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Climate Change Alters Temperate Forest Canopies and Indirectly Reshapes Arthropod Communities

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Global change challenges the adaptive potential of forests. Large-scale alterations of forest canopies have been reported across Europe, and further modifications are expected in response to the predicted changes in drought and windstorm regimes. Since forest canopies are dynamic interfaces between atmosphere and land surface, communities of canopy-dwelling insects are at the forefront of major changes in response to both direct and indirect effects of climate change. First, we briefly introduce the factors shaping arthropod communities in the canopy of temperate forests. Second, we cover the significant impacts of a forest decline on canopy structure and functioning, and more specifically its contrasted effects on insect microhabitats, trophic resources and forest microclimates. Deleterious effects may be expected for several guilds of leaf-dwelling insects. Nonetheless, a forest decline could also lead to transient or long-lasting resource pulses for other canopy-dwelling guilds, especially saproxylic species depending on deadwood substrates and tree-related microhabitats. The novel microclimates may also become more favorable for some particular groups of insects. We pinpoint current knowledge gaps and the technological locks that should be undone to improve our understanding of the canopy biotope and biodiversity in temperate forests. We highlight the need for integrative approaches to reveal the mechanisms at play. We call for cross-scale studies and long-term collaborative research efforts, involving different disciplines such as community and disturbance ecology, plant and insect ecophysiology, and thermal ecology, to better anticipate ongoing functional and conservation issues in temperate forest ecosystems.

Keywords: biodiversity, forest decline, drought, insect, biological conservation

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INTRODUCTION

Forest ecosystems worldwide are currently facing increasing levels of environmental stress, posing severe challenges to their adaptive capacity (Allen et al., 2010; Seidl et al., 2017). Biological invasions (Liebhold et al., 2017), land-use intensification (Seibold et al., 2019), and climate change (Seidl et al., 2017) lead to extended forest diebacks and declines worldwide (Allen et al., 2010). Drought and windstorms have been identified as major drivers of recent forest diebacks and declines in temperate Europe, either through their direct impacts on tree health and survival or by promoting large-scale outbreaks of opportunistic species (Carnicer et al., 2011; Sallé et al., 2014; Seidl et al., 2014, 2017; Biedermann et al., 2019; Senf et al., 2020). The frequency, intensity and spatial extent of both drought and windstorm have been increasing in Europe during the last decades, with a recent acceleration (Gregow et al., 2017; Senf et al., 2020). Damage from these disturbances are predicted to increase even further in temperate areas (Seidl et al., 2014; Samaniego et al., 2018; Spinoni et al., 2018). Consequently, temperate forest ecosystems are expected to undergo major changes in terms of structure and functioning in the near future (Senf et al., 2020).

Depending on disturbance regime, resistance, and resilience level of tree species and/or forest ecosystems, and interactions with other disturbances, the structure and functioning of trees, stands, and forests can be affected to varying degrees of severity (Brodribb et al., 2020). One of the fastest and most conspicuous modifications during forest declines and diebacks is the degradation of tree crown condition (**Figure 1**; Ishii et al., 2004). Droughts and windstorms can directly affect canopy structure by inducing leaf and twig shedding, and provoking branch and stem breakage (Bréda et al., 2006; Mitchell, 2013). They can also have long-lasting effects when they act as inciting factors of forest declines (Manion, 1981). Several long-term forest monitoring studies already highlight large-scale increase in defoliation in the Mediterranean area during the last decades (Carnicer et al., 2011; Senf et al., 2020), and unprecedented modifications of forest canopies will likely occur in the short-term in temperate Europe.

The canopy layer of temperate forests is a treasure trove of diverse plant resources, accumulating large amounts of foliage, wood, floral parts, fruits, cones, and seeds (**Figure 2**). At the interface with atmosphere, it is also the siege of peculiar microclimatic conditions (Leuzinger and Körner, 2007). In addition, the canopy conceals diverse but understudied arthropod communities (Floren and Schmidl, 2008; Ulyshen, 2011). Consequently, decline-driven extended change in canopy structure should dramatically alter the communities of canopy-dwelling arthropods and significantly affect forest biodiversity.

In this essay, we focus on the relationship between the climate-change-induced physical alterations of the canopy and arthropod communities. We briefly review (i) the factors affecting the composition and distribution of canopy-dwelling arthropods, and (ii) the consequences of forest decline on canopy-related microclimates and resources and how it affects arthropod biodiversity. We bring to the attention that a thorough understanding of the physical structure of altered canopies is needed to infer how climate change will reshape arthropod communities. Our aim is to highlight the gaps in our knowledge on the functional response of temperate forest ecosystems to global environmental change, and to stimulate cross-scale studies involving various disciplines to ameliorate predictions that should feed management plans.

FACTORS SHAPING ARTHROPOD COMMUNITIES IN THE CANOPY OF TEMPERATE FORESTS

The large amount of plant biomass in the canopy layer can support abundant arthropod populations and promote species richness according to the more-individuals hypothesis (i.e., higher energy availability promotes higher number of individuals, and higher species richness; Müller et al., 2018), or the resource-availability hypothesis (i.e., arthropod distribution reflects the availability of their resources; Wardhaugh, 2014). This large and diverse biomass may also enhance habitat heterogeneity, provide multiple trophic niches and allow the segregation of arthropod species according to the habitat heterogeneity hypothesis (i.e., species richness increases with increasing habitat heterogeneity due to greater niche dimensionality; Tanabe, 2002 but see Müller et al., 2018). The complex three-dimensional structure of tree crowns also provides ecological space of reduced predation for arthropods, known as an escape or enemy-free space (Lawton, 1983; Wardhaugh, 2014). In addition, the canopy provides a unique set of microhabitats and resources, with specific tree-related microhabitats such as mistletoe, suspended soils, epiphytes, perched dead branches, upper trunk cavities, and fruiting bodies of opportunistic fungi (Ulyshen, 2011; Larrieu et al., 2018), allowing the differentiation of dedicated habitat and/or trophic guilds of arthropods. Ultimately, this results in the establishment of complex food webs (Nakamura et al., 2017).

The temperate canopy layer is characterized by particular microclimates. For instance, the leaf surface of trees can be much warmer than local air temperature at the top of the canopy because they intercept a large amount of incoming radiation (Woods et al., 2018; Miller et al., 2021). Leaf temperature depends on the ecophysiological traits of the plant (Pincebourde and Woods, 2012), and is consequently species specific (Leuzinger and Körner, 2007). Canopy microclimates diverge largely from those of the understory. The shape and range of the vertical air temperature profile of temperate canopies depend on several variables including season, time of the day, canopy architecture, and tree species (De Frenne et al., 2021). This gradient contributes to the vertical distribution of arthropod species in the canopy, according to the physiological-efficiency hypothesis (i.e., arthropod distribution reflects their physiological tolerance to abiotic and biotic conditions, Wardhaugh, 2014). Consequently, resource availability, microhabitat richness, and abiotic conditions can be considered as critical factors affecting the abundance of arboreal arthropods (Mottl et al., 2020).

Forest stands also produce a microclimate in the understory that buffers against the atmospheric extremes for temperature and dryness (**Figure 2**). This buffer effect is present in all forests across latitudes and is relatively independent from tree species (De Frenne et al., 2019), suggesting that this biophysical effect relies almost entirely upon the canopy surface that absorbs or reflects incoming solar radiation. Thus, the amplitude of the buffering effect in the understory is lower when the forest canopy foliage is less dense (Zellweger et al., 2020).

Several studies underlined the vertical stratification of arthropod communities in temperate forests in response to the vertical gradient of resources, microhabitats, and microclimates (e.g., Tanabe, 2002; Bouget et al., 2011; Vodka and Cizek, 2013; Normann et al., 2016; Plewa et al., 2017; Seibold et al., 2018b; Weiss et al., 2019; Urban-Mead et al., 2021). This stratification applies to a diverse range of arthropod taxa and trophic or functional guilds (e.g., saproxylic species, leaf chewers, pollinators, and parasitoids), which results in particular species

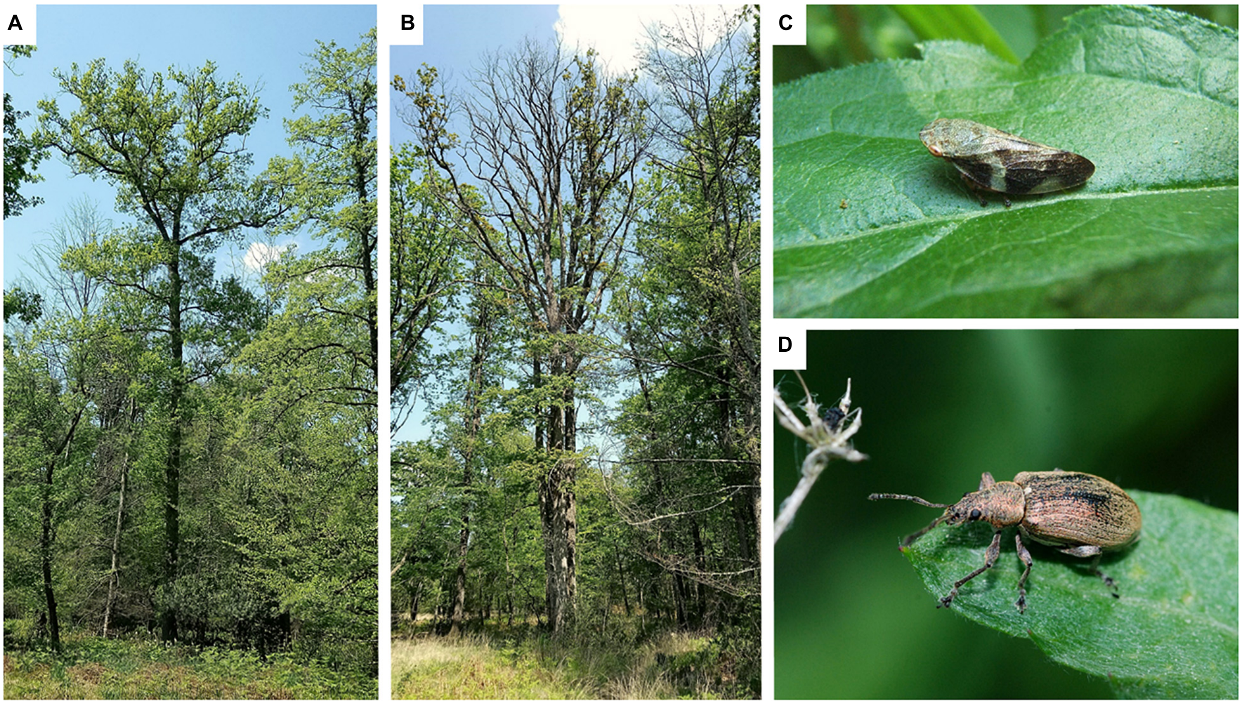

FIGURE 1 | Oaks (*Quercus petraea*) exhibiting moderate **(A)** and pronounced **(B)** symptoms of decline with a reduced foliage density and an accumulation of dead branches. Oak decline will have contrasted effects on canopy-dwelling insects: negative for the sap-feeding *Aphrophora alni* **(C)**, but positive for generalist leaf-feeder *Phyllobius pyri* **(D)**. Photo credits: Aurélien Sallé **(A,B)** and Sébastien Damoiseau **(C,D)**.

assemblages and community structure in the canopy layer (Maguire et al., 2014; Weiss et al., 2016; Šigut et al., 2018; Urban-Mead et al., 2021). Stratification patterns can markedly differ between temperate and tropical forests, but they share similar community structures (Weiss et al., 2019). Temperate forests probably shelter less insect taxa specific to the canopy than their tropical counterparts (Floren and Schmidl, 2008; Ulyshen, 2011), but up to 20–40% of saproxylic beetle species can be considered as exclusive to the canopy (Bouget et al., 2011).

In addition to canopy specialists, other species occasionally or temporarily use canopy microhabitats, as a hunting ground or to find mates for instance, and vertical migrations take place from a stratum to another, depending on the season, the stage of the life cycle, or even the time of the day (Ulyshen, 2011). As an example, several recent studies reported that even common species of scorpionflies (Mecoptera) and earwigs (Dermaptera) were quite abundant in the canopy layer while they were previously rather associated with lower forest strata (Vincent et al., 2020; Martínez-Pérez et al., 2021). Similarly, canopy top can be used by aquatic insects during the imago stage, suggesting cross-ecosystem connectivity involving the canopy layer (Le Naour et al., 2019). This underlines the fact that we still do not accurately evaluate the reliance of the overall forest arthropod community on canopy-related resources and processes.

We still have a limited knowledge of the taxonomic and functional diversity of arthropod communities dwelling in the canopy of temperate forests. Many studies have focused on saproxylic beetle communities, as key components of forest ecosystems (e.g., Bouget et al., 2011; Vodka and Cizek, 2013; Plewa et al., 2017; Seibold et al., 2018b). Other taxonomic groups and/or functional guilds have received comparatively little attention (but see Tanabe, 2002; Leksono et al., 2005; Larrivée and Buddle, 2009; Sobek et al., 2009; Maguire et al., 2014; Sallé et al., 2020; Vincent et al., 2020; Urban-Mead et al., 2021). The canopy of temperate forests may then shelter an underestimated pool of patrimonial species (Plewa et al., 2017; Tillier et al., 2020), and can be considered as a biotic frontier deserving special attention (Bouget et al., 2011).

DECLINE-DRIVEN MODIFICATIONS IN CANOPY HABITATS AND CASCADING EFFECTS ON ARTHROPOD COMMUNITIES

Forest declines and diebacks affect key microhabitats or trophic resources for arthropod communities, through reduced foliage density and flower or seed production (**Figures 1**, **2**; Ishii et al., 2004). For routine surveys of forest health, trees are considered in decline when more than half of their ramification is missing and/or more than half of their main branches are dead in the functional part of their canopy (**Figure 1**; Goudet and Nageleisen, 2019). The dynamic process of crown degradation implies the dieback of branches and twigs, progressing not only vertically from upper to lower levels but also horizontally from outer to

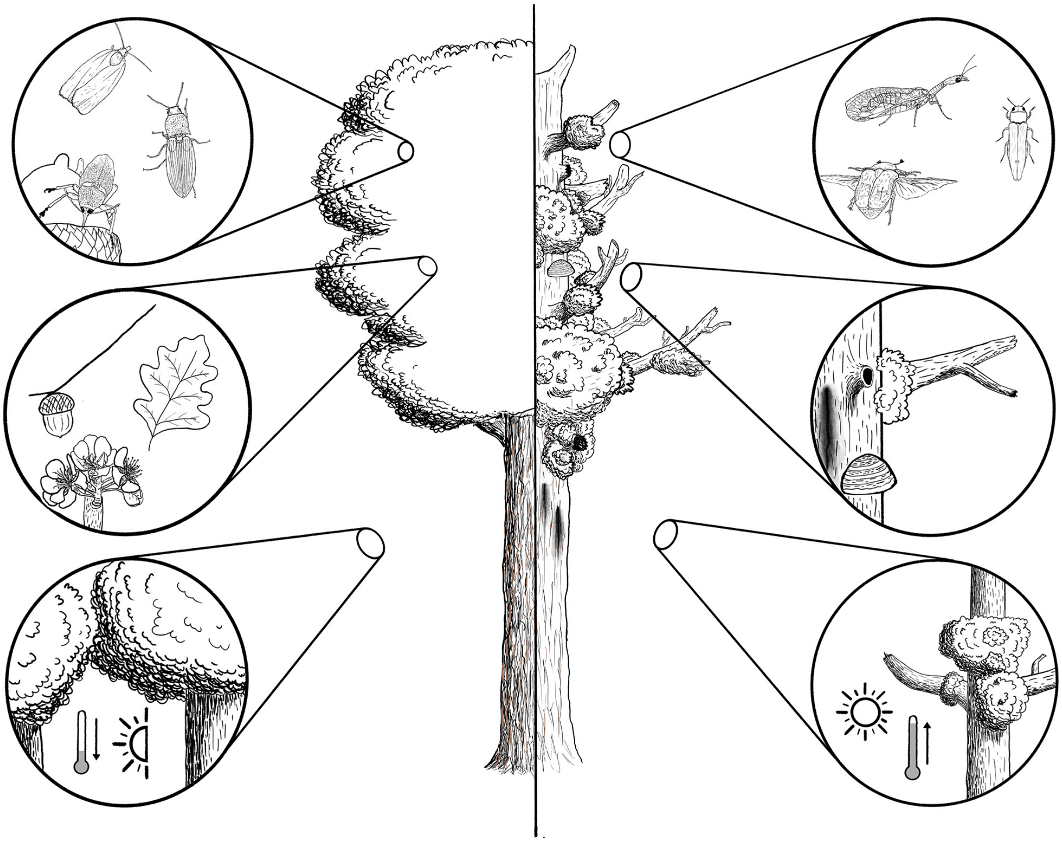

FIGURE 2 | Overview of decline-induced changes in arthropod communities (upper insets), resources and habitats (medium insets), and microclimates (lower insets) in forest canopies. Declining tree crowns (left part) should affect leaf-dwelling species but promote saproxylic species by reducing foliage, flower, and seed amounts but accumulating tree-related microhabitats like perched dead branches, fermented sap exudates, cavities, and fruiting bodies of pathogenic fungi. Reduced canopy cover will also reduce the thermal buffer on lower forest strata but increase the luminosity. Credits: Jérémy Cours.

inner parts of the tree crown (Drénou et al., 2015; **Figures 1**, **2**). This should affect the structure and composition of arthropod communities since experimental manipulations of branch density and structure can affect the abundance and trophic webs of arboreal arthropods (Halaj et al., 2000). Foliage quality, including biochemical and morphological leaf traits, can be also affected by the loss of tree vigor (Günthardt-Goerg et al., 2013; Hu et al., 2013). Likewise, the greater exposure of leaves in opened canopies can alter their phytochemical profile, and promote the accumulation of defensive metabolites (Yamasaki and Kikuzawa, 2003; Lämke and Unsicker, 2018).

Declines and diebacks can generate novel structures and favor the build-up of features uncommon on healthy trees. They promote tree-related microhabitats associated with reduced tree vigor or decaying trees (e.g., cavities initiated by break-offs of scaffold dead branches, perched dead branches and ascending dead branches emerging from the canopy, stress-induced broom-like mass of twigs, fruiting bodies of opportunistic fungi…) (**Figures 1**, **2**; Ojeda et al., 2007; Larrieu et al., 2018; Cours et al., 2021). Consequently, because forest declines and diebacks promote the accumulation of such biological legacies (Cours et al., 2021), they contribute to increase the structural complexity at multiple scales. The magnitude and sustainability of such changes will depend on disturbance regime on the one hand, and on stand characteristics on the other hand (e.g., Brodribb et al., 2020). In particular, tree characteristics such as resistance and tolerance to disturbance, propensity to accumulate microhabitats and decay rate of woody tissues should strongly influence the resources and habitat availability during the decline process. Foliage loss and accumulation of dead branches are frequently quantified during declines and diebacks as crown condition is generally used as proxy for tree health status (e.g., Goudet and Nageleisen, 2019). However, accurate description and quantification of tree-related microhabitats and foliage quality evolution during the entire process of tree decline is still missing.

The reduction of canopy cover negatively impacts the thermal buffering effect of the understory (**Figure 2**; Zellweger et al., 2020). Therefore, declines and diebacks would attenuate and even annihilate this buffer effect in the understory but we currently lack surveys to establish this link directly (Thom et al., 2020). In addition, the degradation of tree crown condition is expected to disturb considerably the vertical temperature profile from the ground to the upper canopy layer. The air temperature layers across the vertical gradient of forest canopies reflect the microclimate experienced by relatively large species. Nonetheless, the vast majority of arthropod species has a body size small enough to be influenced primarily by the microclimatic conditions at the plant surface where they live (Pincebourde and Woods, 2020; Pincebourde et al., 2021), and the influence of tree health status on leaf and bark microclimates is unknown.

The profound structural modifications affect habitat opportunities and trophic resources from micro- to macro-scales, with potentially marked cascading effects on communities of canopy-dwelling arthropods. Few studies have directly investigated how dieback or decline-induced change in canopy resources and microclimates can affect the diversity or functional structure of canopy-dwelling arthropod communities. Changes in foliage abundance and quality can markedly influence leaf-dwelling species, with contrasted effects according to their feeding guild. For instance, the abundance of sap-feeding Hemiptera and leaf-mining caterpillars or weevils can be negatively affected by degraded crown conditions (**Figure 1**; Martel and Mauffette, 1997; Stone et al., 2010; Sallé et al., 2020). However, studies conducted in different declining forests also showed that leaf-chewing beetles, like phyllophagous weevils, could be either promoted (in oak stands; Sallé et al., 2020) or unaffected by degraded crown conditions (in pinyon pine stands; Stone et al., 2010). Likewise leaf-chewing caterpillars were slightly promoted by maple decline (Martel and Mauffette, 1997). The accumulation of biological legacies, like perched deadwood or cavities, generally promotes saproxylic organisms following major disturbances (Beudert et al., 2015; Cours et al., 2021; Kozák et al., 2021). This stands true for canopy-dwelling arthropods as the abundance and species richness of saproxylic species is generally enhanced in the canopy of declining stands (**Figure 1**; Stone et al., 2010; Sallé et al., 2020; Vincent et al., 2020). These changes in sap-feeding, phyllophagous, saprophagous, and xylophagous species have in turn cascading effects on higher trophic levels and affect the community structure within the canopy (Trotter et al., 2008; Stone et al., 2010; Vincent et al., 2020).

The alteration of canopies can also alter their associated arthropod community through cascading effects on lower vegetation strata. The degree of canopy openness markedly influences the epiphyte communities of temperate forests (Nascimbene et al., 2013), and reduced epiphyte abundance have cascading effects on arboreal arthropod communities (e.g., Miller et al., 2007). Likewise, increased canopy openness markedly changes the understory and herbaceous layers (e.g., Dietz et al., 2020). This promotes floral resources and in turn affects some guilds of canopy-dwelling species, relying on below-canopy resources, such as pollinators (Davis et al., 2020; Mathis et al., 2021; but see Urban-Mead et al., 2021).

Declines and diebacks can consequently promote some particular microhabitat-, trophic-, or functional guilds of canopy-dwelling insects. In this regard, arthropod guilds can be arranged as "winners or losers," or "victims or perpetrators" of forest declines and diebacks (Sallé and Bouget, 2020; Sire et al., 2021). Depending on disturbance severity and stand characteristics, these biodiversity pulses could be either transient or long-lasting. Nevertheless, whether and how time scale of the decline process has consequences on decline-driven dynamics of canopy-dwelling communities is still poorly known – and we propose that the difficulty to monitor upper levels of canopy forests explains this gap. This will ultimately result in both biological conservation issues and opportunities that should be urgently assessed before forest declines and diebacks further increase in Europe and other parts of the world.

THE NEED FOR MULTIDISCIPLINARY INTEGRATIVE APPROACHES COMBINING CUTTING-EDGE TOOLS

Monitoring canopy microhabitats and biodiversity is challenging (Nakamura et al., 2017), but monitoring the canopy of declining trees adds further challenges related to safety issues (e.g., fall of tree limbs) compromising climbing. Their crowns are degrading more or less rapidly jeopardizing the installation of permanent monitoring structures and equipment.

To circumvent these issues, either ground-based or aerial surveys should be selected for canopy access. New processes combining drone imagery, airborne LiDAR, deep learning and modeling should be developed to better assess habitat diversity and abundance in the canopy (Müller et al., 2018; Frey et al., 2020; Santopuoli et al., 2020), and microclimates (Duffy et al., 2021). This would also allow to investigate the outcomes of crown diebacks at larger spatial scales, i.e., from tree to the landscape level, which could be more relevant for stakeholders and conservation managers, but also for the study of local biodiversity (Jackson and Fahrig, 2015; Percel et al., 2019). These approaches could be combined with high throughput metabarcoding that allows to characterize arthropod communities over large spatial scales (e.g., Cai et al., 2021; Sire et al., 2021).

We also need to scale-down the investigations at the plant surfaces and organ scale. Since microclimatic conditions are the most relevant for small-bodied organisms like arthropods (Pincebourde and Woods, 2020; Pincebourde et al., 2021), high resolution surveys of microclimate at plant surfaces (leaves and wood) and within plant matrices (e.g., leaves, wood, and galls) are required to better assess the outcomes of changing microclimates across canopy on forest arthropod communities.

Novel sampling and biomonitoring techniques would help to widen the range of arthropod taxa, and guilds, studied and improve their monitoring. This could be achieved by implementing long-lasting and self-contained ecoacoustic or visual monitoring techniques for canopy-dwelling communities (e.g., Rappaport et al., 2020). Approaches based on next generation sequencing and machine-learning could also be used to infer ecological networks and measure the effect of decline of tree canopies on species interactions (Bohan et al., 2017). Developing environmental DNA surveys in canopy-related microhabitats or matrices like cavities, suspended soils, or perched dead wood would also improve our knowledge of arthropod communities in the canopy.

We call for integrated whole-tree approaches, from forest floor to canopy top and from microhabitats to landscapes, to better understand the functional and biodiversity outcomes of canopy degradation on the whole forest ecosystem. This also claims for more integrated studies linking the physiological status of trees to the physical habitats, trophic resources, and microclimatic conditions they provide and ultimately to the biodiversity they shelter. For this, a better exploration of stress-induced horizontal gradient of inner to outer microhabitats in degraded tree crown, and fine characterization of arthropod community distribution within the canopy gradients, and in the above-tree stratum, would be necessary. Several studies have investigated the impacts of forest diebacks or declines on the diversity of specific taxonomic groups or functional, habitat, or trophic guilds (e.g., Martel and Mauffette, 1997; Trotter et al., 2008; Stone et al., 2010; Beudert et al., 2015; Sallé et al., 2020; Vincent et al., 2020; Cours et al., 2021; Sire et al., 2021). Nonetheless, because of the mixed impacts highlighted by several studies, a multi-taxa and multi-guild approach would be necessary to have a holistic view of the conservation and functional outcomes of ongoing climate changes on forest arthropod communities (Seibold et al., 2018a; Swart et al., 2020). Based on this comprehensive ecological assessment, forest management and biodiversity conservation strategies, including the retention of damaged or declining trees (e.g., Kašák and Foit, 2018), shall be designed in order to take advantage of decline patterns and processes for biodiversity promotion while facilitating the forest regeneration at the same time.

AUTHOR CONTRIBUTIONS

AS supervised the writing and wrote the first draft of the manuscript. JC and EL contributed to the writing and prepared the figures. CL-V, SP, and CB contributed to the writing. CB co-supervised the research theme with AS. All authors contributed to the article and approved the submitted version.

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