Surviving in Changing Forests: Abiotic Disturbance Legacy Effects on Arthropod Communities of Temperate Forests

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Abstract

Purpose of Review

The increasing impact of droughts, wildfires and windstorms in temperate areas poses a significant challenge to the adaptation capacity of forests and their associated arthropod communities. Organisms, organic material, and environmental conditions occurring after disturbances, i.e. the disturbance legacies, shape arthropod communities during their transition from pre- to post-disturbance conditions. We describe the contribution of disturbance legacies to the organization of forest arthropod communities following droughts, wildfires, or windstorms. We also highlight how forest conditions, arthropod traits and post-disturbance management influence disturbance legacies and their impact on arthropod communities.

Recent Findings

Key disturbance legacies include surviving arthropods, micro-environmental legacies, and tree- and ground-related resources. Most of these are driven by canopy openness and tree condition. For arthropods, dispersal ability and other biological and demographic traits determine their vulnerability to disturbances, but also their capacity to colonize post-disturbance microhabitats, and withstand micro-environmental legacies. Dominant tree species and management strategies influence disturbance regimes and mediate the pattern of their legacies. Droughts, wildfires and windstorms have idiosyncratic effects on disturbance legacies, and arthropod taxa can have specific responses to legacies, making it difficult to predict the likely composition of post-disturbance arthropod communities.

Summary

This review highlights a particular gap in our understanding of the effects of drought on forest arthropod communities and the need for more research in this area. In addition, a better understanding of how forest arthropod communities are altered by changes in disturbance regimes is urgently needed. Our goal is to foster an improved understanding of the role of disturbance legacies for forest arthropod communities in order to improve management decisions and promote the conservation of forest arthropod species.

Keywords: Drought; Wildfire; Windstorm; Forest management; Microclimate; Trophic resources

1 Introduction

Major abiotic disturbances in temperate forests worldwide include droughts [127, 332, 330], windstorms [131, 114, 331], and wildfires [114, 331, 97]. Climate and land-use changes have increased the incidence and the ecological consequences of these three disturbances across large areas over the last three decades [329, 236, 333, 75]. The frequency, magnitude and intensity (which define the disturbance regime) of droughts, windstorms and wildfires are predicted to increase further in temperate regions with global warming [327, 315, 342], thereby challenging the acclimation and adaptation capacities of temperate forests and their associated communities [236, 3, 368].

Droughts, windstorms and wildfires alter the physical characteristics of forest ecosystems in several ways, including the availability of water and nutrients [116, 328, 341], and the forest microclimate [87, 183]. Likewise, they affect key biotic elements such as the distribution and structural architecture of surviving trees and shrubs, the quantity and viability of their propagules, and decomposer and tree symbiont communities [116, 353, 226]. This in turn affects a whole host of forest features such as soil and litter conditions, canopy and understory cover and the availability and distribution of microhabitats [116, 183, 165,314•]. As a consequence, forest biodiversity also undergoes significant changes [359, 388••].

Arthropods make up the majority of biodiversity on Earth [298]. This makes them a particularly relevant taxonomic group to consider when seeking to better understand and predict the consequences of droughts, windstorms and wildfires on forest biodiversity and ecosystem functioning. Arthropods are: (i) major components of forest biodiversity across multiple strata (i.e. canopy, sub-canopy, forest floor and soil; 298, 396), (ii) important food sources for forest-associated species and vital components of complex trophic webs, (iii) key contributors to vital forest ecosystem functions (i.e. pollination, decomposition, biological control of pests and diseases), and (iv) hyper-diverse, displaying significant variation in traits that are reflected in wide-ranging levels of susceptibility to the direct and indirect effects of disturbances (e.g., 103, 89). In addition, they can (v) cause disturbance feedback effects (e.g., outbreaks of opportunistic pests; 329) and (vi) show rapid responses to disturbance-mediated changes.

Understanding the responses of forest arthropod communities to droughts, windstorms and wildfires is necessary in order to anticipate likely arthropod-induced feedback effects on forest ecosystem structures and processes. This knowledge is crucial to identify management options that may curb any negative feedback effects, especially in a context of changing disturbance regime. An improved understanding is also needed to deliver effective arthropod conservation actions and strategies, considering that arthropods are currently in global decline [141]. We lack a comprehensive overview of the responses of arthropod communities to key abiotic disturbances in temperate forests [359, 388••]. We strive, in this review, to fill this gap and seeking to gain improved insights by considering responses of arthropod communities through the lens of disturbance legacies.

Disturbance legacies can be defined as the post-disturbance physical and biological state of an ecosystem [116, 167]. An example of a disturbance legacy is a physical shelter created during a windstorm or a fire which serves to protect organisms and their propagules from the harmful effects of subsequent disturbances [353, 233, 235]. Disturbance legacies are defined by the amount, availability and diversity of resources and microhabitats left behind following a disturbance [314•, 364, 79]. They are key filters that define how arthropod communities are shaped as they transition from pre-disturbance to post-disturbance communities [116, 353, 293•].

Several factors can modulate the nature, amount and spatio-temporal distribution of disturbance legacies, and ultimately the effects they have on the composition and structure of post-disturbance arthropod communities. A prominent factor is the disturbance regime, as it dramatically affects the amount, distribution and diversity of disturbance legacies [293•, 66, 192]. Other factors include pre-disturbance forest characteristics such as forest stage of development and the taxonomic, functional and phylogenetic diversity of resident tree species. These are themselves influenced by forest management strategies and past disturbances (Fig. 1; 167, 192, 374, 212, 218). Intrinsic traits of forest arthropod communities can also modulate their ability to tolerate disturbances and to exploit the resulting legacies (Fig. 1; 377, 25). Finally, post-disturbance management can markedly modify disturbance legacies (Fig. 1; e.g., dead wood clearance), and consequently, post-disturbance arthropod communities [215, 259, 369].

Our primary aim is to highlight the key roles of disturbance legacies originating from droughts, windstorms and wildfires in shaping arthropod communities in temperate forests. We also consider the contribution of various intensities and methods of both pre- and post-disturbance forest management as an additional filter shaping post-disturbance arthropod communities. Our review is organized into four sections. We first introduce key disturbance legacies associated with droughts, windstorms and wildfires that have a role in shaping forest arthropod communities and explore how each of these disturbance regimes might affect these

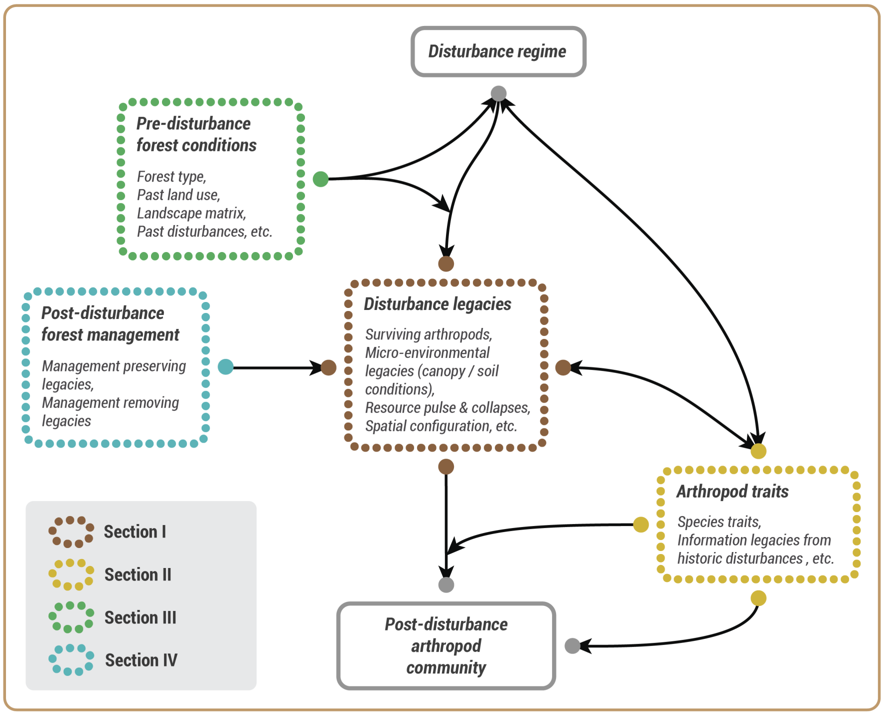

Figure 1: *General structure of this review, with factors affecting disturbance legacies and their exploitation by forest arthropod communities*

legacies. Secondly, we describe how pre-disturbance conditions at tree, stand and landscape scales can affect the nature, distribution and diversity of disturbance legacies. In a third section, we seek to identify the key arthropod traits that influence how arthropods interact with and respond to disturbance legacies. In a final section, we evaluate how post-disturbance management strategies can exacerbate or alleviate disturbance impacts on arthropod communities. We conclude by identifying key knowledge gaps and propose a number of future research directions.

2 Key Drought, Wildfire and Windstorm Disturbance Legacies Influencing Arthropod Communities

Disturbance legacies are a combination of material and information legacies [167]. Material legacies are the biologically-derived materials left in the wake of disturbances, which include surviving individuals, but also the resources and microhabitats available for arthropods (*sensu* 167). Information legacies are ecological traits filtered by the selective pressures exerted by previous disturbances (*sensu* 167).

Droughts, windstorms and wildfires have many similar but also idiosyncratic effects on forest ecosystems, and each type of disturbance can generate a specific set of both material and information legacies for arthropods. Here we describe key disturbance legacies for arthropods and how they specifically influence arthropod communities. These legacies include surviving organisms (including arthropods), micro-environmental conditions, and spatiotemporal dynamics of key resources at local and landscape scales (Fig. 2). How arthropod communities respond to legacies, and how arthropod traits modulate their responses, is detailed in

"Key Drought, Wildfire and Windstorm Disturbance Legacies Influencing Arthropod Communities" section.

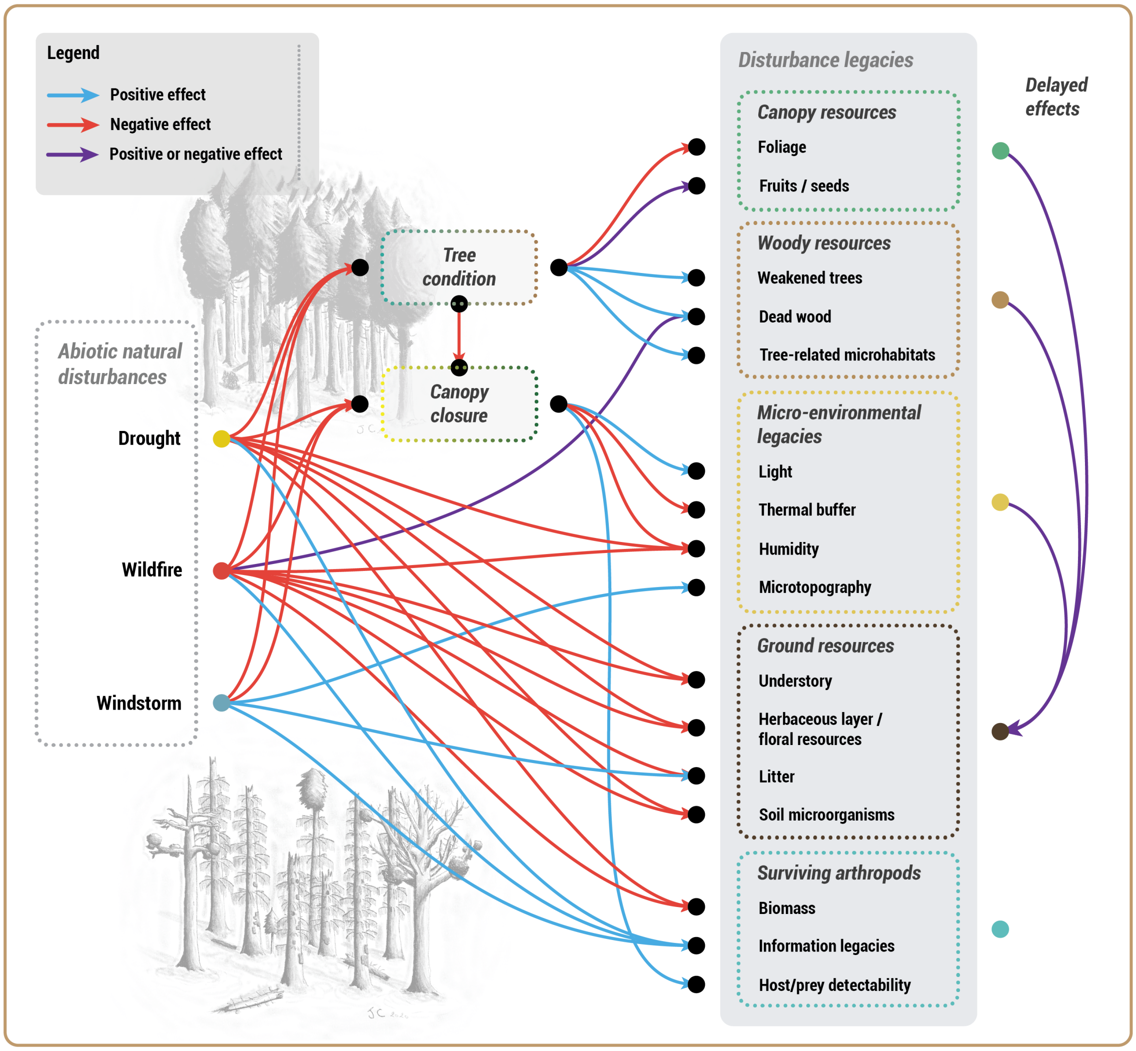

Figure 2: *Effects of droughts, wildfires and windstorms on key disturbance legacies for forest arthropods. Effects can be both direct and indirect through disturbance impacts on tree condition and canopy closure. Some disturbance legacies can also have delayed effects on ground resources. For instance, changes in microclimatic conditions (brighter and warmer conditions) can subsequently enhance the herbaceous layer and floral resources. In general, effects can be positive, negative or both, depending on the context*

2.1 Surviving Arthropods

Large forest disturbances negatively affect populations of many organisms (Fig. 2). Wildfires can cause massive arthropod mortality, and even lead to local extinctions [399, 254]. Windstorms and droughts are less lethal but can severely disrupt the structure of above- and belowground arthropod communities and the structure of forest food webs [213, 124, 275, 395, 171]. Eggs, larvae, pupae, and the adults that survive constitute a major disturbance legacy, and their capacity to survive and subsequently reproduce in the disturbed landscape determines the composition of the post-disturbance community, until immigration takes effect (e.g., 40, 291, 129). Some taxa of surviving arthropods may serve as prey for non-arthropod species, but are also a key resource across various arthropod trophic guilds (i.e. among predatory, parasite and parasitoid species). Disturbances exert strong selective pressures, promoting information legacies in arthropod communities related to survival and colonization processes (see section 2; Fig. 2).

2.2 Micro-Environmental Legacies

Due to their small body size, fine microscales are more relevant to most arthropods than meso- or macroscales [283]. Within forest ecosystems, the canopy, ground vegetation and surface soil layers are key compartments that provide a wide array of resources and microhabitats for a significant proportion of forest arthropods [349]. These compartments can be significantly altered by direct impacts of droughts, wildfires and windstorms (Fig. 2; 243, 38, 250). Canopy structure can be further altered by subsequent tree dieback or decline (Fig. 2; 314•, 310, 13, 20). This increases canopy openness, which is a major determinant of disturbance-mediated effects on arthropod communities. A reduction in canopy cover has a considerable effect on microclimates from the ground level to the upper canopy layer. The higher insolation produces warmer microclimates (e.g., warmer soil surfaces, warmer understory), and a reduced environmental buffer thereby exposing the forest understory to temperature extremes (Fig. 2; 183, 1, 401). Among and within deadwood logs and stumps, sun-exposure increases microclimatic heterogeneity (temperature and moisture), promoting saproxylic beetle species richness at the stand scale [323, 205•]. At the same time, higher insolation can also negatively affect leaf litter arthropods that are sensitive to temperature extremes [139].

Droughts, wildfires and windstorms can have contrasting effects on soil conditions (Fig. 2; 81). For instance, wildfires can entirely remove the litter layer and some portions of the upper organic horizon [65]. This can affect soil biochemical properties, alter soil texture and reduce soil permeability [65, 64, 262, 35]. Windstorms, on the other hand, generally increase the litter cover and add woody debris [104, 392]. The pit-and-mound topography and root plates of uprooted trees in windthrown stands can cause small-scale gradients in soil moisture, temperature and litter accumulation [31]. This provides refuge areas where many arthropod species are comparatively safe from desiccation compared with areas of the forest floor under canopy gaps [388••, 365]. Droughts reduce soil water films and increase soil hardness, which could impede the movement of soil fauna [81]. Disturbance-driven changes in micro-environmental conditions can in turn impact the development, survival and behaviour of ground- and canopy-dwelling arthropods, and ultimately the composition and structure of their community [314•, 388••, 385, 278], but see below (section 2).

2.3 Resource Pulses and Collapses

Disturbances affect the diversity and the amount of resources available to arthropods. In this regard, the timeframe of disturbance effects is important to consider as both the amplitude and direction of resource fluctuations can vary over time (Fig. 2, Table 1; e.g., 288, 15). Some resources may suddenly collapse or increase at the onset of a disturbance (e.g., deadwood after a windstorm), while the temporal dynamics of other habitats and resources may be subject to a timelag and can vary considerably.

Table 1: *Effects of drought on trophic resource and microhabitat availability considering immediate, short-term (weeks/months) and delayed (years/decades) effects. TreMs: tree-related microhabitats*

Habitat / resource	**Drought effects**		
	Immediate	**Short-term (< 1 year)**	**Delayed (1 year +)***
TreMs	(0/+): cavitation can generate dry branches	(+): Partial branch mortality triggers an accumulation of dead wood in the canopy. Tree mortality can occur under severe water constraint and the resulting snags can accumulate diverse TreMs. TreMs associated with living trees may decrease	(+): There can be a lag in drought legacy effects over several years causing progressive tree decline and mortality resulting in an accumulation of TreMs in the canopy and on the trunk (dead branches, loose bark and bark cracks, cavities, etc.). TreMs associated with living trees may decrease
Foliage	(-): premature leaf shedding occurs during severe droughts	Canopy layer (-): (i) partial branch death reduces foliage abundance; (ii) decreased C allocation to non-perennial organs reduces the amounts of buds and foliage	Canopy layer (0/-): (i) gradual increase in dead branches progressively reduces foliage abundance and leads to increased canopy openness; (ii) decreased C allocation to non-perennial organs reduces the amounts of buds and foliage. Resilient trees may compensate crown degradation by forming epicormic shoots
		Herbaceous / shrub layer (±): increased canopy openness can favor ground vegetation regeneration and growth but this can also lead to more exposed conditions (e.g., higher temperatures, lower soil moisture)	Herbaceous / shrub layer (±): increased canopy openness can favor ground vegetation regeneration and growth, but this can also lead to more exposed conditions (e.g., higher temperatures, lower soil moisture)
Fruit and seeds	(0/+): premature abscission or fruit abortion can occur during severe summer droughts	Canopy layer (0/+): large mast events can occur following droughts	Canopy layer (-): (i) fewer branches reduces the number of reproductive structures; (ii) C allocation to perennial organs reduces the size and abundance of reproductive organs
		Herbaceous / shrub layer (+): Increased canopy openness can promote floral resources	Herbaceous / shrub layer (+): Increased canopy openness can promote floral resources in ground vegetation

* variable according to stand resilience. Here it is considered that the expected repeated droughts will compromise tree recovery

Some resources can be markedly reduced or locally depleted as a direct consequence of a disturbance. For example, degraded canopies provide less foliage for herbivorous species [314•]. Similarly, flowers and fruits may abort during a drought [108, 263] and, over longer time scales, weakened trees produce less reproductive organs (Fig. 2, Table 1; 123). Nonetheless, large mast events occasionally occur following disturbances [9, 381, 382, 223], and may provide a pulse of flowers, fruits and seeds that remain hardly predictable. Abiotic disturbances may also alter host plant tissue nutritional content and/or levels of defensive compounds, which in turn can alter host plant resistance to phytophagous insects [124, 300, 152, 158, 69]. In this regard, the immediate and short-term effects of drought have been investigated in several tree species, and the outcomes largely depend on drought severity and duration [124, 152, 158]. Similar modifications probably occur over long-time scales in declining trees, although evidence is lacking [314•]. The pulse in soil nutrient availability following fire may also affect several leaf traits of surviving trees, including leaf mass per area and levels of nitrogen or non-structural carbohydrates [300, 69]. However, Rieske et al. [300] did not observe cascading effects of fire-induced changes in foliage quality on the performance of defoliators. Overall, the quantitative and qualitative fluctuations of these canopy-related resources during decline and dieback processes have been poorly documented [314•, 157].

The reduction of canopy cover stimulates successional dynamics and provides colonization opportunities for early successional and thermophilous plant species [72, 280, 93]. Depending on disturbance type, spatial extent and severity, the change in canopy cover could be important also for late-successional and shade-tolerant species [66, 373, 224]. As a result, windstorms and wildfires may promote plant species richness in the herbaceous layer, but have contrasting effects on plant functional diversity and traits [373, 224, 48, 86, 52], with cascading effects on arthropod communities. For instance, canopy opening can increase ground-related floral resources available for pollinators [48, 305]. This is however a rather short-lived resource pulse, as a few years after disturbance, floral resources tend to decline [288]. In addition, increased canopy openness accelerates decomposition and could provide a pulse of microbial resources and nutrients for soil arthropods [309, 277].

On the ground, wildfires can consume large patches of the litter and superficial organic horizon [64, 88], leaving a charred biomass with altered biochemical properties for long periods [35, 91]. This can profoundly alter the microhabitats and trophic resources for soil-dwelling arthropods, but also for other forest arthropods occupying the forest floor [387]. Wildfires can, however, improve the amount and diversity of ground-nesting sites for some arthropods [48]. The immediate consequences of wildfires on soil microorganisms are a decrease in abundance, biomass and richness, and an alteration of their community structure [15, 290]. Likewise, drought adversely affects microbial communities in forest soils, at least over short time scales [213, 275, 18, 317]. This can be expected to have negative consequences for soil-dwelling arthropods since they rely on soil microorganisms as key food source [275, 285]. However, responses of the soil microbial community can also be complex. Responses may be positive, negative and of varying amplitude, when considering longer time periods following a disturbance [15, 220].

Disturbances may lead to transient increases of resources which are traditionally scarce in managed forest ecosystems, and thus, enhance the structural heterogeneity of the ecosystem [314•, 334, 195, 241]. One of the best examples is the accumulation and diversification of deadwood resources (Fig. 2). Droughts and windstorms promote the accumulation of fallen twigs, branches, stems, uprooted trees and logs on the ground, perched dead branches in the canopy and snags [353, 79, 366]. Another important factor driving arthropod communities is tree-related microhabitats (TreMs; Fig. 2). Canopy openness and compromised tree health can promote the formation of TreMs such as bark scratches, bark cracks, loose bark, mistletoe, and dead branches [264, 190•, 201•]. Snags also offer more TreMs than living trees [267, 8]. As a result, disturbances can significantly affect the abundance and types of available TreMs, thereby generating legacies that could have positive consequences for arthropod species associated with these microhabitats (see below). Disturbances may also occasionally generate very particular substrates and environmental conditions, promoting atypical arthropod communities. For instance, wildfires can produce large amounts of sun-exposed charred deadwood, yielding to specific communities of "burn-associated" saproxylic beetles (e.g., in boreal forests 28). Following disturbances, fallen and weakened trees also constitute a major pulse of suitable breeding substrates for opportunistic pest species [314•, 268, 184, 176]. Similarly, disturbances may favor particular arthropod communities through the process of landscape complementation by spatially combining several habitats occupied by different life stages, e.g. wood-eating larvae with flower-visiting adults [31].

Together with contrasting survival among species, and micro-environmental legacies, resource pulses and collapses contribute to the structural complexity of forest ecosystems over several spatial and temporal scales [192, 157, 241, 321]. This increases the variability of available niches at different ecological scales, changes inter-specific interactions, creates colonization opportunities for novel species and can be major drivers of post-disturbance community structure for arthropods [293•, 157, 149, 378•].

2.4 Composition, Organization and Spatial Patterns of Disturbance Refugia

Disturbances generally do not affect forests uniformly at the landscape scale. They create a mosaic of affected and unaffected habitats of varying ratio depending on the disturbance regime [321]. Forest patches that are not or only minimally affected by disturbances are called disturbance refugia [192, 53]. Depending on the disturbance regime, disturbance refugia can ressemble unaffected islands within a disturbed landscape matrix, but they can also be more diffuse and less clearly delineated [192, 375, 238]. These refugia constitute reservoirs of genetic diversity and propagules from pre-disturbance communities, from which recolonization of disturbed areas can take place [192, 238, 326, 301]. They can also provide resources, suitable microhabitats and micro-environments in an otherwise hostile environment for survivors of the disturbance [192, 238, 301]. In this regard, the spatial pattern of disturbance refugia can be a key driver of forest ecosystem resilience. The spatial distribution of disturbance legacies affects whether post-disturbance arthropod communities stem primarily from recolonization processes, or from survivors. Disturbance refugia also contribute to the spatial heterogeneity at the landscape scale, especially if refugia and the disturbed landscape matrix follow different recovery pathways [238].

2.5 Disturbance Regimes and Disturbance Legacies

Disturbance regimes partly define the type, amount and diversity of legacies that commonly occur in an ecosystem. For instance, the intensity and duration of a disturbance drive its impacts on the number of surviving arthropods, the amplitude of deadwood resource pulses, the impact on soil conditions, and the size of canopy gaps (e.g., 387, 340, 21). Likewise, the spatial extent of disturbances influences (micro-)environmental conditions, and the spatial distribution of refugia in the landscape [372]. Equally, disturbance frequency will affect information legacies. Recurrent disturbances leave evolutionary imprints on communities. Pyrophilous plants and arthropods in fire-prone ecosystems are examples of disturbance-adapted species that improve the ecosystem resilience and resistance capacity of forest communities [178, 273]. Therefore, disturbances can be the catalysts that stimulate adaptation of forest organisms to environmental changes [93, 361].

Through disturbance legacies, successive disturbances can interact and have antagonistic, synergistic or additive effects (e.g., see section 2.2; 329, 193, 219). In this context, legacies from one disturbance can modify ecosystem resistance and resilience to a second disturbance [268, 336, 45, 56]. For example, the pulse of deadwood and litter resources on the ground following a windstorm can promote the spread of subsequent wildfires [261, 94]. Likewise, windstorms may reduce mature tree density and seed production, and consequently delay the recovery following a subsequent wildfire [46]. Severe wildfires can hinder tree regeneration by reducing seed availability thereby altering microclimate and increasing the risk of drought impacts on seed establishment [84]. Successive disturbance events can also generate unusual legacies. For example, disturbance legacies of forests subjects to repeat burns are composed of lower volumes of deadwood, with altered physical and biochemical characteristics, compared with forests burned only once [95].

Changes in climate and silvicultural practices are currently affecting natural disturbance regimes, which are diverging from historical disturbance regimes [131, 315, 83], sometimes leading to so-called "mega-disturbances" [345]. These more frequent, severe and spatially extended droughts, wildfires and storms produce novel types and amounts of disturbance legacies [114, 167]. For instance, increases in the frequency and severity of wildfires can reduce the amount of dead wood and the density of resprouting plants. These changes in available resource can alter the composition of saproxylic beetle communities, potentially lowering diversity and evenness [95, 102, 357].

Changing drought or wildfire regimes can also lead to major ecosystem reorganization through plant community replacement [19, 166, 168, 133]. An example of this is when there is an increase in fire frequency in fire prone ecosystems. This can reduce resilience since serotinous trees can be burnt before reaching sexual maturity and therefore, regeneration is impeded [177, 47, 138]. Ultimately, these regime shifts can disrupt ecological trajectories [84]. In some cases, this may lead to a shift from forests to grassland [345, 19]. These profound ecological changes can occur from the microscale [87] to the landscape scale [50, 376].

3 Forest Arthropod Responses to Disturbance Legacies

3.1 Key Traits of Arthropod Communities Driving Their Responses to Disturbances

Responses to disturbance can be grouped into general strategies according to life-history traits that facilitate population recovery and persistence despite (or because of) disturbance [307]. These strategies include: (i) *invaders* as opportunistic species, taking advantage of disturbance legacies and colonizing recently disturbed areas; (ii) *evaders* that rely on specialized strategies to "get around" the disturbance, being able to immediately re-establish post-disturbance populations; (iii) *resisters* that survive the disturbance itself, using specialized mechanisms to withstand direct, disturbance-induced mortality, or to recover after the disturbance event (e.g., survivors, see section 1) and (iv) *avoiders* which include species that are not considered to be disturbance-adapted and are only found in late successional stages. In this section we review the traits and strategies by which theses four categories of organisms (i) increase their survival to disturbance, (ii) re-colonize and/or exploit spatial refugia, (iii) exploit novel micro-environmental legacies associated with disturbances, and (iv) make use of the pulse and collapse of resources.

3.1.1 Traits Aiding Survival to the Direct Effects of Abiotic Disturbances

Many "resisters" occupy micro-environments that can act as refugia for at least part of their life cycle; e.g. within plant tissues or plant shelters [377, 40, 351, 304], or in patches that remain unaffected by the disturbance (i.e. disturbance refugia; 192). For instance, arthropods that have the capacity to use deeper portions of the soil profile have better chances of surviving a fire or avoiding the impacts of desiccation [291, 81, 234, 173]. Likewise, burrowing spiders, ground- and deadwood-nesting bees and ants, and larvae of saproxylic beetles can survive heat and direct flames within large-diameter logs [377, 234, 386]. Synchronization between disturbance seasonality and arthropod phenology can also influence the chances of surviving negative effects. For instance, in Mediterranean ecosystems, summer wildfires have less impact on soil arthropods as most of them have migrated into deeper soil layers or entered a cryptozoic stage at this time of the year [143].

Some morphological traits also contribute to resistance to disturbance among the "resisters". Drought-resistant species are equipped with specific protective body traits like hairs and thick cuticles [81, 199, 232]. Thick cuticles can additionally enhance resistance to wildfires [399]. Small arthropods such as mites (Acari) tend to be more sensitive to changes in soil temperature and dryness than larger arthropods (e.g., Collembola) [254, 27, 44].

Several "evaders" are able to detect wildfires well in advance, using olfactory or auditory cues, and may rapidly engage in escape behaviors, actively fleeing to disturbance refugia [89, 254]. In this regard, high mobility is a key asset to avoid deleterious disturbance effects. Winged insect orders consequently have higher survivorship to wildfires than less-mobile taxa [89], and smaller-bodied soil-dwelling arthropods are better able to take shelter from wildfires and move to refugia such as underground burrows, beneath rocks, or within tree trunks or roots [81]. Above-ground arthropods may also escape from wildfires by actively burrowing into the soil, or by moving upwards into the cooler canopy during low-intensity surface wildfires [89, 273].

The vulnerability of arthropods to abiotic disturbances depends on their preferred microhabitat [40], especially across the vertical gradient of forests. For instance, arthropods that live in the upper soil layers are likely to experience stronger disturbance-induced fluctuations in temperature and moisture compared to their deeper soil-dwelling counterparts [81], or compared to canopy-dwelling arthropods that may have better chances of surviving ground-level fires [89]. Ferrenberg et al. [109] suggest that aboveground communities are influenced to a greater extent by deterministic processes, while the relative influence of stochastic processes are greater for belowground communities.

3.1.2 Traits Related to Post-Disturbance Colonization Processes and the Spatial Distribution of Disturbance Refugia

Colonization and re-colonization processes depend on the proportion of arthropods that survive in situ or in distant refugia. Post-disturbance arthropod communities can be dominated at first by disturbance-adapted taxa [291]. "Invaders" can also rapidly colonize disturbed areas. This colonization of new habitat patches or newly-created substrates relies on the ability of these arthropods to detect material legacies. Phytophagous arthropods can detect weakened or recently perished trees through the emission of kairomones such as ethanol [248]. Similarly, saproxylic beetles can locate particular types of dead wood at some distance prior to colonization [130]. Pyrophilous insects, seeking burnt substrates, possess specialized chemoreceptors that sense smoke volatiles, and/or sensilla that respond to radiant heat and infrared [103, 273].

Disturbances also lead to the selection of traits related to mobility [253]. "Invaders" are by definition highly mobile, as they exploit ephemeral resources in post-disturbance environments [311]. Similar traits are also selected for in "evaders" and "avoiders", especially when disturbance refugia are highly scattered throughout the landscape. The composition of post-disturbance communities highlights the importance of dispersal in disturbed areas. For example, windthrown and burnt areas generally host lower numbers of brachypterous (small-winged) and higher numbers of macropterous (large-winged) ground beetle species compared with undisturbed forests [29, 316, 339]. Similarly, in recently burnt sites, there can be an increase in the abundance of spiders with greater ballooning dispersal abilities [199] and of wild bees with higher capacities for dispersal [234]. As a result, the spatial scale describing the effect of storms on arthropod communities increases with their dispersal ability [147]. Body size is another trait that is related to dispersal ability; i.e. post-disturbance soil communities often shift from small-bodied to relatively large-bodied, more effectively dispersing species [27, 44].

The colonization of material legacies also involves demographic parameters. The most successful "invaders" tend to have short generation times, high fecundity and long life spans. For instance, eusocial bees can quickly rebound following a fire during the early growing season since they are active across seasons and have several generations per year [337]. Similarly, ants recover rapidly after wildfires and maintain near-stable population sizes due to their large broods, small body size, diverse foraging niches and relatively broad diets [23]. These autecological and demographic parameters might be particularly relevant for recolonization processes when disturbance refugia are small compared to the surrounding disturbed matrix and consequently shelter a small reservoir of "avoiders" and "evaders".

In addition to the availability of space and new trophic resources, the local extinction of certain taxa may constitute an opportunity for the immigration of exotic invasive species into disturbed patches. Examples in support of this hypothesis include *Cacyreus marshalli*, an invasive butterfly, which tends to appear in Mediterranean shrublands after wildfires [319], and also exotic ant species found to have a high probability of establishing colonies in pine forests where there are frequent wildfires [10]. Likewise, arthropods can take advantage of post-disturbance conditions because of likely reductions in predation [147, 274] or competition pressures [297]. *Tentyria grossa*, a rare soil-dwelling beetle species, became dominant after wildfires in Italy partly because of the decreased abundance of almost all other related species [106]. Conversely, for some taxa critical population sizes must be reached before recolonization processes can take place. Resources created by large disturbances in Central Europe led to the return of *Peltis grossa*, a primeval forest specialist beetle, but at a slower rate than two more common, related species [51].

3.1.3 Traits Related to Micro-Environmental Legacies

In general, stand-removing forest disturbances benefit taxa that are adapted to more open, micro-environmental conditions (e.g., open-land ground-dwelling carabids, ground-hunting spiders or some saproxylic beetles), while groups typically associated with shady conditions are negatively impacted (e.g., forest-preferring sheet-web weaver spiders and shade-preferring carabid and saproxylophagous species) [323, 302, 63, 30].

Disturbances also disrupt patterns of humidity. Post-fire environments tend to have drier atmospheric and soil conditions, leading to a predominance of drought-resistant arthropod species [81, 199] and a decline in hygrophilous taxa [365, 316, 339, 380]. In this regard, the phenotypic plasticity of some soil arthropods, and more specifically their capacity to adapt some of their physiological, behavioral, and morphological traits to drier conditions (e.g., urine concentration, thermoregulation strategies, cuticular permeability, etc.) is a major advantage to improve tolerance to these shifting environmental conditions [232].

Open conditions also expose arthropods to higher potential levels of predation [63, 188]. Consequently, for some arthropod taxa the frequency of dark cryptic individuals increases in burned areas [273]. The ability for camouflage may be favored in disturbed forests but there is still limited supporting evidence for this.

3.1.4 Traits Related to Resource Pulses and Collapses

Disturbance legacies generate pulses or collapses in critical resources for arthropods. The largest impacts on arthropod communities are expected in the initial stages of the disturbance, but changes in community structure can unfold over more than a decade [126•]. The responses of arthropod communities to changes in resource diversity, amount and accessibility can be largely mediated by their composition, although idiosyncratic responses at the family or species levels also frequently occur [81, 134, 5, 54, 80•].

A higher diversity and abundance of deadwood-associated arthropods are generally observed in disturbed stands. In response to pulses in the abundance and diversity of deadwood substrates and associated TreMs (Table S1, Fig. 3; 388••). This also affects the taxonomic, functional, and phylogenetic composition of species in disturbed forests [190•, 80•, 338]. In general, saproxylic insects, benefit from these pulses [314•, 359, 365, 366] and this includes saproxylophagous arthropods [80•, 111], cavity-nesting species [80•, 335], and xylomycetophagous and mycophagous insects [29, 80•, 398], unless wildfire has altered wood biochemical properties [356]. The pulse of weakened host trees following severe forest disturbances also promotes xylophagous species (Fig. 3) and may trigger outbreaks of opportunistic pests (cf. III.2.). Impacts of tree dieback or decline on crown-related resources have more contrasting effects on leaf-dwelling guilds. Overall, tree decline has a negative impact on specialized leaf-feeders (Table S1), but has no effect on seed- and fruit-consuming species, although responses to variations in food are generally poorly understood among these guilds (Fig. 3; 314•, 313).

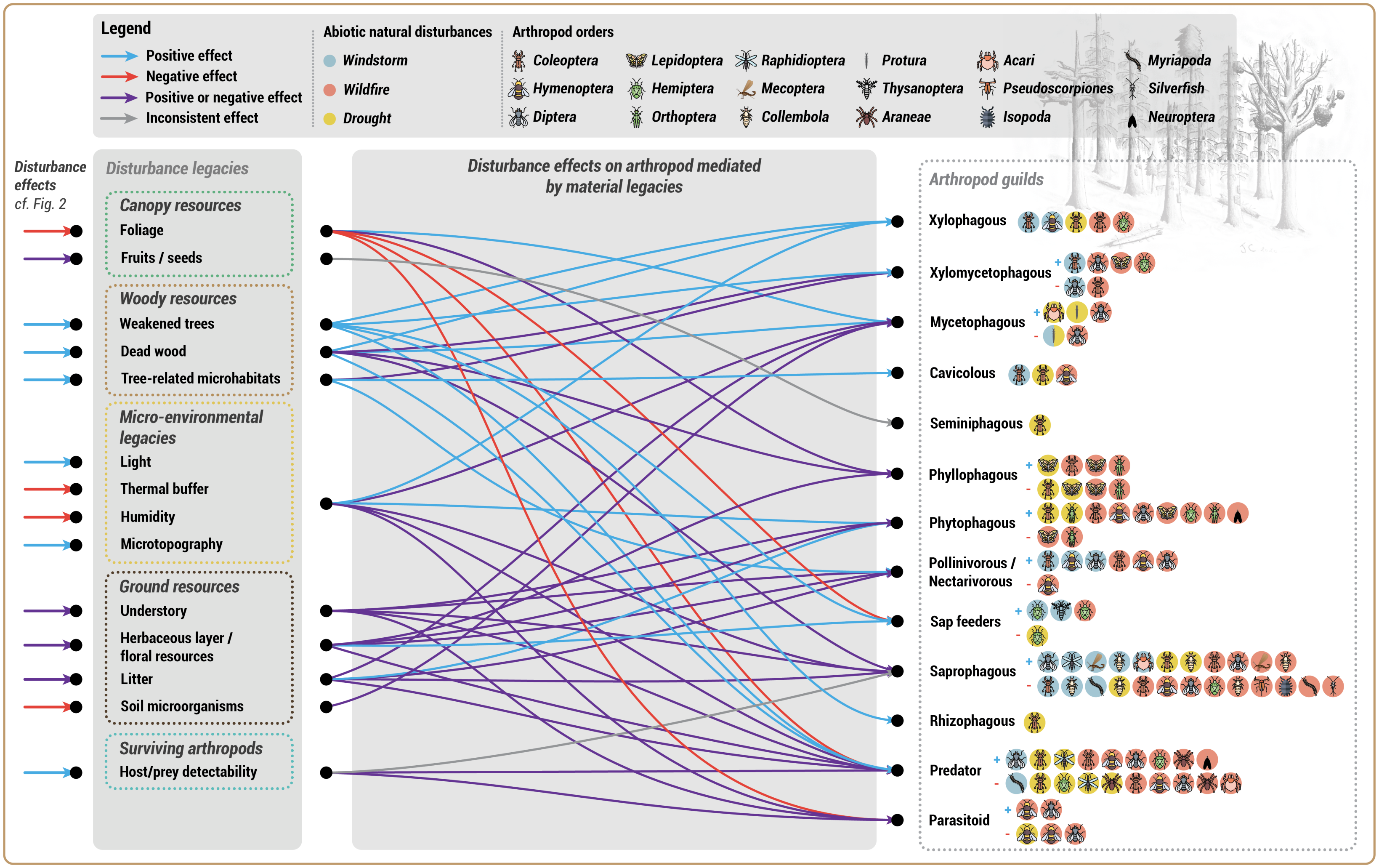

Figure 3: *Responses of forest arthropods to disturbance legacies according to their trophic guild. Details on arthropod groups investigated ($N = 28$), and references ($N = 52$), are provided in Table S1. On the right is a list of arthropod guilds with reported specific effects (positive or negative) against the investigated disturbances (windstorm, drought or wildfire)*

Increased canopy openness and the resulting pulse in herb layer and floral resources, consistently increase understory-associated herbivores and pollinators (Fig. 3; 388••, 112), and potentially also root-feeding insect larvae (Fig. 3). This pulse may also promote generalist leaf-feeders that seek alternative food sources to compensate for thinning tree crowns [313]. However, while cascading effects of wildfires on the herbaceous layer benefit pollinators in general, they also can have negative effects on this guild, or for some vulnerable taxa, when fire frequency is high (e.g., 112, 57). Post-disturbance regrowth of aboveground vegetation additionally increases habitat heterogeneity and can lead to a greater abundance of herbivores in the mid-term [362].

Belowground, soil arthropods exhibit an overall negative short-term response to wildfires (Table S1). This is a consequence of collapses in microbial food resources [197], and detrimental soil conditions (Fig. 3; 139, 297, 197). Their response to wildfire and similar disturbances is often strongly determined by the depth of remaining litter [387, 155, 110]. The response may be different following windstorms as they may benefit both from the pulse in ground-lying resources (e.g., dead wood, litter, etc.) and from the mosaic of soil microhabitats related to windfalls and windbreaks (Fig. 3; 388••, 31). Some guilds of soil arthropods may also benefit from post-disturbance conditions at later stages of the ecosystem recovery process [139, 380, 82]. They may take advantage of the pulse of easily-decomposable organic matter and from the related pulse in microbial activity, but also from changes in micro-environmental conditions related to canopy opening [277]. This latter point is, however, debated and can depend on the taxonomic groups or functional guilds considered [82, 347].

Populations of predatory arthropods may be driven by disturbance-induced variations in prey availability, i.e. prey density and prey detectability. Surviving predators may benefit from surviving prey and an increase in deadwood- and litter-dwelling prey [379]. Conversely, the general decrease in detritivores (Fig. 3) may have cascading effects on higher trophic levels as suggested by reductions in surface predators, such as spiders, centipedes, and predatory ground beetles (e.g., 81, 31; but see 63, 188). Nonetheless, we compiled inconsistent bottom-up effects on higher trophic levels in saproxylic [79, 389] and soil food webs [90]. In addition, predatory arthropods may themselves be affected by higher predatory pressures from higher trophic levels (e.g., insectivorous birds: 217; or bats: 186, 296).This means that predaceous groups can both increase or decrease in disturbed forest stands compared with undisturbed forests (Table S1, Fig. 3), and the drivers of the direction of effects still requires further research.

3.1.5 Spatiotemporal Changes in Community Structure

Post-disturbance community patterns hinge on spatio-temporal dynamics of microhabitats and resources. The increase in within-patch heterogeneity in disturbed areas may play an important role in community organization by niche partitioning among species [31]. Post-disturbance conditions may result in an increased range of food sources and breeding substrates for some arthropod guilds, expanding their trophic and reproductive niche space and resulting in a potential functional divergence in the disturbed area [80•, 255]. At the same time, micro-environmental legacies could lead to niche filtering and a decrease in trait variations, by reducing abiotic niche space and selecting species with narrow microclimatic requirements, i.e., xerothermic, heliophilous, and diurnal species [255]. The spatial extent of disturbed areas can also affect the response of arthropod communities to a disturbance. As an example, flower-visiting saproxylic beetles were more abundant in mid-size and large windthrow gaps than in small ones [29].

At the landscape scale, local variations in disturbance regimes increase habitat heterogeneity [238] and should consequently promote local and regional biodiversity, according to the habitat heterogeneity hypothesis [358]. In this regard, landscapes with a high diversity of fire histories (i.e., a high pyrodiversity *sensu* 230) support a greater abundance and diversity of pollinators [378•, 286]. The total amount of habitat over a landscape can also modulate communities at a local scale, according to the habitat amount hypothesis [105]. For instance, in declining silver fir forests, the local abundance and richness of saproxylic beetles responded positively to local forest dieback only if the landscape level of forest dieback was high [80•].

Environmental effects of disturbance on forest arthropod communities can be ephemeral or long-lasting, immediate or delayed, or even cumulative over time. Saproxylic insect assemblages associated with older burned forests were found to consist of a mix of pyrophilous specialists and non-pyrophilous secondary users, i.e. opportunistic generalist saproxylic species which are not restricted to freshly burnt wood but which benefit from fire-induced pulses of deadwood after a delay [311]. In windthrown areas, reinvigorated community dynamics of ground-dwelling arthropods are also a matter of time since wind disturbances: i.e. positive effects are observed in response to short-term pulses of litter after windstorms, and then mid-term with a reduction in the quantities of litter generated from weakened trees [81].

3.2 Disturbance Legacy, Insect Outbreak and Arthropod Community Interactions

The pulse of weakened host trees following severe abiotic disturbances may promote outbreaks of opportunistic bark and wood-boring insects, bark beetles being a prime example. These outbreaks are major biotic disturbances causing forest diebacks sometimes over large spatial scale [26, 22, 306, 258, 312]. These opportunistic insects can also act as aggravating elements in complex multifactorial forest declines, further deteriorating stand conditions in previously disturbed forest areas [312]. Severe droughts and windstorms are major initial drivers of such outbreaks [329, 26, 22, 312, 284]. Wildfires, however, only occasionally contribute to large-scale pest outbreaks as a function of their severity. This is because high-intensity crown fires generally destroy the breeding substrate which hinders any pest outbreaks [112, 194, 289, 164, 61]. Nevertheless, low intensity ground fires are less destructive, and weakened trees can provide ample substrates for breeding outbreaks of opportunistic pests [39, 222, 354].

Compound disturbances can lead to a situation when a disturbance alters ecosystem response to a subsequent disturbance (see 3.1; 268). Large-scale outbreaks of opportunistic pests trigger or contribute to extended forest diebacks and declines [26, 22, 312, 284]. They consequently compound the effects of wildfires, windstorms and drought since pest outbreaks increase the severity and spatial extent of abiotic disturbances [221, 282]. Therefore, pest outbreaks can amplify some of the disturbance legacies left by previous disturbances such as the volume of deadwood, abundance of TreMs, and canopy openness [79, 366]. Cascading effects on arthropod communities are consequently similar to those of abiotic disturbances: flower-visiting insects [79, 203, 24, 360, 187] are stimulated in canopy gaps as a result of micro-environmental legacies and related pulses of plant resources [85]. Conversely, taxonomic groups linked to closed-canopy forests, such as Mycetophilidae, might suffer from canopy opening and the desiccation of decaying litter [203]. Increases in deadwood volume, in sunnier environments, fosters the diversity of saproxylic beetles [323, 205•, 130, 24], although the trend varies with the dynamics of dieback [79]. Several soil-dwelling groups (i.e., ground beetles, harvestmen, springtails) seem, however, to be unaffected in bark beetle infestation areas [24, 400] compared with undisturbed forests. The response of fungus-dwelling arthropods to bark beetle-induced diebacks depends on inconsistent variations in wood-dwelling fungi [79, 80•, 24] and in a very significant decline in the biomass of the forest soil fungi community, reflecting both the disappearance of fungi that form symbiosis with tree roots and the changing availability of needle litter [235, 350]. Overall, eruptive pests, like the spruce bark beetle in Europe, may be considered as keystone ecosystem engineers, providing habitat structures that promote the occurrence of other species, including endangered species [51, 258, 17, 146, 245]. Outbreaks of opportunistic pests are triggered by abiotic disturbances, but through their disturbance legacies, they can also, in turn, have additive or synergistic effects on these abiotic disturbances [329]. For instance, fuel accumulation and changes in microclimatic conditions (e.g., temperature, moisture, etc.) following outbreaks may promote subsequent wildfires, but depends on the time that has passed since a pest outbreak, and also the characteristics of available fuels and of the fire (e.g., 61, 145, 140; but see 240). Likewise, increased canopy openness may amplify the impact of subsequent droughts on forest stands [219, 182], and similar effects could be expected following large-scale outbreaks. Pest outbreaks may also compound the effects of wildfires since depending on disturbance severity and forest type, they may alter recovery processes following a subsequent wildfire [58, 181, 320].

4 Pre-Disturbance Forest Conditions: from Forest Characteristics to Long-Term Legacies

4.1 Pre-Disturbance Forest Type

4.1.1 Pre-Disturbance Vegetation

Initial stand characteristics modulate the composition of post-disturbance vegetation [374, 166]. For instance, the maintenance of trees and understory seedlings and saplings after a disturbance significantly contribute to the vegetation composition (Fig. 4; 92, 119, 394, 299). Depending on the degree of reorganization undergone by pre-disturbance vegetation and disturbance type, forest ecosystems could follow different pathways leading to resilience (no change in structure and composition), restructuring (structure changes but not composition), reassembly (composition changes but not structure), or replacement (both structure and composition change; 325). While forest resilience may also promote the resilience of forest arthropod communities, the three other pathways should reshape arthropod communities to varying extents. In this regard, Iida et al. [155] found that, following a volcanic eruption, pre-eruptive vegetation influenced post-disturbance communities of ground-dwelling arthropods. Nonetheless, this effect was strongly mediated by disturbance severity and/or type, and by the depth of remaining litter.

At the tree species and individual tree levels, several characteristics can affect tree resistance to droughts, windstorms or wildfires, and there is significant intra- and interspecific variation among trees in their susceptibility to these disturbances (e.g., 55 for windstorms; 70 for drought; 14 for wildfire). For instance,

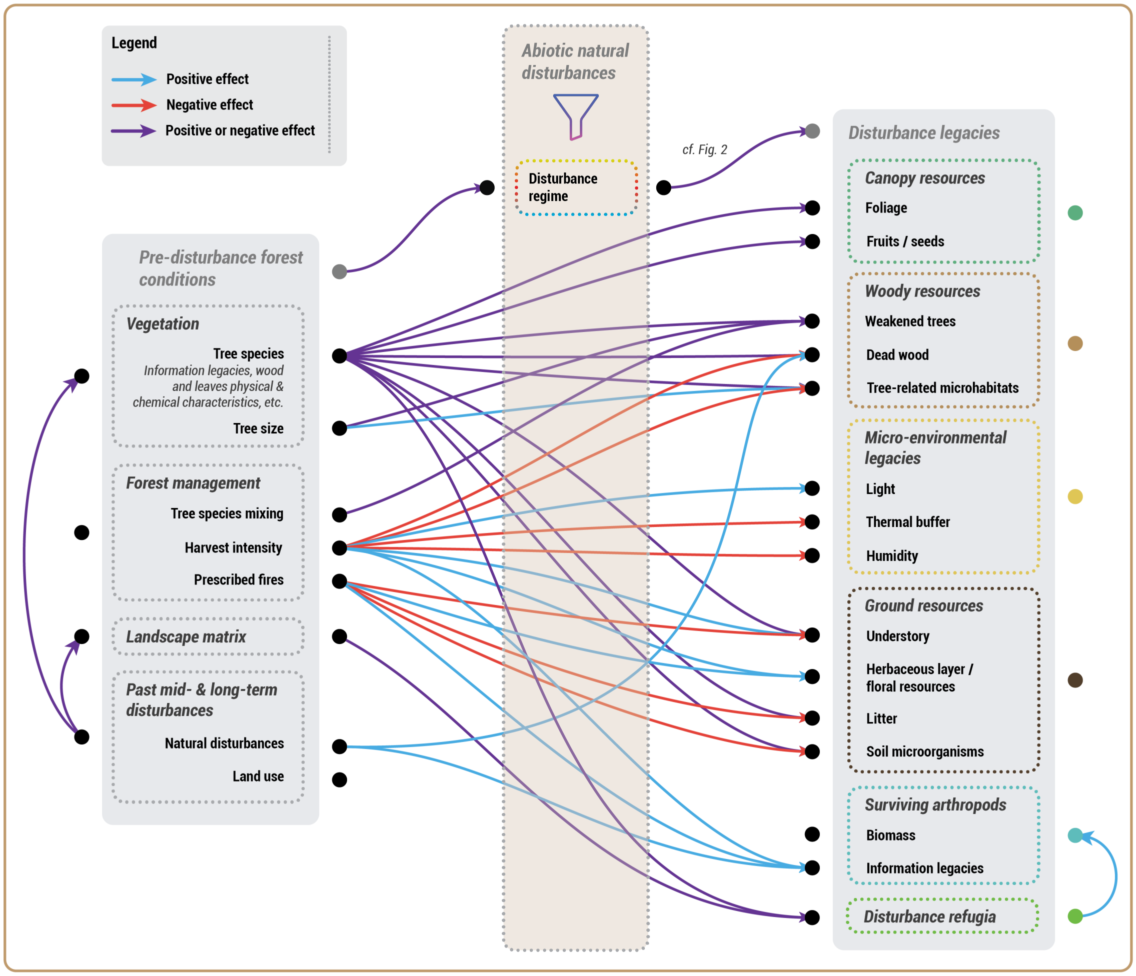

Figure 4: *Effects of pre-disturbance forest conditions on key disturbance legacies for forest arthropods. Pre-disturbance forest conditions modulate the impact of disturbances on the amount and diversity legacies, by altering disturbance regimes, modulating initial amounts and diversity of resources and initial micro-environmental conditions, and by imprinting information legacies on forest organisms*

large and more mature trees are generally more resistant to fire damage [374, 67], while they are frequently more susceptible to wind damage [161] (Fig. 4). Trees may also have traits that confer resilience to specific disturbances, especially if these disturbances are reoccurring [16]. For example, resistance and resilience to wildfires typically occurs via the emergence and relative success of trees with fire-resilient traits such as serotiny, thick bark, high resprouting capacities, and lignotubers, providing resistance and resilience to wildfires [178, 122, 74]. These information legacies (Fig. 4) can be paramount drivers of ecosystem resilience [36] as they modulate the nature and spatial pattern of disturbance refugia on scales ranging from the tree to the landscape [192, 326]. Resistant trees can serve as disturbance refugia for arthropod communities since they ensure the persistence of suitable micro-environmental conditions and trophic resources for arthropod communities during the disturbance, and in the post-disturbance environment. For instance, fire-resistant grass trees in Australia (*Xanthorrhoea* sp.) have tightly packed leaves around their apical stem, which provide micro-climatic refugia for several arthropod taxa [40].

Conversely, some characteristics of disturbance-adapted tree species may also increase the intensity, severity or spatial extent of disturbances. For instance, leaf moisture content, leaf area and leaf chemistry affect the flammability of trees and influence the spread of wildfires within stands [287] and at landscape scales (59; Fig. 4). Highly flammable tree species may also provide disturbance refugia for arthropods (e.g., 40), but forests dominated by such tree species should promote disturbance-prone arthropod communities, and communities associated with open habitats.

Tree characteristics also influence key resource pulses (Table 2). For instance, there is a significant interspecific variability in decomposition rates of deadwood [174, 137]. This affects the amount, diversity and persistence of deadwood resources, and modulates post-disturbance communities of saproxylic arthropods [324]. Tree species, and some morphological features like trunk diameter, also significantly influence the ontogenesis, and ultimately the assemblages of TreMs [201•, 267, 78]. Interestingly, early-successional tree species promoted by stand-replacing disturbances, develop different TreMs than mid- and late-successional tree species promoted by low- and mid-severity disturbances [78, 196]. Therefore, the complex interplay between tree characteristics and disturbance regime may lead to peculiar assemblages of TreMs [229], and significantly contribute to the organization of post-disturbance arthropod communities [190•, 189]. Likewise, species-specific physical and chemical characteristics of leaves differentially affect their flammability, e.g., long curly leaves containing high amounts of terpenes are highly flammable [266, 383]. Consequently, depending on dominant plant species, litter can be more or less severely affected by wildfires, which implies more or less extended impacts on soil arthropod communities [387].

Table 2: *Examples of interactive effects of tree species and drought on two key resources for arthropods, tree-related microhabitats (TreMs) and foliage. * TreMs profiles vary among species, and depending on tree status (e.g., 201•); ° Depending on drought regime*

Tree species	**TreMs abund. & diversity [390, 6, 7]***	**Susceptibility to drought [101]**		**Decomposition rate [174]**	**Post-disturbance accumulation pattern of TreMs**	**Post-disturbance foliage loss**
		Acute stress	**Repeated stress**			
Beech	Medium	High	High	High	Rapid & ephemeral	Rapid
Oak	High	Low	Low	Low	Slow & persistent	Slow
Pine	Low	Low	High	Low	Slow / rapid° & persistent	Slow
Spruce	Low	High	High	Medium	Rapid & moderately persistent	Rapid

4.1.2 Pre-Disturbance Forest Management

Pre-disturbance forest management can modulate both disturbance regimes and stand susceptibility to disturbances (e.g., for windstorm: [161]; for wildfire: [346, 363, 211]; for drought: [128, 99, 62, 227]; Fig. 4). For example, dense plantations of easily flammable species promote severe wildfires [212, 346, 363, 211]. Conversely, landscape fuel reduction treatments can decrease wildfire severity and promote post-fire seedling regeneration [84, 371]. Following a high intensity fire in south-eastern Australia, Bowd et al. [36] showed that old-growth forests recovered better than younger ones, because old-growth forests displayed a higher abundance of seed-tree species. Likewise, mixing tree species can affect stand susceptibility to windstorms [370], and, depending on tree mixing characteristics, increase stand resistance to drought and wildfire [159, 271]. Mixing tree species also provides associational resistance to herbivores, by increasing predation / parasitism pressures, and may prevent outbreaks of opportunistic pests in response to pulses of weakened host trees (159, 160; Fig. 4). The inflection of disturbance regimes by forest management could modulate the amount and diversity of disturbance legacies such as stand structure (e.g., complexity of vertical stratum), micro-environments and resources (e.g., soil, burned pieces of deadwood, etc.), with cascading effects on post-disturbance arthropod communities. Pre-disturbance management can also interact with disturbance regime and influence the amount of disturbance legacies. For instance, green tree retention during harvest increased the amount of deadwood following prescribed fires, and promoted red-listed saproxylic insects (e.g., in boreal forests [154]).

Forest management modulates the initial amount of microhabitats and trophic resources and consequently filters ecological traits in pre-disturbance arthropod communities, which may promote or hamper their resilience to disturbances (Fig. 4). At the tree level, pruning and pollarding promote the formation of tree cavities [322]. At the stand level, thinning can reduce the amount of dead and living trees carrying large arrays of TreMs [390, 78, 200, 77]. Thinning may also promote particular TreMs, such as bark injuries occurring during harvesting operations, or dendrotelms [390, 78]. As a result, thinning and logging may alter the initial supply of critical resources like deadwood and TreMs, and initial environmental conditions in the canopy and ground layers through increased canopy openness [68]. More generally, intensive forest management negatively affects the community of saproxylic arthropods [334, 132, 348], and could therefore limit their response to deadwood pulses following a disturbance. On the contrary, by regularly creating canopy gaps, forest management maintains populations of forest pollinators [135], allowing them to rapidly exploit the post-disturbance pulses in floral resources [142] (Fig. 4).

4.1.3 Pre-Disturbance Landscape Matrix

Landscape matrix influences disturbance regimes. For instance, patterns of wildfire spread and severity are an interactive function of topography, vegetation, management and land use [374, 212, 60, 303]. Likewise, large forest gaps increase the likelihood of windstorm damage at the landscape level [370, 136, 270]. Forest edge exposure also results in a disruption of the microclimatic buffer and therefore exacerbates the effects of drought on vegetation and arthropod communities [87, 275, 182, 352]. Consequently, the landscape matrix can be seen as a mosaic of habitats more or less prone to disturbances. This will markedly influence the spatial distribution of disturbance refugia, and the recolonization processes by arthropod communities (Fig. 4).

4.2 Material and Information Legacies from Past Disturbances

Past disturbances can directly influence current arthropod communities in forests through changes in forest structure. Kozák et al. [190•] showed that current saproxylic beetle assemblages are influenced by the historical disturbances that occurred over the last 250 years. Overall, the recency and the severity of the last disturbance increased the current species richness, although maximum disturbance severity had negative effects [190•]. The changes in current insect assemblage were mainly mediated through past changes in deadwood resources and canopy openness [12].

Pre-disturbance conditions are also influenced by changes in land-use that occurred a long time ago (Fig. 4).

For example, Mollier et al. [252] showed that the forest area of 150 years ago is a better predictor of current beetle communities than the current forest area. This is probably mediated by ancient forest legacies related to forest maturity and continuity [162]. Past land-use also significantly determined current forest vegetation, due to the trees historically favored by man [76], colonization credit [252, 144], and nutrient availability (e.g., generally higher in former agricultural lands; 117), which largely affect the dynamics of the post-disturbance vegetation [292].

5 Post-Disturbance Forest Management Influences on Disturbance Legacies and Arthropod Communities

Post-disturbance forest management encompasses an array of strategies, ranging from intensive to passive approaches [96]. Following drought, wildfire, or windstorm disturbances, salvage or sanitation logging are typical management strategies in production forests [216] and can also be implemented in forests with high conservation value [71, 247, 265]. Salvage logging is the practice of extracting trees in disturbed forests and it is frequently conducted to minimize the economic loss of timber [215]. Sanitation logging aims to harvest dead and weakened trees to prevent the build-up of opportunistic pest populations and subsequent outbreaks, but also to reduce the risks of further wildfires [344, 118]. The effectiveness of salvage and sanitation logging in mitigating subsequent disturbances remains unclear [209]. These management strategies can be considered to compound disturbances, as forests are more likely to be harvested after a natural disturbance than if there was no disturbance [207].

Most disturbance legacies are affected by logging (215; Fig. 5). The extent of any negative consequences for forest arthropod communities depends on disturbance severity, as well as on the intensity and extent of logging and the time lag following a disturbance [79, 208, 242]. Logging removes dead and weakened trees, and woody debris. This affects the amount and diversity of material legacies that are essential for saproxylic arthropods. While the amount of deadwood in a stand logged after a disturbance may remain high [79, 126•, 242, 125], the diversity of deadwood resources is generally reduced compared to unlogged stands (392; Fig. 5). For instance, rare types of disturbance-induced deadwood resources, like charred snags and large logs are a key target for salvage logging [28, 153]. Post-disturbance logging also affects the diversity of TreMs as microhabitat-bearing weakened trees and snags are targeted for salvage harvesting despite the many microhabitats they likely provide (79, 392; Fig. 5). Logging can affect species succession by disrupting colonization and recolonization patterns, and by affecting the community of surviving arthropods. For instance, the removal of deadwood disturbance legacies can effectively be ecological traps [32], negatively affecting saproxylic arthropods that have taken shelter from a disturbance within deadwood, but also those arthropods that subsequently colonize the deadwood [126•, 146, 367, 73]. Conversely, increased canopy openness promotes the colonization of logged areas by arthropod species that are associated with open habitats, preferring warmer and sunnier environments, and by species associated with floral resources [338, 142, 125, 33].

Post-disturbance logging also affects micro-environmental legacies. Removal of dead and weakened trees further increases canopy openness (115, 279, 179; Fig. 5). The impact of logging on soil conditions is highly context-dependent, and it is influenced by logging intensity and the construction and distribution of roads

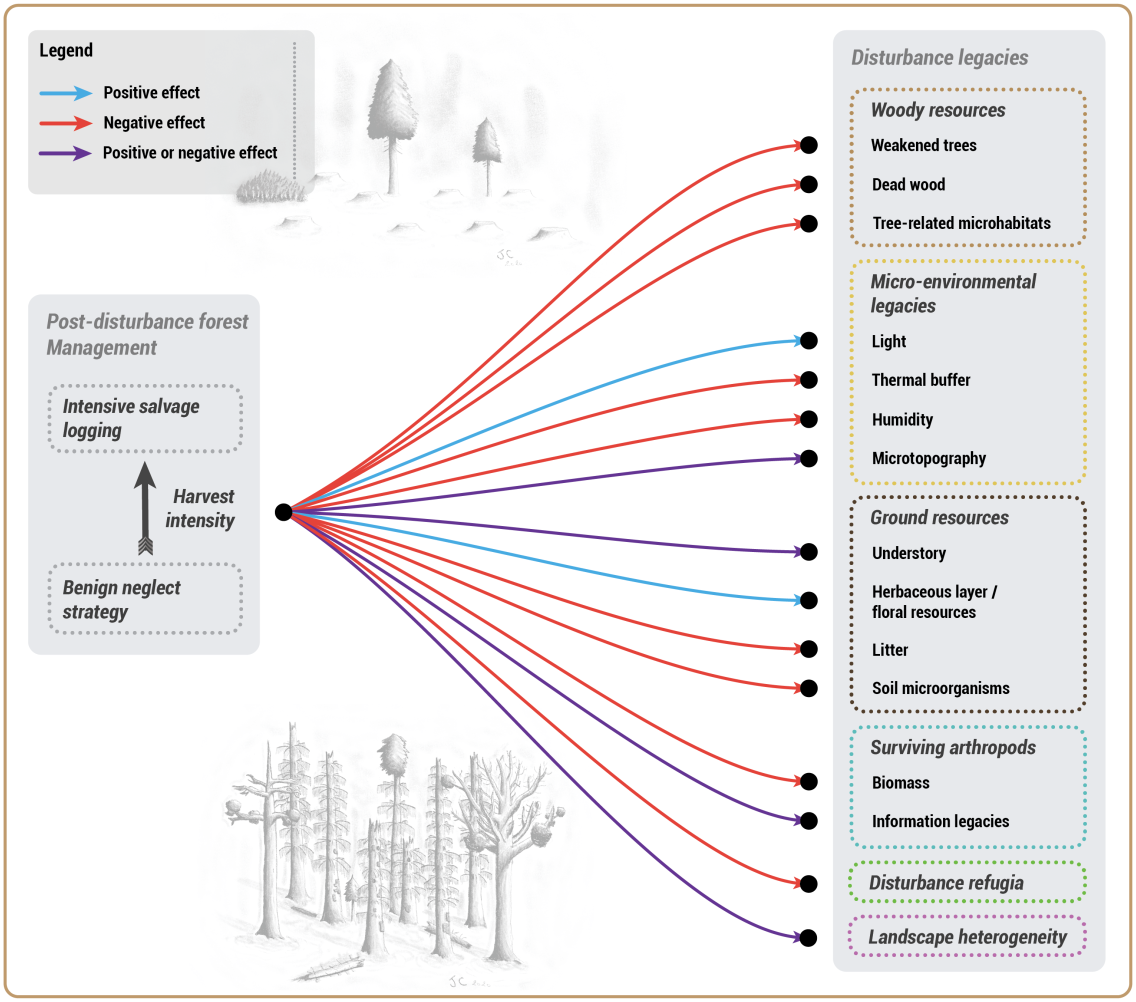

Figure 5: *Effects of post-disturbance forest management on key disturbance legacies for forest arthropods. Increasing harvest intensity from benign neglect strategy to intensive logging largely affects a wide array of disturbance legacies*

(279, 225, 231; Fig. 5). Increased canopy openness and the removal of downed deadwood generally results in increased soil temperature, and decreased soil moisture [237], thereby affecting soil microbial communities (235; Fig. 5). Removal of downed deadwood also reduces the amount of available nutrients compared to stands that retain their legacies [228, 121, 276, 172]. In addition, the use of forestry machinery generally increases soil compaction [225, 121, 295, 391]. Together with the removal of woody debris, it modulates the pattern of soil microsites and microtopography, with a decrease in pits and mounds but an overall increase in microsite richness (392, 279, 393, 355; Fig. 5). These effects on soil properties can persist for a long time (e.g., 10 years in boreal forests; 180). These changes in micro-environmental conditions can negatively affect soil arthropods [251].

At the landscape scale, logging increases habitat diversity if it creates a mosaic of undisturbed, disturbed and logging-disturbed patches [397, 281]. The alteration of local deadwood composition can increase β-diversity of saproxylic organisms across salvaged areas, compared to unsalvaged and undisturbed forests (e.g., 126•, 397). This may in turn promote the γ-diversity of arthropod communities [397, 281]. The configuration and size of such mosaics certainly are important to define the extent to which these mosaics can help certain insect communities maintain their populations, but we lack knowledge about this issue. Nonetheless, logging may also increase habitat fragmentation, putting disturbance refugia further away from each other [247, 246], which may also affect the dispersal and colonization processes of disturbed areas by arthropod species [311]. It is often conducted extensively, in a way that the landscape ends up dominated by a burnt and clearcut matrix with some patches of deadwood only in inaccessible areas [207].

Following post-disturbance harvest, different reforestation strategies can be implemented, from natural regeneration to full planting of new tree species. While post-disturbance logging does not produce a generalized effect on the density or height of subsequent tree regeneration, there can be a variety of local responses [210] and effects on composition are generalized [355]. Logging often promotes early-successional resprouting species, but disfavors late-successional seeder species [355, 169, 269, 206, 113, 244]. However, these immediate effects generally fade in the longer term (e.g., [210, 308, 318]; but see 256). Reforestation leading to the plantation of novel, and potentially exotic, tree species may increase habitat diversity at the landscape scale, but result in a dramatic shift of tree-related resources and habitats for arthropods at a local scale [294]. Shifting tree species during post-disturbance reforestation may result in a major resource collapse for the community of plant-feeding arthropods [37, 384, 204], but also for saproxylophagous species [324, 260, 175], at least at initial stages of the saproxylation process [324, 170]. This would be particularly true if native tree species are replaced by exotic and phylogenetically- and functionally-distant tree species [175, 34, 249]. At the landscape scale, this may however increase β- and γ-diversity of arthropod communities [42, 4, 148]. Nonetheless, natural regeneration following disturbance is heterogenous and naturally produce landscape diversity [373, 321].

In contrast, the absence of active management, within the frame of a "benign neglect" or passive strategy, allows the retention of disturbance legacies [259]. The latter strategy is mainly implemented in conservation forests [259, 96, 150, 151]. Forest managers can retain some disturbance legacy features that may be of interest [146, 96, 163] to achieve a compromise between fully preserving disturbance legacies and virtually eliminating them through clearfell. They also may implement variable management strategies in different part of the landscape to prioritize different functions ans services. Compared to logged stands, saproxylic arthropods greatly benefit from the retention of deadwood following disturbances [79, 24, 125]. Even though logged areas are generally favorable to open-habitat arthropod species, Galbraith et al. [120] observed greater α- and β-diversity of wild bees in unlogged than in logged areas. Furthermore, passive post-disturbance strategy also maintains greater network connections between pollinators and plant species than salvage logging [49]. Only a few studies considered the effects of intermediate forest management strategies after a natural disturbance, such as retention harvesting or close-to-nature forestry [96, 207]. Scattered trees or groves retained during clear-cuts generally support intermediate communities composed of both species from intact forest and clear-cut areas but do not support specialists (e.g., interior forest species; 107, 214). Even when retention levels are high, the community of saproxylic arthropods exhibits substantial changes compared to those of intact forests [187, 202]. According to Müller and Bütler [257], minimum threshold values of 30 to 50m^3.ha-1 are needed to ensure a relatively high richness of saproxylic organisms. In addition, Thorn et al. [369] found that 75% of disturbed forest areas must be retained to maintain 90% of the species richness present in those disturbed areas.

6 Conclusion

One of the main similarities between droughts, windstorms, and wildfires is their direct and indirect impacts on canopy openness. Increased canopy openness, and its cascading effects on forest microclimates at different strata, and on understory and herbaceous layers, sets in motion the transition of forest arthropod communities towards communities adapted to sunnier/warmer and drier conditions, with a reduced thermal buffer, and to the exploitation of resources related to the herbaceous layer, like floral resources. The impacts of disturbances on canopy resources and microhabitats has received little attention to date [314•], but seems to generally have null to negative effects on canopy-dwelling arthropods depending on their ecological guild. The three disturbances considered in our review increase the amount and diversity of weakened trees and deadwood resources, and consequently have positive cascading effects on saproxylic species, including opportunistic pests. However, compared to drought and windstorms, wildfires tend to alter the quality of deadwood resources, which are consequently preferentially exploited by a specialized pyrophilous fauna. Likewise, the impacts of these disturbances on soil conditions are quite variable. While droughts and wildfires have an overall negative impact on soil organisms and their micro-environmental conditions, disturbance legacies of windstorms are generally beneficial for soil arthropods. Through their material legacies, abiotic disturbances may have positive outcomes on forest arthropod communities, at least for certain guilds like saproxylic and flower-visiting arthropods, although responses of arthropod taxa may be frequently idiosyncratic. Considering that with our current knowledge it is still difficult to predict the likely composition of post-disturbance arthropod communities, we call for more comprehensive investigations on disturbance impacts on arthropod diversity. These investigations should include several taxa and guilds and consider the taxonomical, functional and phylogenetic responses to changes in microhabitat amount and diversity, at various spatial scales.

Pre-disturbance forest conditions influence the amount and diversity of several disturbance legacies such as the amount of surviving arthropods and the amount, diversity and temporal dynamics of several of their key resources, like deadwood and TreMs. Fostering silvicultural practices which promote TreMs in stands at risk might prove useful to promote the resilience of forest arthropod communities. Since they can modulate local disturbance regimes and consequently the post-disturbance habitat heterogeneity at landscape scales, they are also of paramount importance for recolonization processes of disturbed areas. They either allow the resilience of pre-disturbance arthropod communities, or lead to a recolonization by communities dominated by large, highly mobile, fecund and long-lived arthropod species. Post-disturbance management, especially logging, considerably alters the amount and diversity of both deadwood resources and TreMs, and soil conditions. Consequently it restricts beneficial disturbance effects on saproxylic taxa and further affects soil arthropods. Conversely, it also exacerbates some disturbance impacts like canopy opening and habitat heterogeneity at the landscape scale and may therefore have beneficial impacts on certain arthropod guilds such as pollinators. For biological conservation purposes, an optimal management of disturbed forest areas should therefore aim at conserving benefits provided by (i) the accumulation and diversification of deadwood resources and TreMs for saproxylic taxa, (ii) by canopy opening for pollinators and some saproxylic and soil-dwelling taxa, and

(iii) habitat diversification at the landscape scale. To achieve this, sanitation logging could be limited to a restricted proportion of disturbed forest areas at the landscape-scale, to prevent bark beetle outbreaks [11], especially when harvesting costs are lower than the selling price [98, 185]. Conversely, since maximizing the retention of disturbance legacies limits the detrimental effects of logging on biodiversity and subsequent successional process, it should become an increasingly common response to disturbances, especially when timber prices are low [148].

A majority of the studies investigating the impact of forest disturbances on material and information legacies, and/or more specifically on arthropod communities, have focused on wildfires, and on windstorms, to a much lower extent (e.g., Fig. 3; Table S1). Comparatively, fewer studies have evaluated the impacts of drought on legacies and on forest arthropod communities, although there is a growing body of literature highlighting the increasing involvement of this disturbance in forest diebacks and declines worldwide [330, 236, 2, 41]. Heatwaves also frequently co-occur with droughts, and are also expected to become more frequent, intense and longer lasting in the second half of the twenty-first century [236, 239]. However, both disturbances can have idiosyncratic impacts on forest ecosystems and their associated communities [150], which may be difficult to disentangle under field conditions. We therefore call for more studies on the impacts of drought and heat waves on forest resources and microhabitats, and their cascading effects on arthropod communities. In our review, we focused on the three main disturbances for temperate forest ecosystems. Nonetheless, additional disturbances with more localized impacts could also be considered, like flooding events which are expected to increase and affect floodplain forests and their arthropod communities in Central and Northern Europe in the future [156, 191, 198].

Several shifts in disturbance regimes occurred in forest ecosystems during the last centuries with sometimes major ecological impacts [372, 357, 343, 100, 43]. For instance, a recent shift in the disturbance regime in Alaska towards more severe wildfires led to a modification of the plant community from coniferous to deciduous species [166, 168]. However, the speed of current changes in disturbance regimes appears to be unprecedented and largely questions the future of world's forests and their associated communities [167, 372, 376, 272]. We therefore need a better mechanistic understanding of disturbances and compounded disturbances impacts on arthropod communities to better forecast how changes in disturbance regimes will affect disturbance legacies and the arthropod communities their shelter.

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