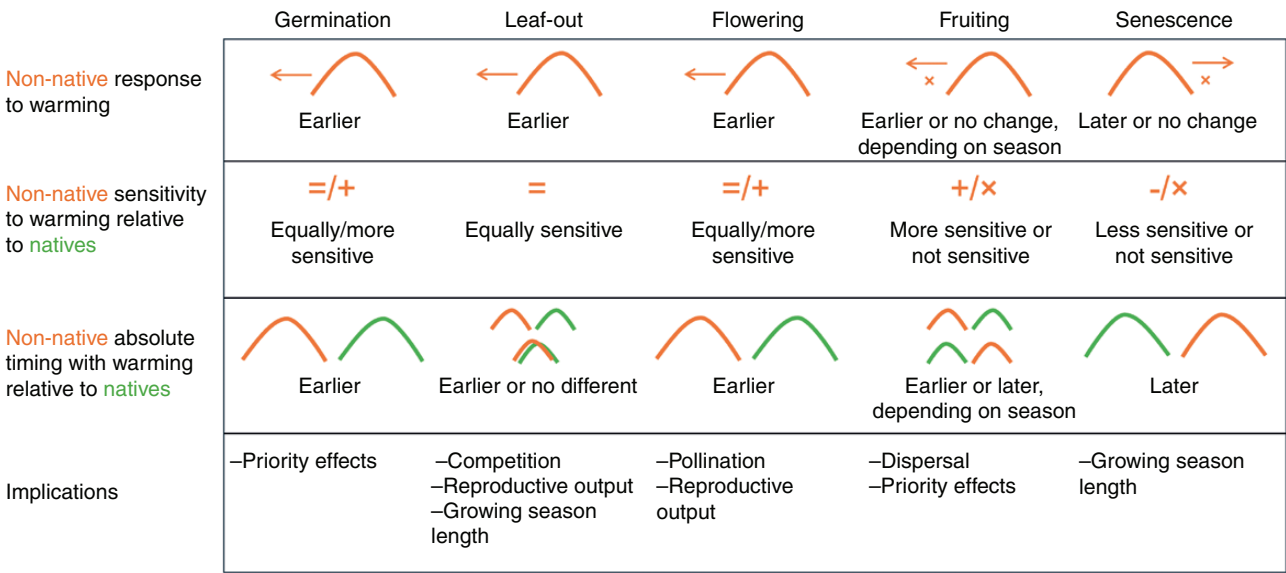|	Germination	Leaf-out	Flowering	Fruiting	Senescence
Non-native response to warming	Earlier	Earlier	Earlier	Earlier or no change, depending on season	Later or no change
Non-native sensitivity to warming relative to natives	=/+ Equally/more sensitive	= Equally sensitive	=/+ Equally/more sensitive	+/✗ More sensitive or not sensitive	-/✗ Less sensitive or not sensitive
Non-native absolute timing with warming relative to natives	Earlier	Earlier or no different	Earlier	Earlier or later, depending on season	Later
Implications	–Priority effects	–Competition –Reproductive output –Growing season length	–Pollination –Reproductive output	–Dispersal –Priority effects	–Growing season length

FIG. 3. Most non-natives surveyed in the studies we reviewed advanced or maintained early-season phenophases (including germination, leaf-out, flowering and early season fruiting) in response to warming. Late-season phenophases (like late season fruiting and senescence) were typically less sensitive or delayed (but were also less well studied). Non-natives were usually equally or more sensitive to warming relative to natives, though this pattern was less evident in late-season phenophases. As a result, non-native phenology was typically earlier than native phenology for early-season phenophases, and later for late-season phenophases. We highlight areas where these responses are likely to be important.

systems, and in plants with perennial life histories, is critically limited. As is so often the case with ecological dynamics, many factors drive the responsiveness of non-native plant phenology to warming, including region of origin, time of introduction, environmental conditions within the invaded range, and plant traits. Further study on, and accounting for, this variability would greatly improve our understanding of non-native responses to warming.

Impacts of warming-induced non-native phenological shifts

Critically, the ability of non-native species to advance or delay phenological transitions with the changing climate can confer benefits to these species, sometimes with knock-on consequences for the invaded ecosystem. These shifts impact not only the non-native species themselves, but also co-occurring natives, and can even scale up to ecosystem-level processes. These effects are most pronounced when the phenological sensitivity of non-natives outpaces (or lags) that of natives within the community (a phenological mismatch; Box 1). In fact, the literature provides diverse evidence that such shifts can influence many aspects of invaded systems, from population dynamics to interspecific interactions, and ultimately ecosystem function (Fig. 3). However, our understanding of the implications of non-native phenological shifts is still lacking as most studies to date have focused solely on documenting phenological shifts. Studies that do explore the implications of phenological shifts have primarily explored demographic responses. Additional studies of the consequences of shifts in non-native phenology for communities and ecosystems are a vital next step. Such studies might include assessments of shifts in nutrient/carbon dynamics (Fridley, 2012), community

composition (Dawson-Glass *et al.* 2025) and multitrophic species interactions (Gallinat *et al.*, 2020).

CONCLUSIONS

While the impacts of warming on phenology are variable across species and geographies, broad evidence is emerging that many non-native species are shifting the timing of life history events in response to warming, and sometimes (but not always) do so more effectively than native species. Such changes are likely critical drivers of how warming will reshape natural systems. However, additional research in these areas will enhance our ability to predict such responses, particularly exploring a greater diversity of phenological responses in a greater diversity of species in more habitat types and locations around the globe.

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