

**OPINION**

# Buffering and phenological mismatch: A change of perspective

Jamie C. Weir  | Albert B. Phillimore Institute for Ecology and Evolution,  
University of Edinburgh, Edinburgh, UK**Correspondence**Jamie C. Weir, Institute for Ecology  
and Evolution, University of Edinburgh,  
Edinburgh, UK.  
Email: [jamiweir@outlook.com](mailto:jamiweir@outlook.com)**Abstract**

The potential for climate change to disrupt phenology-mediated interactions in interaction networks has attracted considerable attention in recent decades. Frequently, studies emphasize the fragility of ephemeral seasonal interactions, and the risks posed by phenological asynchrony. Here, we argue that the fitness consequences of asynchrony in phenological interactions may often be more buffered than is typically acknowledged. We identify three main forms that buffering may take: (i) mechanisms that reduce asynchrony between consumer and resource; (ii) mechanisms that reduce the costs of being asynchronous; and (iii) mechanisms that dampen interannual variance in performance across higher organizational units. Using synchrony between the hatching of winter moth caterpillars and the leafing of their host-plants as a case study, we identify a wide variety of buffers that reduce the detrimental consequences of phenological asynchrony on caterpillar individuals, populations, and meta-populations. We follow this by drawing on examples across a breadth of taxa, and demonstrate that these buffering mechanisms may be quite general. We conclude by identifying key gaps in our knowledge of the fitness and demographic consequences of buffering, in the context of phenological mismatch. Buffering has the potential to substantially alter our understanding of the biotic impacts of future climate change—a greater recognition of the contribution of these mechanisms may reveal that many trophic interactions are surprisingly resilient, and also serve to shift research emphasis to those systems with fewer buffers and towards identifying the limits of those buffers.

**KEYWORDS**

asynchrony, climate change, environmental change, life history, perturbation, resilience, stability, synchrony, timing

## 1 | INTRODUCTION

Phenology—the timing of life history events—often plays a central role in structuring interaction networks, including food-webs. Where resource inputs are pulsed, such as in temperate forests and lakes in the spring, bursts of primary productivity and trophic interactions can be highly ephemeral (i.e. short-lived); a scenario that is expected to place the phenology of consumers under strong selection for synchrony with key resources (Cushing, 1969, 1990; Durant et al., 2007).

Outside of the tropics many primary producers use spring temperatures as a phenological cue indicating the arrival of benign conditions, with primary and secondary consumers often converging on similar (Thackeray et al., 2016) or correlated (Shutt, Cabello, et al., 2019) cues to track the timing of their respective resources. The emergence of widespread evidence that on average consumer species are advancing their phenology by less than the resources they rely on (Roslin et al., 2021; Thackeray et al., 2016) has led to concern that rising temperatures could result in consumers becoming ‘asynchronous’

and mismatched with their resources (Durant et al., 2007; Samplonius et al., 2020; Visser et al., 2021; Visser & Gienapp, 2019).

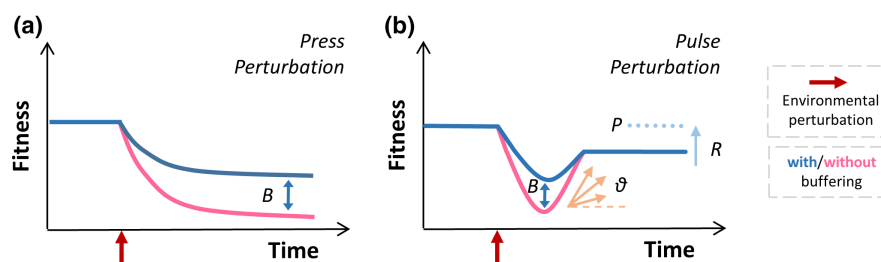
Amid the attention given to the risks of climate-mediated phenological asynchrony, there is growing but scattered evidence that a wide range of mechanisms can serve to buffer consumers against the impacts of asynchrony (Bartomeus et al., 2013; Macphie et al., 2020; Reed et al., 2013; Weir, 2022). Our impression is that the breadth and impact of such buffering mechanisms is not widely appreciated or reflected in the phenological mismatch literature. Therefore, in this piece we attempt to assimilate the evidence, synthesize the different forms that buffering can take, and identify implications for the stability of interaction networks in the face of climate warming. In the context of phenological interactions, we define ‘buffering’ as any mechanism that softens the impact of phenological mismatch on the focal species (Figure 1), where the metric of performance can be adjusted according to the organizational level (e.g. individual fitness, population growth rate, etc.). We note that “buffering” has been discussed elsewhere in the ecological literature, with respect to demography (Hilde et al., 2020), populations (Milles et al., 2023), communities (Hegland et al., 2009; Rudolf & Ekeland, 2021), and ecosystems (Jeltsch et al., 2000). Buffering is related, but not identical, to concepts of ecosystem stability and resilience (Figure 1), which are also widely discussed in the literature (Grimm & Wissel, 1997). Across different ecological contexts, “buffering” is consistently used to imply mechanisms that promote the stability of a state in the face of press and pulse environmental perturbations (Figure 1).

We identify three ways in which the buffering of phenological interactions can operate: (i) by reducing the degree of asynchrony between consumer and resource (Figure 2b); (ii) by reducing the performance cost that the consumer incurs from asynchrony (Figure 2c); and (iii) from portfolio effects whereby weak or negative covariance among individuals and/or environments dampens year-to-year variation in consumer performance at an aggregate level (Figure 2d,e; Childs et al., 2010; Dempster, 1955; Milles et al., 2023; Schindler et al., 2015; Slatkin, 1974).

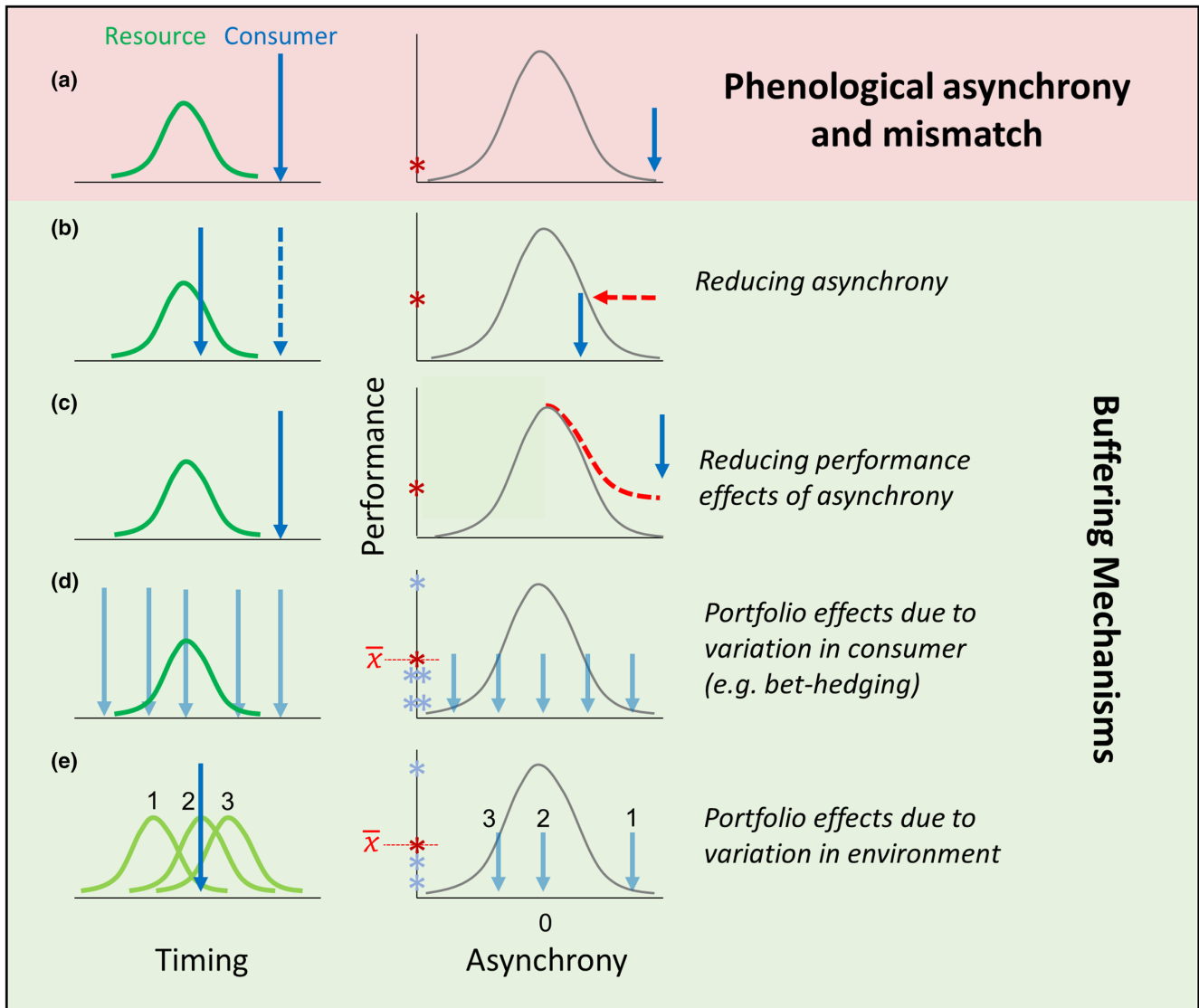
In this perspective, we present the phenology-mediated trophic interactions between a single caterpillar species—the winter moth (*Operophtera brumata*)—and its host plants as a case study to highlight the diversity of buffering mechanisms that can exist within a single system. Our motivation for focusing on this species is that its trophic interactions are paradigmatic in the study of phenological mismatch, and we can draw on decades of research that has been conducted in the field and the laboratory. First, we outline the life history of the winter moth in detail, discussing the potential for asynchrony and phenological mismatch to occur. We then identify mechanisms at each developmental stage (e.g. adult, egg, caterpillar, etc.) that might serve to buffer offspring, parents, populations, and meta-populations (a ‘population of populations’; Levins, 1968) of this consumer species against the fitness consequences of asynchrony with its food resources. We follow the case study by examining the extent to which the buffering mechanisms that we identify in this system are likely to generalize to other caterpillar species, and more broadly. Finally, we identify research priorities and opportunities to better understand the nature and consequences of buffering in ecological interactions.

## 2 | CASE STUDY: PHENOLOGICAL MISMATCH AND BUFFERING IN THE WINTER MOTH

Much work on the phenological (a)synchrony of the winter moth and its resource emphasizes oak (*Quercus* sp.) as a host-plant (van Asch & Visser, 2007). Oaks leaf-out in the spring as benign conditions for growth arrive and the risk of late frost recedes, with the time of leaf-out for an individual tree able to differ by several weeks from year-to-year depending on spring forcing and winter chilling temperatures (Roberts et al., 2015). Winter moth caterpillars that hatch from eggs in synchrony with buds breaking on oak (Figure 3) have access to a short-lived but plentiful resource



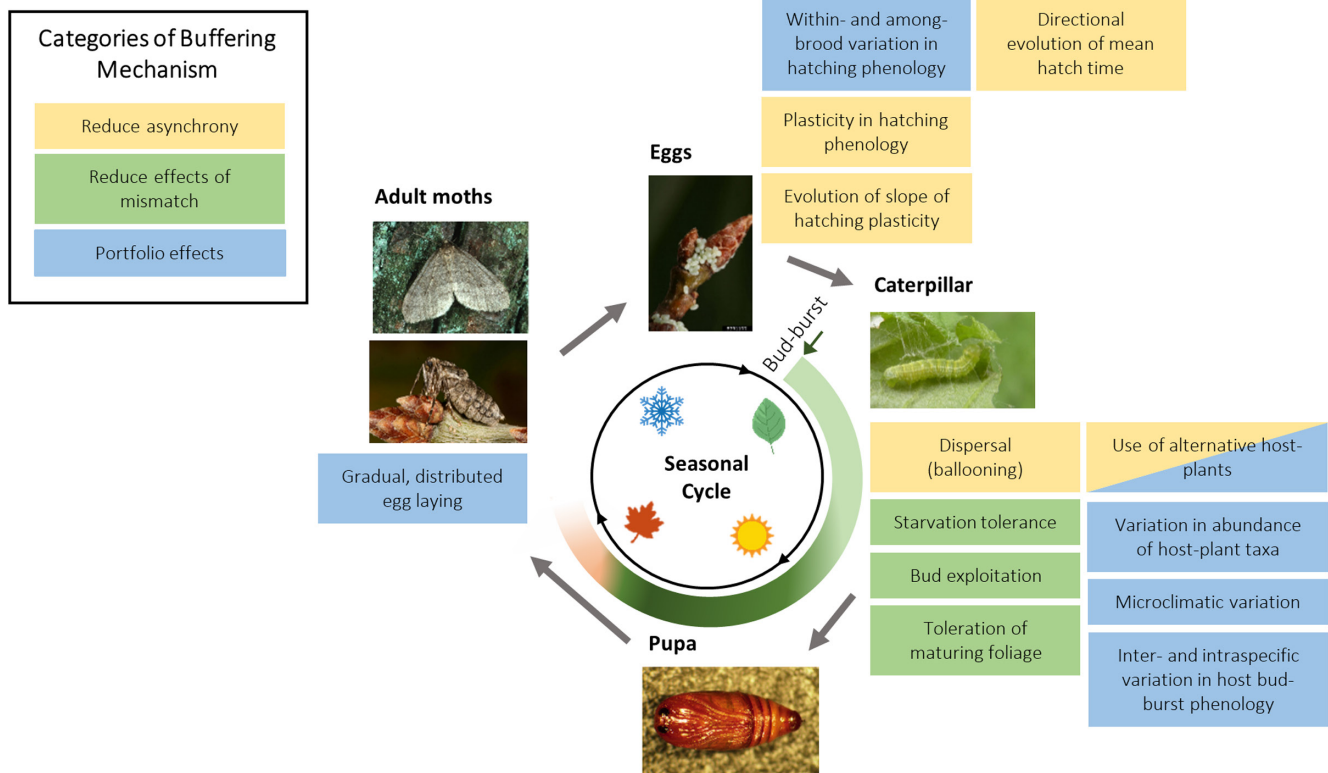
**FIGURE 1** Buffering and stability concepts under different models of environmental perturbation. For simplicity, these figures show the fitness of an individual organism as the response variable. However, performance, abundance, biomass, biodiversity, and so forth could be substituted for fitness, depending on the particular question being addressed and the organizational level in question within the ecosystem (individual, population, etc.). A press perturbation (Plot a) describes a consistent, directional shift in environmental conditions. A pulse perturbation (Plot b) describes a temporally ephemeral period of changed environmental conditions. Buffering ( $B$ ) acts to reduce the fitness costs of an environmental change, and the extent of that buffering is described by the difference in fitness between an individual with/without that mechanism. Under a pulse perturbation (Plot b), the resilience ( $R$ ) of the individual is the extent to which fitness returns to the pre-perturbation baseline ( $P$ ). The speed with which the individual returns to the pre-perturbation baseline is known as the elasticity ( $\theta$ ), and is likely to be affected positively by the extent of buffering ( $B$ ).



**FIGURE 2** A schematic of the effect of the timing of a consumer (blue arrow/s) relative to resource availability (green distribution/s; left column) on the degree of trophic asynchrony and performance (right column). The position of the red asterisk on the y-axis indicates the realized performance (this corresponds to mean performance in plots d and e). The example in (a) shows typical phenological asynchrony and mismatch, where the consumer phenology is later than resource phenology (though note that in the winter moth case study the consumer is often earlier than the resource), resulting in low consumer fitness, while (b–e) show various different forms of buffering. (b) shows a reduction in asynchrony, for example where a consumer switches to an alternative resource. (c) shows a reduction in the performance cost of asynchrony. (d) shows a portfolio effect (such as diversified bet-hedging) where variation in timing among consumer individuals means that some individuals are highly synchronous with the resource. (e) corresponds to an alternative portfolio effect where individuals are distributed across resources that vary in timing, meaning that some individuals are highly synchronous with the resource while others are less synchronous (shown is the possible fitness of an individual on each of three alternative numbered resource curves).

to fuel growth and development before the leaves mature, and become tougher and more chemically defended over the space of a few weeks (Feeny, 1968, 1970; Wint, 1983). After feeding and growing, winter moth caterpillars descend to the ground to pupate among leaf litter where they pass the summer and autumn (Figure 3; Henwood et al., 2020). Experimental studies have found that even a few days of asynchrony (too early or too late) between larval hatching and the bud-burst of oak trees may result in greatly reduced survival and growth for winter moth caterpillars (Tikkanen & Julkunen-Tiitto, 2003; van Asch et al., 2007; Van

Dis et al., 2023). Tikkanen and Julkunen-Tiitto (2003) found that the fitness costs of asynchrony were asymmetric, with hatching early and starving being more costly than hatching late and feeding on poor quality foliage. On the basis of this observation, Singer and Parmesan (2010) identified that under such asymmetric fitness costs the mean phenological trait is predicted to evolve to be slightly later than perfect synchrony, a scenario they termed 'adaptive asynchrony'. However, intriguingly, most field data support winter moth caterpillars hatching slightly earlier than the leaf-out of oak trees (van Asch et al., 2013; van Dis et al., 2023).



**FIGURE 3** Buffering mechanisms in the life history of the winter moth *Operophtera brumata*. Caterpillars hatch as buds break in spring, feeding up and pupating by summer. Pupae pass the summer in leaf litter and adults eclose in midwinter. Mating takes place, and the wingless females ascend their host-trees, laying eggs as they go. Eggs pass the remainder of the winter dormant. Hatching is stimulated by temperature increases in spring. Buffering mechanisms discussed in the text are summarized here, and classified as to whether they act to reduce asynchrony itself (yellow), reduce the negative effects of asynchrony/mismatch (green), or arise through portfolio effects (blue).

Relative to the effects of mismatch on individual fitness, much less work has considered how mismatch might negatively impact winter moth population size. However, population density data collected in Hoge Veluwe, in the Netherlands, reveals that where the mean larval hatch date is much earlier than the timing of oak bud-burst, the population growth rate is lower (Van Dis et al., 2023).

To place the buffering mechanisms of the winter moth in their ecological context, it is also important to emphasise the extent of the variability in the timing of leaf-out that caterpillars of this species face. In a single year the timing of leaf-out will vary among locations (Tansey et al., 2017), tree species (Cole & Sheldon, 2017), individual trees (Cole & Sheldon, 2017; Crawley & Akhteruzzaman, 1988) and even within a tree. While the leaf-out phenology of deciduous trees can be highly plastic in response to spring temperatures, the slopes of these reaction norms can themselves be highly variable (Vitasse et al., 2009). This variation in resource timing across time and space will be a recurring theme throughout this piece, and illustrates the challenge to local synchrony that winter moth caterpillars face.

How, then, might winter moths be buffered against the effects of phenological mismatch (Figure 3)? Some buffering mechanisms arise from attributes of the moths themselves (Figure 2b–d), whereas others arise as a property of the environment and hosts

(Figure 2e). In the next few paragraphs, we will describe some of these mechanisms and identify when they arise during the life history of this species.

## 2.1 | Egg-laying

The female winter moth ascends the trunk of a single host tree in the late autumn/early winter, mating en route, and laying eggs at a steady rate over a period of several days, depositing them throughout the trunk, branches, and buds of that tree (Embree, 1961; Hibbard, 2014; Maitland Emmet & Heath, 1992). This behavior gives rise to a portfolio effect, by introducing variation in the environmental conditions experienced by the eggs of a single female, such that although some individual caterpillars may find themselves hatching asynchronous with adjacent foliage in spring, others in a different location may be synchronous (Figure 2d). Regardless of synchrony, caterpillar fitness can vary between different parts of the same host tree (Suomela et al., 1995), such that distributing offspring throughout an individual tree may have evolved as a diversified bet-hedging strategy—an evolutionary strategy whereby phenotypic variation among offspring generates a portfolio effect in uncertain or variable environments (Childs et al., 2010; Dempster, 1955; Schindler et al., 2015).

## 2.2 | Egg development

The phenological plasticity of egg hatch times in response to spring temperature is a major buffering mechanism in this system. By responding to similar temperature cues as those used by their host-plants (Buse & Good, 1996; Visser & Holleman, 2001), winter moths partially track spatial and temporal variation in the timing of leaf-out, thereby reducing individual asynchrony. Egg development times vary substantially within and among broods, such that hatching can extend over several weeks even in a constant lab environment (Buse & Good, 1996; Ivashov et al., 2002; Kimberling & Miller, 1988; Speyer, 1938; Tikkanen & Julkunen-Tiitto, 2003; van Asch et al., 2007; Watt & McFarlane, 1991). This intra-clutch phenological variation may provide a portfolio effect in the face of the inherent unpredictability of leaf-out timing, where the cost of asynchrony is spread among the offspring of a single female such that at least some of the offspring of any given female moth are likely to hatch in synchrony with the resource (Figure 2d).

## 2.3 | Caterpillar behavior and physiology

Where caterpillars hatch prior to budburst they are able to employ: (1) *Dispersal*. When faced with adverse conditions, neonate caterpillars can spin a thread of silk and 'balloon' to new locations (Bell et al., 2005), either on the same host tree or a new tree—perhaps even successively until they find a host tree at a suitable phenological stage (Figure 2b; Edland, 1971; Holliday, 1977). However, this strategy presents considerable risks and arises only under the most stressful conditions, such as a lack of available food or maternal effects arising from high population density (indicating future competition; Tikkanen & Lyytikäinen-Saarenmaa, 2002). (2) *Starvation tolerance*. Winter moth caterpillars can survive for several days without food, which may allow them to simply wait for budburst on their host-plant if they hatch too early (Figure 2c) (Cuming, 1961; Hunter, 1990; Patocka, 1972; Tikkanen & Julkunen-Tiitto, 2003; van Dis et al., 2023; Weir, 2022; Wint, 1983). Although some degree of starvation tolerance has been recorded in a range of Lepidoptera (Reavey, 1992), its extent is negatively affected by increasing temperature (Wint, 1983). (3) *Use of plant buds as food*. Finally, winter moth caterpillars hatching before buds have broken on their host tree can still establish on bud tissue and in some cases exploit buds in an early stage of development (Porter, 2010; Stokoe, 1948), though, as a food resource, this seems to be sub-optimal (Weir, 2022). This behavioral and physiological buffering mechanism minimizes the cost of asynchrony to individual fitness (Figure 2c), and, although widely appreciated in the entomological literature, appears to have been somewhat overlooked in the phenological mismatch literature (Weir, 2022).

A range of buffering mechanisms also exist for caterpillars that hatch late compared to leaf-out on their host. While the role of oak as the "primary" or most significant host-plant of the winter moth in the field is often emphasized in the literature (e.g. Feeny, 1970;

Hinks et al., 2015; O'Donnell et al., 2019; van Asch & Visser, 2007; Varley et al., 1974; Wint, 1983), the species is a trophic generalist and its caterpillars have been recorded feeding on plants from over 15 taxonomic families (Robinson et al., 2010). Among these different host-plant species, there is considerable variation in the rate at which caterpillar fitness declines as foliage matures, with fitness declines found to be steeper on oak than on many other species (Weir, 2022). In the case of the winter moth, there are clear and strong declines in fitness with late hatching asynchrony, averaged across taxonomically and morphologically diverse host-plant species (Weir, 2022). However, fitness has been found to decline steadily over weeks rather than days (Weir, 2022), with caterpillars found to be able to *tolerate and utilize maturing foliage* to a considerable extent (Figure 2b,c). This contrasts with the generally steeper declines in fitness associated with early-hatching asynchrony and arising from starvation, although the slope of these declines is temperature sensitive, for example up to 12 days at 5°C to 3 days at 20°C (Patocka, 1972). The restrictive taxonomic lens through which mismatch has been studied in this system may have resulted in an over-emphasis on the fitness costs of asynchrony for the winter moth. Host-plant tree species can vary substantially in their average timing and the extent to which they shift their phenology in response to spring forcing temperature and winter chilling (Roberts et al., 2015). In light of the limited dispersal and host choice employed by adult female winter moths, the ability of the caterpillars to effectively exploit a diversity of host-plant taxa (O'Donnell et al., 2019; Tikkanen et al., 1999; Weir, 2022; Wint, 1983) could also enable individual caterpillars to move to a tree with which they are synchronous (Figure 2b), or give rise to a population-level portfolio effect, where at least some individuals are synchronous with some host trees (Figure 2e).

## 2.4 | Environmental variation

Winter moths may also benefit from portfolio effects that arise as a result of the properties of their woodland environment (Figure 2e). The structural complexity of woodland habitats can present considerable microclimatic variation on a local scale and even between different parts of the same individual tree (De Frenne et al., 2021; Nicolai, 1986; Prinzing, 2001). This may generate variation in caterpillar phenology by affecting developmental rate (Hibbard, 2014; Hibbard & Elkinton, 2015), or indirectly by adding to the general phenological variation in host-plant development to be found in the environment. On a larger spatial scale where the effects of spring temperature on phenology at two sites are sufficiently uncoupled (e.g. between early and late sites at different elevations or latitudes), the meta-population may be buffered by a portfolio effect, where some populations are synchronous even when others are asynchronous (Burgess et al., 2018; Milles et al., 2023). Evidence that gene flow extends over large distances across the range of the winter moth (Andersen et al., 2017; Legget et al., 2011) suggests some ability to disperse across a landscape—despite the apparent limitations

on both male and female dispersal (van Dongen et al., 1996)—which may allow for recolonization or demographic rescue at the metapopulation level.

## 2.5 | Evolution

Temporal and spatial variation in resource timing is the baseline state for systems like this and, over longer time periods, adaptation in response to selection provides an additional buffer for populations (Milles et al., 2023). In fact, a common garden experiment on winter moths replicated in time found that the population mean phenology-temperature reaction norm slope and elevation had evolved over time in the direction that facilitated better tracking of the resource (Figure 2b; van Asch et al., 2013). This evolutionary mechanism has been described as ‘repelling’ buffering (in contrast to ‘damping’ buffering mechanisms, such as portfolio effects) elsewhere (Milles et al., 2023).

## 2.6 | Conclusions from the winter moth

Although winter moths partially track the spring phenology of their host trees from year-to-year, broad phenological differences between different parts of a woodland site, differences in mean phenology between host species, among individuals of the same host species, and even differences among parts of the same individual make precisely synchronising their phenology a difficult task. Two caterpillars hatching at the same time in spring on two adjacent trees could suffer vastly different fates depending on the phenological particularities of those two trees. Viewed in this light, it would indeed be surprising if winter moths did not possess some suite of buffering mechanisms, specialized as they are to feed on foliage in the early weeks/months of spring—a temporally restricted phenological window. It is difficult to imagine how they could persist if, on the one hand, they could not reliably track host phenology and were, at the same time, extremely sensitive to phenological asynchrony. In the context of climate change, we argue that buffering mechanisms will provide a level of in-built resilience to the impacts of rising temperatures on phenological asynchrony (Weir, 2022).

## 3 | THE GENERALITY OF BUFFERING IN OTHER PHENOLOGICAL INTERACTIONS

We have seen how winter moth caterpillars may buffer themselves against mismatch by reducing asynchrony (e.g. through dispersal via ballooning), reducing the performance costs of being asynchronous (e.g. by using the un-opened or opening buds of their host-plant as food), and through portfolio effects (e.g. bet-hedging within the brood of an individual female, where variation in hatching phenology ensures at least some offspring will be synchronous). To what extent are analogous buffering mechanisms found beyond the winter

moth? Here, we consider first the buffers found among other spring-feeding caterpillar species and then across trophic interactions in other taxa.

## 3.1 | Buffers in the spring arboreal caterpillar guild

The winter moth may have received the most attention in the literature on phenology and synchrony (van Asch & Visser, 2007) but, in fact, a diverse guild of arboreal caterpillars share the phenological niche of hatching in approximate synchrony with the timing of bud-burst and leafing in spring (Kulfan et al., 2018; Shutt, Burgess, & Phillimore, 2019; Smith et al., 2011), and these species share many similar buffering mechanisms. For instance, substantial intra-brood variation in hatching phenology, as well as the ability to adjust phenology plastically in response to temperature, is found in many spring-feeding species (e.g. Fitzgerald, 1995; Ivashov et al., 2002). Ballooning in search of more favourable resources has been widely observed in young caterpillars across species in this guild (reviewed in Zalucki et al., 2003, though Lepidopteran species vary in the extent to which they employ this strategy, e.g., Capinera & Barbosa, 1976; Johns & Eveleigh, 2013). We also see variation in the duration across which Lepidopteran caterpillars can survive without food (Reavey, 1992), ranging from several days (e.g., quaker moths *Orthosia* spp., Reavey, 1992; gypsy moth *Lymantria dispar*, Patocka, 1972; Hunter, 1993) to weeks (e.g. tent caterpillars *Malacosoma* spp., Abarca & Lill, 2015; oak processionary moth *Thaumetopoea processione*, Wagenhoff et al., 2013), with that duration being temperature-sensitive (Weir, 2022). Finally, many species of Lepidoptera have been recorded feeding on plant buds, both as specialists or opportunistically (as in the winter moth). The caterpillars of the hairstreak butterflies, for example, feed in early spring, and commence their larval development by burrowing into flower and shoot buds, sometimes feeding exclusively or preferentially within these structures until they are too big to do so (Eeles, 2019). Additionally, many microlepidopteran species exploit buds, successively feeding until they pupate (Langmaid et al., 2018; Maitland Emmet & Heath, 1992).

Most arboreal spring-feeding caterpillars are trophic generalists, able to exploit a range of different host-plant species, though diet breadth does vary (Maitland Emmet & Heath, 1992). Naturally, all spring-feeding species also experience the inherent heterogeneity and patchiness of woodland environments which gives rise to portfolio effects in the hatching phenology of these species. This includes environmental attributes (such as microclimatic variation), alongside factors related to the host-plants they exploit, such as variation in spatial distribution, abundance, inter- and intraspecific variation in phenology, etc.

That the members of this guild share similar buffering mechanisms should not be surprising since they share a phenological niche and the same challenge of tracking the timing of their resource. However, it is also notable that the relative importance of different buffering mechanisms varies among species, and there is the

potential for different mechanisms to be traded-off against one another. For example, a decreased propensity to disperse in the green oak tortrix, *Tortrix viridana*, accompanies a more specialist diet, but a corresponding increase in starvation tolerance, relative to the winter moth (Hunter, 1990).

### 3.2 | Buffers in other trophic interactions

Several of the buffering mechanisms we have identified as operating in the winter moth-tree interaction are likely to be general to phenology-mediated trophic interactions across systems. For instance, as we discussed in the introduction, we see broad evidence that consumers outside of the tropics exhibit phenological plasticity in response to temperature that at least partially tracks the timing of their resource (Roslin et al., 2021; Thackeray et al., 2016). We also have some evidence that the phenology of secondary consumers, such as pied flycatchers, has evolved over recent decades to better track climate-mediated advances in resource timing (Helm et al., 2019).

We suspect that in many systems trophic generalism and prey switching will provide some buffering against pairwise asynchrony. For example, among insectivorous passerine birds such as tits and flycatchers (important consumers of arboreal caterpillars), variation in the precise spring hatching phenology and rates of development among different caterpillar species may give rise to a portfolio effect that buffers nestlings from the negative impacts of asynchrony with any one prey species. However, many studies focusing on insectivorous birds consider the caterpillar guild as a whole (e.g., via frass-fall, Smith et al., 2011), which precludes investigation of diet switching, but also means that this buffering mechanism is already incorporated into analyses of the impacts of mismatch (e.g., Reed et al., 2013). To date, very few studies have examined the phenology of resource taxon availability and the fitness consequences of diet switches in the detail required to infer whether this is an important and general buffer (but for exceptions see Burger et al., 2013, and Deacy et al., 2017). We also expect portfolio effects that aggregate at the meta-population scale (e.g. arising out of environmental heterogeneity) to be general across systems (Milles et al., 2023). For great tits *Parus major*, interannual variation in mismatch between chick food demand and peak caterpillar availability has been shown to be a very poor predictor of the tit population growth rate, with density-dependent compensation of post-fledging juvenile survival acting as a buffer in years where mismatch reduces fledging success (Reed et al., 2013). The extent to which this mechanism buffers the population level impacts of mismatch in other systems is unknown, though it is likely to assume greater importance for populations that are more sensitive to density-dependent regulation, and may be less important for populations that, like the winter moth, have faster life history strategies.

Passerine birds such as great tits are income breeders, and provision their growing offspring with resources gathered from the environment during development. This makes their breeding success

highly sensitive to the abundance of local, ephemeral resources. In Greenland's arctic tundra environments, while reproductive performance declines steeply with increasing mismatch in income-breeding caribou *Rangifer tarandus*, it appears to be unaffected in capital-breeding muskox *Ovibos moschatus* (Kerby & Post, 2013). Capital breeding may therefore act as a buffer against mismatch in some instances, reducing the fitness costs associated with asynchrony (Figure 2c)—although in the case of muskoxen, performance does seem to be subject to knock-on effects of historical mismatch in previous years (Kerby & Post, 2013).

Beyond the mean timing of the consumer phenological distribution, characteristics of the shape of that phenological distribution that act to buffer impacts of asynchrony are also likely to be widespread. For example, among-individual variation in phenology in the butterfly *Euphydryas aurinia* and its specialist parasitoid *Cotesia bignelli* mean that, despite having different phenological sensitivities to temperature, changing temperature conditions need not necessarily result in mismatch (Klapwijk et al., 2010). High baseline resource abundance or inter-annual variation in resource abundance can act to alleviate the strength of selection for synchrony either consistently or in high-abundance years, respectively, and therefore buffer taxa against mismatch (Cushing, 1990). In a marine system comparing trophic interactions among plankton taxa, Atkinson et al. (2015) attributed a lack of any effect of mismatch on population size to food abundance overriding the impacts of temporal asynchrony. Atkinson et al. (2015) also noted that prolonged seasonal food availability likely also acted as a buffer in their marine system, by limiting the ephemerality of the resource taxa and therefore the extent of any asynchrony. Similarly, the survival of soay sheep *Ovis aries* on the island of Hirta (UK) is influenced by the availability of vegetation but not mismatch relative to the timing of peak vegetation growth (Durant et al., 2005).

Some of the buffering mechanisms we see in winter moths have analogs elsewhere but are not general. For instance, the ability to reduce asynchrony through movement, akin to ballooning by winter moth caterpillars, has been suggested for some migratory birds (Hušek et al., 2014; Lamers et al., 2023) and fish (Chust et al., 2023), but this mechanism is likely to be limited to species with strong dispersal abilities and those that are not philopatric. Also, it remains to be established in different systems whether such dispersal is directed toward locations that would reduce asynchrony, thereby benefiting the individual, or is non-directed, where benefits may accrue at an aggregate level. Equally, we find some buffering mechanisms that do not have an analogue in the winter moth system, such as behavioral plasticity in incubation exercised by parent tits (Simmonds et al., 2017).

## 4 | SYNTHESIS AND FUTURE OUTLOOK

Despite considerable attention given to climate-induced phenological mismatch over the past two decades, there remain surprisingly few studies, and of limited taxonomic breadth, that demonstrate

a widespread negative impact of asynchrony on consumers at the population-level (Kharouba & Wolkovich, 2020, 2023; Samplonius et al., 2020). One explanation for this lack of evidence for detrimental impacts on consumers is that ephemeral consumer-resource interactions may be inherently more buffered than has been hitherto appreciated. If this is the case, we may be overestimating the severity and frequency of the short-term threat that climate change-induced mismatch poses to consumer populations.

We suggest that there are two priorities to establish the contribution and impact of buffering. First, for a diverse sample of systems, we need studies that quantify the magnitude of different buffering mechanisms on performance, that is  $B$  in Figure 1—the magnitude of the difference in a given performance metric with and without that mechanism in operation. This would enable us to establish the degree to which buffers might quantitatively change our predictions of future population size, the metric that is of most importance to conservation and policy. For some buffering mechanisms, experiments that manipulate the degree of buffering can be envisaged (e.g., heterogeneity in resource timing). Whereas, for other buffering mechanisms (e.g., plasticity and evolution of the phenology-temperature reaction norm) the absence of the buffer is a hypothetical state, and we may need to rely on models to assess differences in performance metrics with and without the mechanism (e.g., Briedis et al., 2024; Vedder et al., 2013).

Second, we lack a general understanding of the occurrence and importance of different buffering mechanisms across different interaction types, environments, and taxa—this topic would greatly benefit from phylogenetic comparative analysis. For instance, we hypothesize that the species and populations that are most often exposed to temporal asynchrony with resources will tend to have evolved the most buffering mechanisms, though there have been few tests of this. One such study examined the pollen diet of *Osmia* bees, and found a tendency for species with earlier phenology to be more generalist (Pelletier & Forrest, 2023). We might also expect to find a trade-off in the extent to which different buffers are important in different species; for example, those species that show least phenotypic plasticity may show most evidence for an evolutionary shift in phenology. A comparative approach could reveal cases where climate change may have the most detrimental impact, i.e. where trophic asynchrony has deleterious consequences for the consumer and buffering has limited impact or becomes reduced or exhausted (e.g., limits to phenological plasticity, or changes to biodiversity which reduce portfolio effects). Indeed, it appears that in the winter moth, a reduction in population growth rates becomes much more apparent beyond a threshold level of asynchrony (Van Dis et al., 2023).

To conclude, we acknowledge the potential for climate change to have severe phenology-mediated impacts, and that buffers may clearly become exhausted if temperature (or other environmental) changes are extreme (Simmonds et al., 2020). However, as we have tried to illustrate in this paper, there are insights to be had from conceptualising the effects of those climatic changes through a different lens—one that de-emphasizes the fragility of species interactions

and highlights the mechanisms that confer stability and resilience in the face of environmental stress and variation. We hope that this change in perspective will stimulate future research to determine the ubiquity of buffering across a range of taxa and its significance in a changing climate.

#### AUTHOR CONTRIBUTIONS

**Jamie C. Weir:** Conceptualization; writing – original draft; writing – review and editing. **Albert B. Phillimore:** Conceptualization; supervision; writing – review and editing.

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#### CONFLICT OF INTEREST STATEMENT

We declare that there are no conflicts of interest regarding the publication of this paper.

#### DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

#### ORCID

Jamie C. Weir  <https://orcid.org/0000-0003-0182-2332>

Albert B. Phillimore  <https://orcid.org/0000-0002-6553-1553>

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