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Review

Seasonality of forest insects: why diapause matters

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Insects have major impacts on forest ecosystems, from herbivory and soil-nutrient cycling to killing trees at a large scale. Forest insects from temperate, tropical, and subtropical regions have evolved strategies to respond to seasonality; for example, by entering diapause, to mitigate adversity and to synchronize lifecycles with favorable periods. Here, we show that distinct functional groups of forest insects; that is, canopy dwellers, trunk-associated species, and soil/litter-inhabiting insects, express a variety of diapause strategies, but do not show systematic differences in diapause strategy depending on functional group. Due to the overall similarities in diapause strategies, we can better estimate the impacts of anthropogenic change on forest insect populations and, consequently, on key ecosystems.

Highlights

Diapause is a strategy in insects to mitigate seasonal stress and synchronize lifecycles with favorable times.

Forests are 3D, dynamic ecosystems with contrasting microhabitats where numerous insects enter diapause and the duration of diapause affects their phenology.

Ecologically important forest insects, like defoliators, bark breeders, or soil/litter-dwelling species have diverse diapause strategies.

Anthropogenic change, like climate change and urbanization, has and will have substantial impacts on forest insects. Some species may increase their impact on ecosystems, while that of others may be reduced.

Understanding how climate change or urbanization factors, like artificial light at night and the urban-heat-island effect, affect diapause may help develop generalizable rules to predict which species will show population expansion and which are likely to contract.

Seasonal adaptations and diapause

Most forest insects experience predictable periods of seasonal stress every year [1,2]. Numerous species use dormancy to mitigate stressful times and synchronize lifecycles with times of the year favorable for development and reproduction [3,4]. Often dormancy is associated with overwintering and cold conditions in temperate habitats, but dormancy can also occur in tropical or subtropical climates in response to hot or dry conditions [1,4]. Dormancy as a life-history strategy can be broken down into a suite of tactics (Box 1). Diapause is a programmed alternative developmental trajectory, a state of developmental suppression that insects enter prior to the onset of stressful conditions [1]. Diapause can either be induced facultatively in response to predictable seasonal cues (e.g., photoperiod, temperature, or humidity) or can be obligate, induced every generation regardless of environmental conditions [5]. Not all insects use diapause to survive unfavorable seasons. Some species become quiescent, wherein the normal lifecycle is slowed down or suppressed directly by the immediate environment [4]. Some insects even use a combination of tactics over the course of an unfavorable season; for example, by beginning their dormant period in a programmed diapause, but ending that diapause before the onset of the growing season and remaining quiescent until favorable conditions return [1,6,7]. Ending dormancy in quiescence allows insects to immediately resume their lifecycle once stressful conditions end, to exploit the growing season and synchronize individuals across a population.

Forests are complex habitats for dormancy

Forests offer variable habitats across space and time (Box 2) [8]. The vertical profile of forest layers [9], including soil, litter, herbaceous stratum, shrubs, trunks (including wood cavities or galleries), canopy, and internal gradients [10,11], modulates light penetration, radiation, airflow, and consequently temperature and humidity [12]. All these factors likely contribute to the stratification of insect fauna [13] (Figure 1). Although the complexity and height of vertical gradients can vary depending on latitude, elevation, tree species richness, and density, the averages and magnitudes of microclimatic conditions can vary within each stratum [12,14]. For example, the canopy

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Box 1. Key concepts for insect diapause

Many insects incorporate diapause as part of their lifecycles [1], although research effort is often skewed towards pest species. Dormancy is an umbrella term to describe any major slowdown in insect lifecycles. Dormancy can either be induced directly by harsh conditions in the environment, a state termed quiescence, or programmed to begin preemptively before conditions become unfavorable for growth or reproduction, a state termed diapause. Prevention of growth or reproduction by environmentally induced quiescence is common in lifecycles of many insects. From cold winter temperatures or hot summer conditions to lack of food sources, insects enter quiescence rapidly and also exit from quiescence rapidly to reengage in growth or reproduction as soon as conditions become permissive again. By contrast, diapause is a pre-programmed form of dormancy insects enter prior to the onset of adversity. Whereas quiescence can be entered in any lifecycle stage in response to the environment, diapause is a distinct developmental trajectory within the lifecycle that follows a stereotypical series of developmental phases and is typically only expressed in particular, species-specific life stages (Figure I). These phases include induction, a developmental window when the insect becomes responsive to environmental cues that will cause it to enter the diapause trajectory. Preparation is a phase that might overlap with induction where the insect changes its physiology to accumulate additional nutrients or induce mechanisms of stress hardiness. Diapause initiation corresponds to the phase when the insect will enter the state of developmental slowdown. Diapause maintenance is a state in which progression of the lifecycle is arrested. During the maintenance phase, insects are refractory to environmental cues that cause them to resume growth or reproduction. During diapause termination, insects become receptive to environmental cues that end diapause and induce growth or reproduction (followed by postdiapause). For some insects, diapause only ends once favorable times have already begun. Other insects will end diapause during unfavorable times (e.g., in mid-winter) and remain dormant due to environmentally induced quiescence but can readily resume their direct development or reproductive maturation as soon as conditions become permissive again. In multivoltine species, diapause is typically a facultative plastic response, induced by cues that predict oncoming unfavorable conditions (e.g., short-day photoperiods that portend the onset of winter). Diapause is an obligate part of the lifecycles of most univoltine insects and is expressed every generation regardless of environmental cues, thus obligate-diapausing insects lack the induction phase.

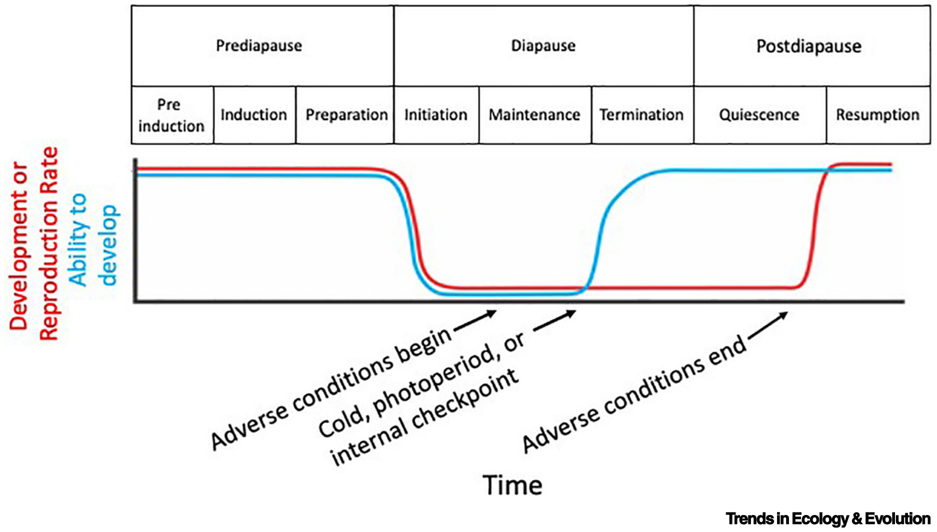

Figure I. Insect diapause is an alternative developmental trajectory with a series of physiologically distinct sequential phases that define the extent to which an insect is both dormant and receptive or refractory to cues that would end dormancy and restart the lifecycle.

intercepts and absorbs most of the sunlight while being exposed to the highest airflow, whereas ground level strata receive much less light or wind and can collect moisture from the strata above. A diverse range of contrasting habitats at a relatively small spatial scale means that seemingly sympatric forest insects can experience distinct environments even when they share the same plant in the same forest, depending on their **phenology** (see Glossary), lifespan, age, typical feeding substrates and microrefugia, and their ability to behaviorally navigate along the vertical gradient to mitigate immediate conditions [8,13,15].

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Forests are long-lived ecosystems whose biophysical characteristics change cyclically over mid- and long-term timescales. In temperate deciduous forests, for example, autumnal foliage loss and associated changes in evapotranspiration alter light and microclimatic conditions from canopy to ground, while accumulation of dead leaves can modify the sheltering properties and **microclimate** of litter [16]. Finally, forests undergo profound changes over decades to centuries [17] due to tree growth, mortality, natural succession, and regeneration, as well as human interventions [18] (Box 2). Seasonal and long-term variation alters vertical gradients of forests by either exacerbating or disrupting microclimatic properties and structure of particular strata.

The multidimensionality of forests in space and time can modulate environmental factors that cue diapause initiation and termination, influencing the timing and duration of dormant and nondormant lifecycle stages. Consideration of the multidimensionality of subhabitats within forests is therefore crucial to understand the ecology of forest insects [2], especially because insects can in turn play a major role in altering microclimate regulation of forests by defoliating or killing trees.

Significance of forest insects

Insects play multiple roles in forest ecosystems. They feed as herbivores on plant tissues, pollinate plants, disperse seeds and pollen, decompose organic matter, or prey on/parasitize other species [19,20]. Additionally, some insects, particularly herbivorous species, interfere with anthropogenic interests for certain ecosystem services and resources provided by forests [21].

From an ecological perspective, three functional groups including species from numerous taxa are of high significance in forests: (i) canopy-dwelling insects feeding on leaves/needles; (ii) trunk-associated species living on the phloem/xylem of trees; and (iii) litter/soil-dwelling insects (Figure 1). The first group includes lepidopteran larvae and larvae of hymenopteran sawflies as well as hemipterans that can degrade the canopy and affect trees through defoliation. The second group includes phloem-feeding insects, particularly **bark beetles**. Some conifer bark

Box 2. Forest management, climate change, and diapause

Forests capture and store carbon in tree biomass, deliver societal requirements for timber, and harbor and conserve biodiversity. As 3D, long-term, and complex ecosystems, forests vary significantly from agricultural systems focused on annual row cropping. Tree canopies buffer low and high temperature extremes by filtering incoming solar radiation and regulating evapotranspiration, and the structural complexity of vegetation creates multiple microclimates that deviate from the background atmosphere (Figure I) [103,104]. Many organisms including forest insects do not experience climate at a coarse scale, and instead live in microclimates where conditions can vary dramatically from those recorded at weather stations [105,106]. Forest microclimates among the soil, understory vegetation, tree bole, and canopy harbor different functional groups of insects and often different life stages of the same species. For example, eggs of the pine processionary moth (Box 3) are frequently deposited on lower pine branches, neonate larvae feed gregariously for a few weeks, then more mature larvae spin a silken tent and feed in the canopy for several months, after which pupae overwinter in the soil, a well buffered environment [107]. Logging in closed canopy forests removes leaf density and creates gaps, thereby changing thermal and solar radiation levels, resulting in hotter, drier, and more variable microclimates in the understory [108,109]. Mean air temperatures are higher in newly created forest-edge microclimates relative to forest interiors and soil temperatures can increase more dramatically than air following tree removal due to solar radiation [108,110]. Because even slight changes in microclimate can influence changes in individual and population-level traits [111], forest management can greatly impact insect fitness and population success. Specifically, diapause induction and termination, which are often regulated by temperature and photoperiod [1], might be altered by changes in temperature and solar radiation [112] that can occur following logging. Effects on diapause will be species- and life stage-specific as timing of diapause induction, termination, and postdiapause development vary across species. Not all microclimates will be affected equally due to the spatial and structural complexity of forest ecosystems. Tree removal is a form of localized climate change and species living in postmanagement forests face the combined forces of global climate change on top of management-induced changes in microclimate [109,113]. Microclimate regulation should be considered an important ecosystem service that is incorporated into forest management strategies in a changing climate.

Glossary

Abiotic stressor: variation in the non-living world that can negatively influence biological processes, for example, high or low temperature, strong wind or low humidity.

Bark beetle: subfamily within weevils, that is, Curculionidae, Scolytinae. The term bark beetle can be confusing as it is used taxonomically (i.e., subfamily Scolytinae) and ecologically, describing their main habitat and food source (i.e., phloem of trees). Apart from phloem-feeding/inhabiting bark beetles, other feeding modes and microhabitats are found, like xylem-inhabiting and fungus-farming species (i.e., ambrosia beetles), or species utilizing herbs, seeds, wood, pith or fungi. So far, >6300 bark beetle species have been described worldwide, with the majority living in dead/dying plants. A small number of species are able to colonize hardly stressed plants and are therefore known as pests.

Microclimate: climate variation on small scales, important for insects. For instance, the south or north side of a stone, or tree, can have dramatically different temperature and humidity.

Phenological traps: lifecycle-timing mismatches with the biotic and abiotic environment, resulting in fitness costs, worse performance, or mortality when a species does not meet its critical resources in a certain time window. Timing mismatches can result from phenological changes of players of various trophic levels and can be related to climate change.

Phenology: temporal occurrence and/or succession of lifecycle events over the course of a year; for example, dispersal, mating, or entry into dormancy.

Phenotypic plasticity: capacity of a single genotype to produce multiple phenotypes. This includes irreversible developmental changes (e.g., solitary versus gregarious locust morphs), but also reversible changes (e.g., seasonal increases in cold tolerance that decrease later).

Seasonality: habitats, for example, in temperate and polar regions are characterized by changing environmental conditions throughout a year. Organisms must adjust their lifecycles to biotic and abiotic resources to increase fitness and avoid harmful consequences.

Sensitive developmental stage: diapause induction generally occurs in species-specific lifecycle stages where

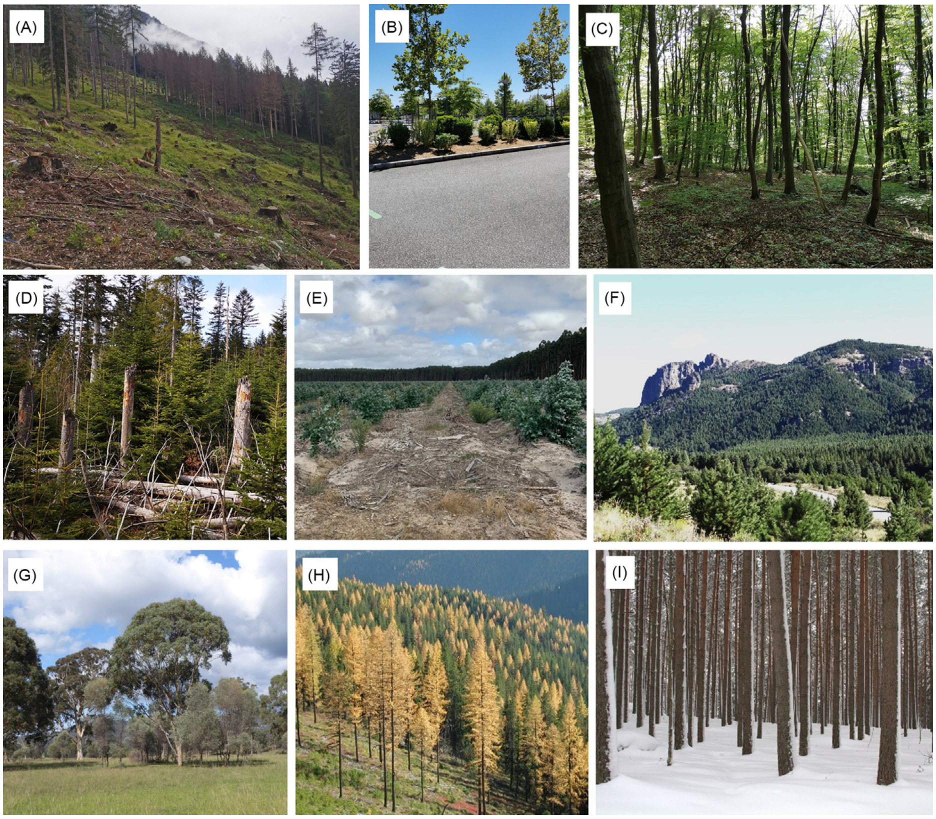

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Figure I. (A) Mountainous conifer forest in Central Europe, consisting of Norway spruce and European larch. Forest management after infestations of the spruce bark beetle *Ips typographus.* Clear cuts result in an immediate change of abiotic conditions (Gstatterboden, Austria). (B) Trees and associated forest insects in urban and suburban landscapes face extreme abiotic conditions (e.g., drought and heat) and are exposed to artificial light at night (Rennes, France). (C) Deciduous forests differ from conifer forests in environmental conditions over various spatiotemporal scales and provide specific microclimates for forest insects (Vienna, Austria). (D) Natural, unmanaged forest ecosystems have a high structural variety with multiple microhabitats showing complexity of microclimates on a small scale (National Park Bavarian Forest, Germany). (E) Plantation of bluegum, *Eucalyptus globulus*. Environmental conditions in young stands of these highly managed forests strongly differ from buffered, heterogeneous natural forest ecosystems (Green Triangle Region, South Australia, Australia). (F) Unmanaged *Pinus ponderosa* forest in Argentina. Multiple pine species were introduced to various regions in the Southern Hemisphere where they grow in both managed plantations and unmanaged ecosystems (Patagonia, Argentina). (G) Natural stand of acacia and eucalypt where trees are intermingled with clearings exploited for grazing. The area is exposed to frequent droughts that are affecting phenology and diapause of insects (New South Wales, Australia). (H) Managed mountainous forest, consisting of western larch (*Larix occidentalis*) and other conifer species, showing the effect of seasonality on leaf fall (evergreen versus deciduous trees), which ultimately affects the climatic conditions of forest stands (Lolo National Forest, Montana, USA). (I) Managed Scots pine forest in Northern Europe during winter. Boreal forest ecosystems are often characterized by high and long-lasting snow cover, which has implications on the microclimate of insects hibernating belowground (Öby, Finland). Photos: (A–D) by Martin Schebeck, (E) by Dianne Patzel, (F) by Victoria Lantschner and Juan C. Corley, (G) by Andrea Battisti, (H) by Barbara J. Bentz, (I) by Philipp Lehmann.

beetles of the Northern Hemisphere show eruptive population outbreaks under suitable environmental conditions, resulting in large-scale tree death [22,23]. Additionally, larval feeding of many cerambycid and buprestid beetles (many saproxylic species) initially occurs in the phloem before they proceed into woody tissues as development progresses. The third group includes **wood ants**, which are key elements of forests across the Northern Hemisphere. These social insects

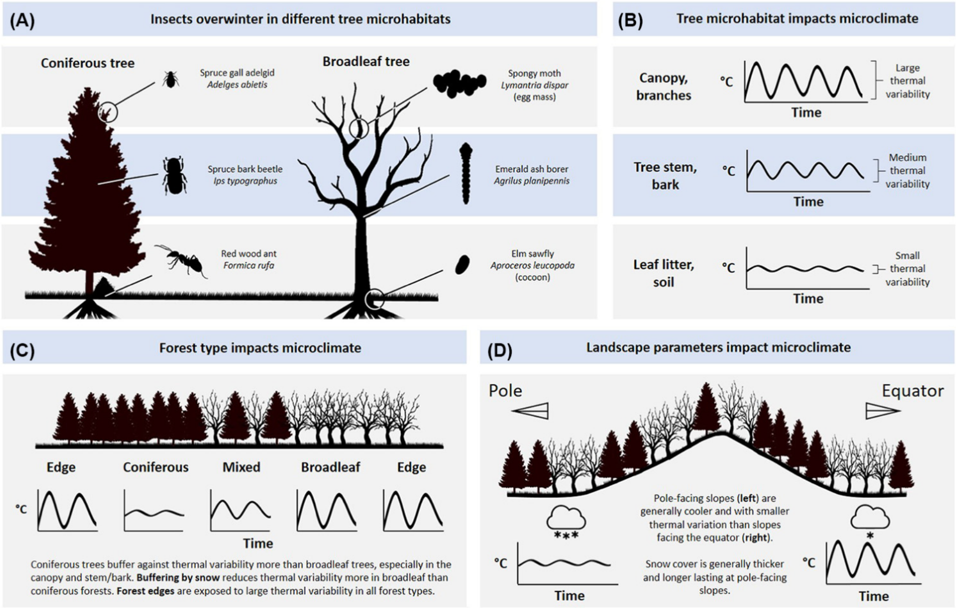
an insect is perceptive to internal or external cues (see also token stimulus) to start the diapause program.

Synchronization: intrinsic or extrinsic processes that unify lifecycles so that most individuals of a population are simultaneously active and available to time their occurrence with critical resources; for example, mating partners or food.

Token stimulus: external environmental signal that is strongly correlated with a future, unfavorable seasonal event. The token stimulus itself is not adverse, but it programs an insect to enter diapause. Common token stimuli for insect diapause are photoperiod or temperature.

Voltinism: number of generations produced per year. Univoltine: one generation/year; bivoltine: two generations/year; multivoltine: more than two/year; semivoltine: lifecycles that are completed in two years or longer.

Wood ants: eusocial insects belonging to the hymenopteran family Formicidae, and the genus *Formica*. In particular, wood ants comprise species of the *Formica rufa* species group that are widely distributed in the Holarctic. The majority of species inhabit forest ecosystems and are characterized by their mound-building behavior. They fulfill pivotal functions in forests, ranging from soil bioturbation, to seed dispersal, predation of other animals, etc.



Coniferous trees buffer against thermal variability more than broadleaf trees, especially in the canopy and stem/bark. **Buffering by snow** reduces thermal variability more in broadleaf than coniferous forests. **Forest edges** are exposed to large thermal variability in all forest types.

Pole-facing slopes (**left**) are generally cooler and with smaller thermal variation than slopes facing the equator (**right**).

Snow cover is generally thicker and longer lasting at pole-facing slopes.

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Figure 1. Spatial and temporal microclimatic variations across contrasted forest microhabitats. Simplified conceptual overview showing (A) insects overwintering in three different microhabitats. Note that some species (e.g., soil-overwintering moth species) are restricted to a single microhabitat, while others (e.g., the spongy moth *Lymantria dispar* or the spruce bark beetle *Ips typographus*) can overwinter in multiple microhabitats. (B) Thermal variation over a certain time-span (e.g., a day) is shown as a function of tree microhabitat. This microclimatic variation can have significant impact on insect performance. (C) Effect of forest structure and type on thermal variation. (D) Highlights of some important landscape impacts on microclimate.

are abundant in multiple ecosystems and perform pivotal functions including predation on insects, bioturbation of soil or decomposition of plant biomass [24,25].

Lifecycle regulation and diapause of forest insects

Lifecycles of insects are strongly shaped by abiotic factors. Temperature affects many life-history traits, including developmental time, reproduction, survival, and **voltinism** [26]. Additionally, lifecycles of numerous forest insects are affected by dormancy, particularly diapause. Although diapause expression in canopy-dwelling, trunk-inhabiting, and soil/litter-inhabiting insects is phenotypically diverse, there are common strategies and overlapping tactics across taxa.

Both facultative and obligate diapause occur among forest insects. For example, obligate diapause is expressed in the spongy moth *Lymantria dispar* (native to Eurasia and invasive in North America) [27]. This common species of Holarctic broadleaf forests enters obligate diapause as a fully developed first-instar larva still inside its eggshell and hibernates in egg batches on trunks (or branches). Larvae hatch and begin growth the following spring when temperatures allow for development and food is available [27]. Likewise, the emerald ash borer *Agrilus plannipennis* (native to Asia and now highly invasive in parts of North America and Eurasia) enters obligate diapause as late-instar larva to survive unfavorable cold conditions [28].

Furthermore, the ecologically significant group of wood ants enter an endogenously regulated dormancy during winter, regardless of environmental conditions [29,30]. Queens stop laying eggs in late summer/early fall and prepare for overwintering. Only adult females (queens and workers) overwinter in belowground nests prior to reproduction the following spring. Although this dormancy resembles an obligate reproductive diapause, it is difficult to put these long-lived insects (particularly queens) in the standard framework of diapause classification because they enter dormancy repeatedly during their lifecycles.

Many forest insects from the aforementioned functional groups enter environmentally sensitive, facultative diapause. The most common cues for diapause induction are photoperiod (i.e., day length) and temperature, or a combination of both. Photosensitive species respond to short day-lengths in late summer/early fall to prepare for the upcoming winter and to synchronize lifecycles with the favorable growing season [1]. For example, bark beetles in the genera *Ips* and *Pityogenes* that are common in Northern Hemisphere forests enter a photoperiod-regulated diapause [3,31,32]. Defoliators of both Northern and Southern Hemisphere forests, such as the eastern spruce budworm *Choristoneura fumiferana* [33], the autumn gum moth *Mnesampela privata* [34], and some hymenopteran sawflies of the genera *Diprion* and *Neodiprion* [35] also enter diapause in response to short photoperiods.

Photoperiod changes predictably across the year, allowing organisms to anticipate seasonal low temperatures and adjust resistance, or to enter the unfavorable season in a specific developmental stage that withstands cold. Thus, photoperiod is a reliable intra- and interannual indicator for upcoming adversity. Temperature-regulated diapause is common in *Dendroctonus* bark beetles, which express facultative prepupal diapause cued by thermoperiod (seasonal and daily fluctuations of temperature) [36,37]. Diapause-driven developmental delays ensure that the most cold-resistant ontogenetic stage enters winter. Induction by temperature provides more flexibility compared with photoperiodic diapause, potentially allowing plasticity in voltinism that might track changing climates across latitudes and altitudes [38].

The process of diapause termination determines the duration of diapause and is often temperature-sensitive; many forest insects require a certain duration of cold exposure to successfully terminate diapause [31]. Diapause often ends by mid-winter, when conditions are still adverse, and is followed by postdiapause quiescence. In this state, an overwintering insect can rapidly resume development, activity, and reproduction as soon as conditions become favorable. This combined diapause/quiescence strategy is very effective at synchronizing lifecycles so that most of a population is simultaneously active and available for reproduction in spring.

Beyond low temperatures, some forest insects enter diapause to mitigate heat or drought. For example, the bag shelter moth *Ochrogaster lunifer*, feeding on leaves of acacias and eucalypts in Australia, undergoes prepupal diapause to survive the dry season [39,40]. Conifer-associated aphids of the family Adelgidae (native to the Northern Hemisphere) enter diapause as so-called sistentes, which have morphological adaptations, like heavy sclerotization, to overcome hot and dry periods [41]. For example, the hemlock woolly adelgid *Adelges tsugae* (native to Asia and Western North America, and invasive in Eastern North America where it causes mortality on eastern hemlock) prefers cool conditions in spring and fall and expresses diapause during summer to mitigate high temperatures [41,42].

Some forest insect species also show remarkable forms of diapause with implications for lifecycle regulation. For example, in several species part of a population expresses prolonged diapause beyond one year, helping to spread risks across years within a population [43–45] (Box 3). Additionally, there are examples where both facultative and obligate diapause occur within a single species [3,31,36], a strategy to respond to diverse environmental conditions across a wide geographic range.

Climate change and alterations of diapause-related environmental factors

Climate and anthropogenic change can have substantial effects on insect dormancy. In temperate regions, some of the general trends for climate change are a shortening of the duration of winter, an increase in night-time temperatures across the year, and an expansion of seasonally warm conditions [46]. Climatic variability is also increasing, particularly in autumn and spring, with potential negative effects on the timing of entry into or exit from diapause [46].

Photoperiodic cues are well known to induce diapause [1,6]. Due to climate-change-induced shifts in the phenology of some tree species, photoperiodic cues that once signaled the onset or the end of unfavorable conditions and the timing of bud break might no longer accurately reflect the timing of the onset or end of winter [47]. The duration of photoperiod that cues diapause can rapidly evolve to track changes in **seasonality** of climatic variables [47,48]. However, the extent to which rapid adaptation in photoperiodic cues for diapause will allow forest insects to mitigate the effects of climate change is a multi-faceted problem and we lack generalizable rules for which species have more or less capacity for rapid adaptation [49,50].

Adapting to novel climatic conditions is especially challenging for species with range expansions into novel habitats where they encounter new thermal and photoperiodic conditions; for example, due to introductions or release from previous low-temperature constraints during winter [51,52]. While temperatures can rapidly change due to ongoing warming, photoperiods do not, leading to asymmetries among drivers that can challenge seasonal adaptation and potentially lead to **phenological traps** [38].

Urbanization might interact with changing climates to influence seasonality and dormancy cues in forest insects in urban and suburban landscapes [53,54]. These landscapes tend to be warmer than surrounding rural areas and form urban heat islands, where trees and insects are also exposed to an excess of artificial light at night [55–57]. Forest insects inhabiting urban/suburban habitats therefore experience seasonality very differently than their rural counterparts, leading to

Box 3. Prolonged diapause in forest insects – the pine processionary moth as an outstanding example

Prolonged diapause is a long-term, bet-hedging strategy by which insects can mitigate risks posed by year-to-year variation in conditions, from temperature and rainfall to food resources or disease. The pine processionary moth (*Thaumetopoea pityocampa*) is a pine-defoliating insect typical of the Mediterranean region, although it is currently expanding north and retracting from some of the southernmost areas of its range [51]. Prolonged diapause occurs in the pupal stage. Each year, some fraction of individuals from a population enter multiyear diapause that can last as long as 7–9 years in the soil before emergence [43,44]. During prolonged diapause, metabolism is maintained at a minimum level except for short peaks evidenced by an increase of oxygen consumption and body temperature that are observed every year in spring, ~1.5 months before the expected emergence of adults [114]. After each peak, some individuals continue to ramp up metabolism and emerge as adults while others suppress their metabolism again until the following year. The mechanisms behind the ultimate duration of prolonged diapause are unknown, although fat body reserves might be a factor.

Considering the high inter-individual variation in the number of years spent in prolonged diapause within populations, including siblings of a single colony, prolonged diapause likely allows some larvae to escape lethal temperatures in the case of extreme events and mitigate local population crashes during unfavorably hot or cold years [67,107]. Larvae are gregarious and occur on trees from late summer to spring, depending on local populations and climatic conditions. Larvae spend the day inside a silk tent and feed outside the tent at night (Figure I). Temperature is the major driver of activity as larvae feed only when they experience a temperature >9°C during day, and when night-time temperatures are above 0°C, but only if both conditions are met concurrently. If daytime and night-time temperature thresholds are not met, larvae do not feed and starve to death (although they can survive up to four weeks without feeding). Extreme cold or warm winter temperatures were found to be the best predictors of the probability of individuals entering prolonged diapause, indicating that prolonged diapause could be a general bet-hedging, or risk-spreading, mechanism in unpredictable climates [67]. The physiological mechanisms driving prolonged diapause and the associated ecological and management consequences in *T. pityocampa* and other forest insects remain poorly understood, highlighting the need for future research on this topic.

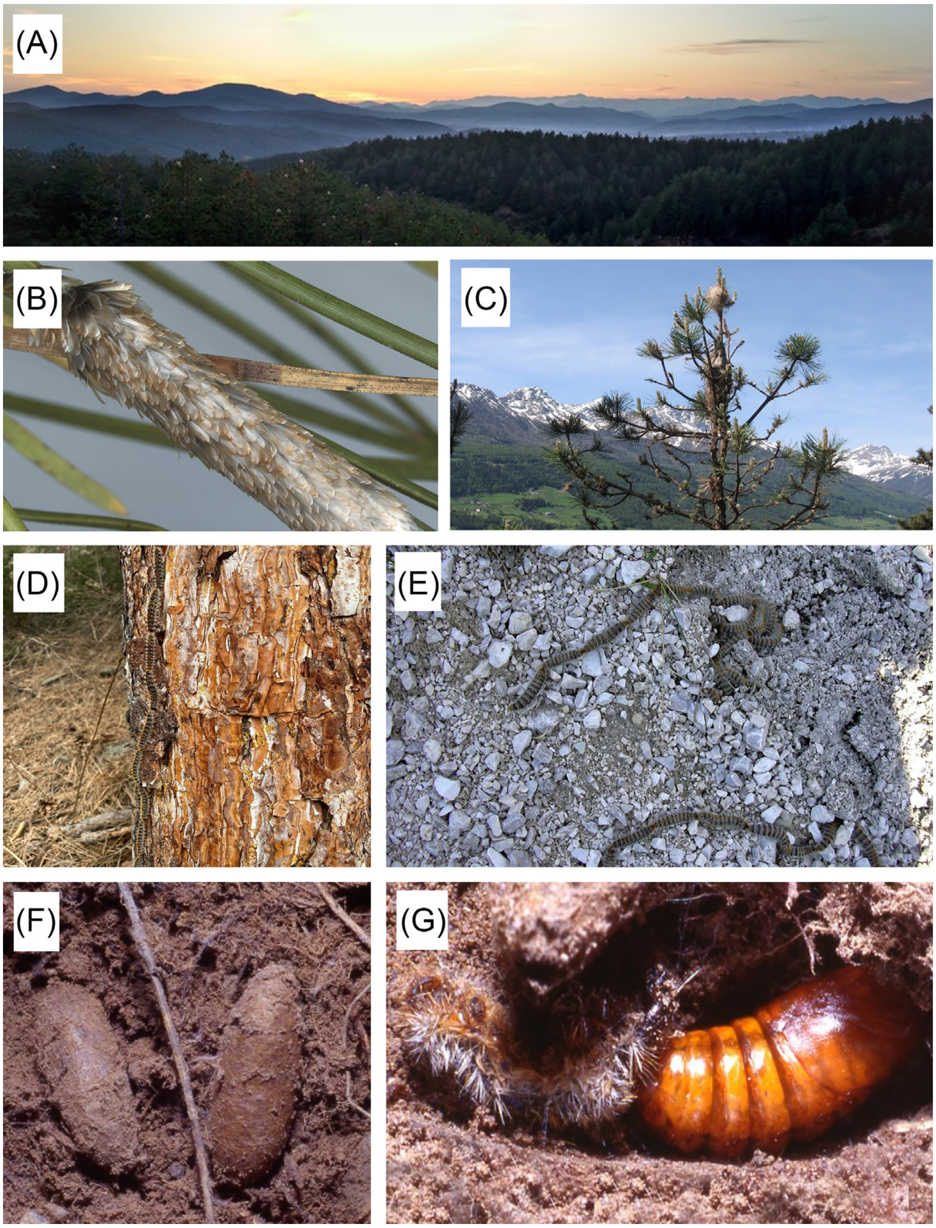

Figure I. Overview of (A) canopies in a pine stand in Southern Bulgaria showing how pine processionary moth (*Thaumetopoea pityocampa*) nests are spun to be well exposed to radiation. (B) Eggs deposited on pine needles, which can be exposed to intense heat in summer, but scales are assumed to help thermoregulating/buffering the microenvironment. (C) Pine with nests. (D) Procession of larvae crawling down their host tree (band heading to suitable habitats). (E) Larvae looking for pupation and subsequent diapause sites in the soil. (F) After burying down at the end of their procession, larvae spin a silken cocoon where they pupate and undergo obligate diapause. (G) Pupa as well as its former larval exuvia without the cocoon. Photos: (A, B) by Mathieu Laparie, (C–G) by Andrea Battisti.

different sets of selective forces on seasonal dormancy [58–60]. Thus, urbanization can combine with climate change to have unexpected effects on forest insect dormancy, from urban forest insects foregoing dormancy, having truncated dormancy or undergoing more intense or longer dormancies [61–63].

Effects of climate change on performance of diapausing insects

Forests can buffer environmental variation in some microhabitats, but changing climates are likely to influence diapause performance [64]. Three central dormancy-related traits influenced by climate change are: (i) timing mismatches; (ii) direct temperature-related stress; and (iii) energetic stress.

Effects on seasonal timing have been discussed earlier and can result in mismatched timing of entry into and exit from dormancy [47,48]. Depending on the life stage, diapause includes a block [1] or a heavy suppression [65] of morphogenic and/or reproductive development. The block or suppression of development is a key feature of diapause because it protects against premature development during the favorable season (late summer and fall for winter-diapausing insects), and acts to synchronize postdormancy emergence in local populations [66]. Because accumulation of a threshold quantity of low temperature is a common driver of diapause termination, warming winters are expected to reduce the ability of some insect species or populations to accumulate adequate amounts of cold for a timely diapause termination and subsequent resumption of development [1,67]. This can lead to emergence mismatches, and will likely have multiple thus-far poorly understood effects later in the season [47].

Most dormant insects, including forest-dwelling species, increase abiotic stress tolerance as part of the diapause phenotype [4]. This includes increased resistance to low and high temperature, ice formation, and desiccation [66]. Mounting these stress responses is often costly. Therefore, insects tend to show resistance in relation to the level of stress found in a region, including a buffer or safety margin between their tolerance limits and local conditions [68,69]. Climate change can thus lead to maladapted responses through costly energy drain during dormancy, for example, when winter temperatures are warmer (see later). Snow cover also affects the dormancy performance of insects overwintering in microhabitats that are below snow. Snow cover buffers direct **abiotic stressors**, and reductions in snow depth or complete absence of snow cover can expose dormant insects to thermal variability and extreme thermal events [70]. Insects overwintering in the trunk or the canopy are less affected by changes in snow cover than are insects dormant in the leaf litter or soil; for example, wood ants, some bark beetles, and moth pupae [3,32,71]. Because forest type influences snow cover accumulation across microhabitats (forest edges vs. inner parts of stands, or continuous versus fragmented forests), overwintering in deciduous, coniferous, or mixed forests each has distinct implications for the nature of the cold stress dormant insects experience (Figure 1).

Changing climates can increase energy drain in overwintering insects because they generally do not feed during winter, regardless of the dormant stage [72,73]. Thus, the dormant phase uses energy stored prior to the onset of dormancy [72], and most insects display substantial metabolic suppression during diapause [74–76]. While many insects show a reduction in the thermal sensitivity of metabolism in their dormant state [70,77], higher temperatures nevertheless will lead to greater metabolic demand. Thus, increasing temperatures are expected to lead to severe energy drain and to reduced post-dormancy fitness [78,79]. Reduction of snow depth/cover might further exacerbate energy drain by decreasing thermal buffering [71]. Such extra energy expenditures due to warmer conditions could become particularly significant in insects undergoing prolonged diapause spanning multiple seasons and years [43,67].

Effects of climate change and diapause on phenology and voltinism

While advancing spring phenology is one of the most well-documented responses to warming climates [80], phenology is not advancing in all insects. In some species there is little evidence of any phenological change [81], whereas in others, fall phenology is altered rather than spring phenology [82]. Distinct geographic populations of the same species can differ in the directionality or magnitude of changes in seasonal timing [31,83]. Thus, the phenological alterations of forest insects with climate change can be a complex mosaic of responses [84]. Given the central role of dormancy in forest insect lifecycles, further understanding of how each of the components of dormancy responds to changing microclimates could provide generalizable rules that can be used to untangle this mosaic of responses more clearly and more accurately predict how forest insect populations will be affected by climate and other sources of anthropogenic change. Further, the small-scale microclimatic variation in forests contrasts with other terrestrial ecosystems that are less buffered; for example, agricultural systems. Comparing habitat conditions and insect responses across multiple ecosystems will be needed to develop generalizable concepts of how dormancy affects population processes across habitats.

Often acting as a central mediator of lifecycle timing, diapause can modulate phenology in two nonmutually exclusive ways: (i) there is **phenotypic plasticity** in diapause regulation with respect to temperature, thus changing temperatures affect the onset, duration and end of diapause; and (ii) heritable variation in diapause regulation evolves in response to changing climates. Documented and predicted responses of forest insect phenology to climate change are largely based on responses to temperature, though diapause is known to be highly variable among populations and rapidly evolving in insects [85–87].

Climate-change-related temperature increases can have a range of effects depending on the different phases of diapause in which thermal increases occur, consequently affecting phenology, synchrony, and voltinism [84]. Induction of photoperiod-regulated diapause can be modified by temperature, for example, in the bark beetle *Ips typographus* [3,32,88]. Temperature increase in late summer/early fall, when **sensitive developmental stages** perceive the **token stimulus**, can postpone diapause induction resulting in an extended reproductive season. Together with warmer spring conditions and an earlier onset of activity, this lengthening of the growing season and shrinking of the dormant season will likely increase voltinism. For example, the bark beetle *Dendroctonus rufipennis* has a temperature-regulated facultative prepupal diapause that is induced by low temperatures in late summer [3,37]. Diapause can be averted under warm conditions which ultimately results in a shorter lifecycle and a shift from semivoltinism to univoltinism [89].

Photoperiod-mediated induction or termination of diapause often occurs over a small developmental window, a sensitive developmental stage, and changes in phenology caused by changing temperatures can disrupt developmental synchrony of the sensitive stage from the photoperiodic cue, resulting in altered phenological timing and consequently changes in voltinism [1,3]. Because many forest insects must experience some period of cold to terminate diapause, warmer winters might postpone diapause termination. Therefore, warming temperatures could actually delay spring phenology, or possibly lead to no change if the delay is offset by more rapid post-diapause development [90].

As mentioned earlier, climate change can cause phenological mismatches. For example, the timing of emergence from larval diapause does not change with increasing temperature in the spruce budworm *C. fumiferana*, possibly facilitating a shift from the primary host to another secondary host tree because budburst is temperature sensitive in the primary host [91].

Defoliating moths including the winter moth (*Operophtera brumata*) experience changes in phenology, population dynamics, and geographic range due to changes in winter diapause termination and synchrony with food sources the following spring [92–94]. The larch bud moth (*Zeiraphera griseana*) requires **synchronization** between hatching of overwintering eggs and flushing of the larch needles they feed on [95,96]. Because the lack of cold during winter is altering the timing of egg hatch more than leaf flush, larch bud moth populations are shifting to elevations where synchronization still is possible [95]. Once the tree line has been reached, however, finding suitable trees will be less likely, unless a shift in the tree line to higher elevations also occurs. The latter will take decades, and therefore local extinctions of the larch bud moth seem likely. Other voltinism-related phenological mismatches can occur when certain developmental stages that are not suitable to cold enter the winter season [38,46]. For example, although an extended reproductive season increases voltinism in the bark beetle *I. typographus*, preimaginal stages (which are less resistant to cold than adults) that do not become adults in time will suffer from cold-related mortality over a wide part of the range of the species [3,32]. Similarly, *Dendroctonus* bark beetles synchronize their lifecycles such that the most cold-hardy developmental stage enters winter. Thus, climate change-related phenological shifts can result in increased overwinter mortality if conditions deteriorate while the insect is in a less hardy stage [3,97].

Finally, a few forest insect species exhibit potentially heritable, and therefore evolvable variation in diapause strategies. For example, populations of the bark beetles *I. typographus, Dendroctonus simplex, Dendroctonus ponderosae*, and *D. rufipennis* vary across a range of environmental sensitivity from effectively obligate to highly facultative diapause [31,36,98]. An extended favorable season for reproduction and development due to higher temperatures might increase the proportion of facultative diapausing lineages within and across populations over obligate diapausing conspecifics [1]. This could result in evolutionary changes in environmental sensitivity of dormancy, possibly accompanied by alterations in voltinism.

Concluding remarks

Forest insect dormancies have both plastic and adaptive potential and are responding to changing environmental conditions, with significant impacts on forest ecosystems, including carbon sequestration [99]. Insects are a tremendously successful group of animals occupying all continents on Earth and show remarkable responses for adapting to climate change. Probably due to the strong selection imposed by mortality in individuals making poor timing decisions in seasonal environments, evolutionary pressures on entry into and exit from diapause include some of the most famous cases of rapid adaptation known, including responses to climate change and urbanization [60,100]. Large-scale range shifts are also becoming ever clearer, with strong associations between dormancy type and extent of range expansion [101,102]. In addition, local adaptation in physiological traits, including metabolic suppression and tolerance to low temperatures, are apparent in forest insects; indicating high potential for rapid evolution and strong selection on dormancy-related traits [64,87]. As such, insects clearly possess the capacity to respond to changing seasonality and an understanding of how diapause tactics are affected by environmental parameters is needed to predict potential impacts of insects on forests under future climates (see Outstanding questions).

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Outstanding questions

Although still difficult to collect, would microclimatic data with fine spatiotemporal resolution improve our estimates of dormancy performance; for example, phenology or winter survival, of forest insects?

Climate change can result in an asymmetry in abiotic conditions regulating diapause, for example, temperatures in a given habitat might change while photoperiod does not. Do photoperiod-regulated traits evolve faster than temperature responses in forest insects? Can we use data on the asymmetry of different drivers to predict range changes?

Will information on phenotypic plasticity and adaptive potential of diapause responses allow us to understand the effects of seasonality on insect performance in a changing climate?

Whether urban or rural, managed or unmanaged forests, insects face a broad spectrum of diapause-regulating conditions and diapause responses might consequently vary depending on forest type. Can we use information on diapause tactics and diapause responses of insects across habitats to get insights into possible adaptations to different environments?

Some species do not fit into the standard framework of insect diapause; for example, eusocial insects, like ant queens of some *Formica* species that live >20 years and go through dormant and reproductive cycles multiple times during their life. How are diapause and/or dormancy regulated in long-lived eusocial insects and how does this affect the response of perennially long-lived insects to seasonally changing environments?

Our current understanding of forest insect dormancy is based on economically relevant species from the Northern Hemisphere. Can we infer generalizable rules and concepts about forest insect diapause by studying species from numerous taxa and functional groups across a diversity of ecosystems worldwide?

Declaration of interests

No interests are declared.

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