Forest canopies as nature-based solutions to mitigate global change effects on people and nature

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Abstract

1. Via sheltering, decoupling and buffering mechanisms, tree canopies have the capacity to mitigate impacts of multiple global-change drivers on below-canopy processes and organisms in forests. As a result, canopies have an important potential as nature-based solution.

2. The optimal combinations of forest canopy structural attributes to jointly mitigate the impacts of multiple global-change drivers on below-canopy organisms and processes have received little attention to date.

3. To help solving this research gap, here we review how forest canopies modulate the effects of four important global-change drivers - climate warming, drought, air pollution, and biological invasions – on below-canopy conditions. Particular attention is paid to mitigating canopy attributes that can be influenced by forest management, including canopy cover, tree species composition and vertical and horizontal structure.

4. *Synthesis*. We show that the potential of forest canopies to mitigate global-change effects is highly context-dependent and that optimal canopy-based solutions strongly depend on the environmental context and the targeted subcanopy organisms. Hence, holistic approaches, that maximize synergies and minimize trade-offs, are needed to optimize the solution-potential of forest canopies.

Introduction

Tree canopies are a specific structural feature of forests, not present in open ecosystems. Canopies create a physical, chemical and biological boundary between the atmosphere and the ground, its characteristics shaped by the trees that make up the forest overstorey. Due to this boundary, tree canopies shelter below-canopy organisms and processes from external influences. Indeed, canopies govern the amount of solar radiation reaching the forest floor, decouple and buffer microclimates from the atmosphere, affect nutrient and water cycles, and determine habitat conditions of plants and animals (De Frenne 2023). Via these sheltering mechanisms, canopies have the capacity to mitigate impacts of global change on below-canopy processes and organisms, but also on forest functioning and services provided to society. Hence, proper management of forest canopies can be considered a cost-effective, nature-based solution to deal with societal challenges related to, among others, climate change adaptation, human health, and biodiversity loss.

Global environmental change is not only affecting societies, but is also putting forests under increasing pressure (Senf & Seidl 2021). Hence, the strong focus of forest management on creating resilient, future-proof forests (Keenan 2015). However, most efforts go to solutions to maintain forest productivity in the future (e.g. Ammer 2019), and less attention is being paid at finding optimal combinations of forest canopy structural attributes to mitigate the impacts of several global change drivers on multiple below-canopy organisms and processes now and in the future.

To help solve this attention gap, here we review how forest canopies can mitigate the effects of four important global change drivers - climate warming, drought, air pollution, and biological invasions – on below-canopy conditions, with potential benefits for people and biodiversity (Fig. 1). Our review describes general effects of trees, but focusses on the canopy as the structural feature of forests that mainly drives the mitigating effects and that therefore deserves special attention by researchers, forest managers and policy makers. Particular focus is given to mitigation-impacting canopy attributes that can be influenced by forest management, like (1) canopy cover, (2) species composition of the trees that make up the canopy and (3) vertical and horizontal structure of the canopy. By integrating current understanding on the mitigating potential of canopies, we aim to explore synergies and trade-offs among the above-mentioned canopy attributes and their effects on below-canopy conditions, and assess how context-dependencies, pertaining to both environmental context and targeted organisms and/or processes, may determine optimal canopy structures. Note that we confine our review in terms of space and time, in the sense that we mainly focus on patterns and processes at the local stand scale only and do not explicitly address canopy dynamics, trees outside woodlands or landscape scale effects.

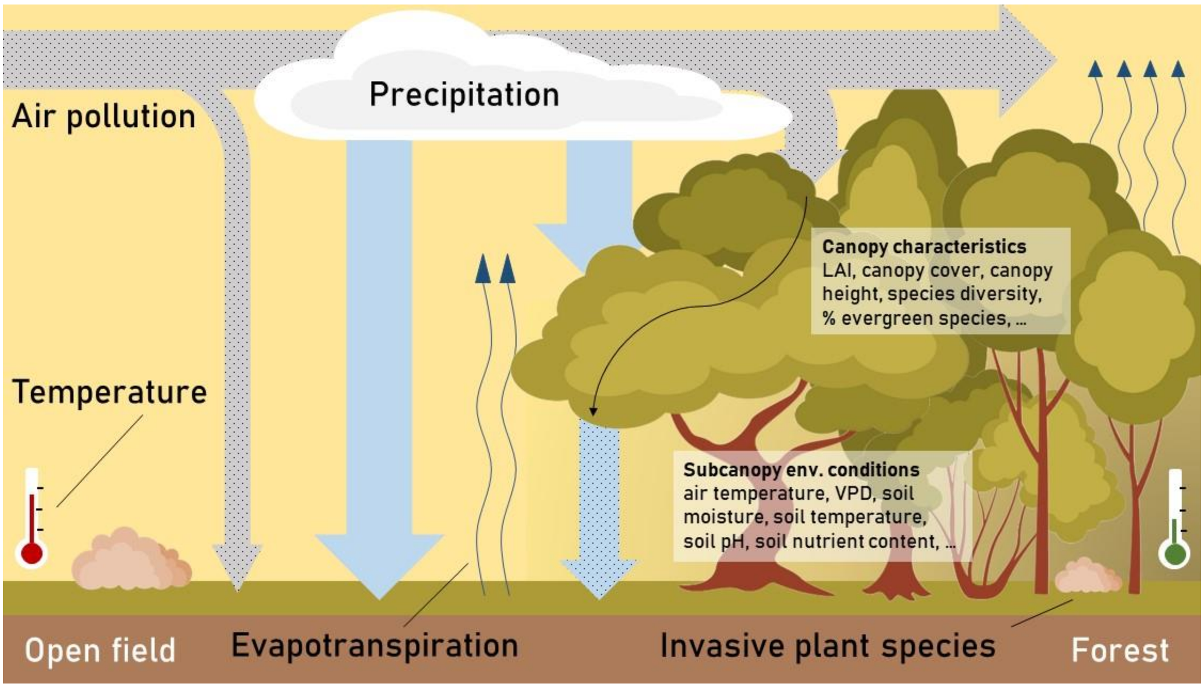

Figure 1: Overview of the four reviewed global change drivers (warming, drought, air pollution, and biological invasions), their interaction with forest canopies, key-canopy characteristics and sub-canopy environmental conditions addressed in this paper. Forest elements by macrovector on Freepik.

Mitigation of temperature at the forest floor

Temperatures are usually measured in synoptic weather stations following the World Meteorological Organisation's guidelines (De Frenne and Verheyen 2016). These so-called "macroclimatic" conditions, however, do not represent the thermal conditions below forests canopies. Forest organisms experience "microclimate" temperatures, i.e. highly variable, fine-grained thermal conditions that are determined by the joint action of macroclimate, landscape-scale determinants (e.g. forest fragmentation degree), and local environmental characteristics such as micro-topography, soil, and canopy structure.

While macroclimate land temperatures have warmed globally by on average +1.16°C over the past decades (1993-2022 mean annual anomaly, compared to the 1881-1900 baseline according to NASA GISTEMP data), microclimatic temperature changes are often strongly depending on other environmental conditions, such as changes in canopy cover (De Lombaerde et al., 2022; Zellweger et al. 2019). Importantly, while macroclimate warming provides a strong indicator of temperature evolutions over longer time scales and across large spatial extents, it is the change in microclimate temperatures that is often most relevant for people and nature (Dayi et al. 2019; Sanczuk et al. 2023).

Due to their size and highly complex structure, trees and shrubs are ecosystem engineers that attenuate variation in microclimatic conditions, and hereby shelter organisms living below the canopy from macroclimatic temperature extremes. The main mechanisms driving this attenuation are the shading from direct solar radiation, evapotranspiration and the reduction of wind speeds (De Frenne *et al*., 2021). Wind speeds are lower in forests. Gillerot *et al*. (2022), for example, measured wind speeds reduced by a factor 4.5 within forests compared to open field conditions. However*,* the absolute difference depends strongly on prevailing wind conditions with increases for higher external wind speeds (Chen *et al*., 1995; Renaud *et al*., 2011). On average, maximum temperatures are 4.1 °C lower below tree canopies relative to macroclimate temperatures (De Frenne et al., 2019; De Frenne and Verheyen, 2016), and during extremely hot summer days, air and human-perceived temperatures can be up to 10°C lower than outside forests (Gillerot et al. 2022, Meeussen et al. 2021). Winter and minimum air temperatures are buffered too, with minima being on average 1.1 °C higher in forests.

The magnitude of summer and winter temperature buffering is strongly linked to key canopy characteristics, like canopy closure, height and structure, dominant tree species and their shade casting ability, and forest stand basal area. Across Europe, structurally complex multi-layered forest stands with a dense canopy and shrub layer, buffer maximum temperature extremes by 0.6 °C more than simple-structured, recently thinned forests (Meeussen et al. 2021). Buffering by tree species with a high shade casting ability (e.g., beech - *Fagus sylvatica*) can be approximately 1°C higher than by tree species with a lower shade casting ability (e.g. ash – *Fraxinus excelsior*) with the same overall canopy closure (Zellweger et al., 2019). Tree species diversity can also lead to additional buffering through overyielding when tree species are complementary or when high-performing species dominate without fully outcompeting lower-performing species (Loreau *et al*., 2001; van der Plas *et al*., 2016). For example, maximum temperatures were lower in stands with higher tree species richness in young tree plantations, caused by the higher canopy cover and structural diversity in mixtures than in monocultures (Zhang et al., 2022). Forest microclimate buffering can thus be used by forest managers as a tool to mitigate climate change impacts on people and nature (Gillerot et al., 2022; Sanczuk et al., 2023), for example by adopting continuous cover forestry with stands with high canopy closure, consisting of shade-casting tree species and with gaps that are smaller than one tree height (den Ouden & Mohren 2020), to limit abrupt temperature increase. In urban contexts, people and nature are confronted with amplified heat exposure due to the urban heat island (Tuholske *et al*., 2021), further increasing the value of this nature-based solution in urban landscapes. Urban green managers can maximize the mitigation potential by providing sufficient canopy cover in highly urbanized and vulnerable neighborhoods (Ziter *et al*., 2019), thereby reducing negative health impacts and even heat mortality (Iungman *et al*., 2023; McDonald *et al*., 2020). Neighbourhood canopy cover levels of 30%

lead to very significant cooling effects (Iungman *et al.*, 2023), but especially levels of 40-50% and higher drastically reduce local urban temperatures (Gillerot *et al*., 2024; Ren *et al*., 2021; Ziter *et al*., 2019).

Mitigation of drought

Drought is commonly defined as any prolonged period with a meteorological water deficit, being a precipitation anomaly relative to the long-term local climatic conditions (Slette et al. 2019). Droughts are intensifying under climate change, with an estimated fivefold increase in global drought frequency for the coming decades compared to the second half of the 20th century (Thiery et al. 2021; Xu et al. 2019). Droughts are increasingly accompanied with heatwaves (Overpeck 2013), leading to more frequent 'hot droughts' that stress plants and increase mortality (DeSoto et al., 2020; Hammond et al., 2022; Senf et al., 2020). Drought stress on plants is driven by both low soil moisture supply and high atmospheric water demand (Liu et al., 2020), both of which are mediated by canopies - but via different mechanisms and with different outcomes.

The impact of forest canopies on **soil moisture** is not as consistent nor well understood as their impact on temperature (see above and Goeking & Tarboton, 2020; Smith-Tripp et al., 2022). The dominant paradigm states that with afforestation, or with increasing tree densities, soil moisture decreases due to water losses from canopy transpiration and interception (Ellison et al., 2017). Indeed, numerous studies have shown that soil moisture content in forest gaps is higher than under closed canopies (Gray et al., 2002; Kovács et al., 2020), and a meta-analysis concluded a positive effect of forest thinning on soil moisture (Sohn et al., 2016). However, tree canopies can on the other hand also enhance soil moisture through reducing surface run off and soil evaporation, and improving soil infiltrability (Ilstedt et al., 2016; Jones et al., 2020). The final impact of tree canopies on soil moisture will depend on the balance between these negative and positive effects, which are also mediated by environmental context.

Forest canopies affect **vapour pressure deficit (VPD ~ atmospheric drought)** mainly through their effect on temperature. Forest canopies reduce maximum temperatures, which in turn reduces VPD (Davis et al., 2019; Von Arx et al., 2013). VPD is also strongly coupled to soil moisture availability: increased VPD results in a higher evaporative demand which can lead to decreases in soil moisture (Seneviratne et al., 2010). Similarly, canopy buffering of VPD depends on the local water balance, and forests might lose their capacity to buffer VPD when soil moisture decreases as sites become water limited (Davis et al., 2019; Von Arx et al., 2013).

Canopy structure and composition are key in mitigating drought effects (Jones et al., 2020; Sohn et al., 2016). Overstorey structural complexity can attenuate drought via shading, through a lower subcanopy VPD, which is – however – also contingent on the moisture retention capacities of the soil (Michalet, Nemer, & Delerue, 2023). Contrastingly, lower canopy density generally enhances soil moisture by promoting throughfall and reducing foliar transpiration during drought (Sohn et al., 2016). While the canopy's mitigating role on drought is context-dependent, promoting drought-tolerant compositions is crucial for sustaining this role (Baeten et al., 2019; Blondeel et al. 2024). A canopy composed of diverse tree species could reduce drought vulnerability through complementary water uptake and hydraulic redistribution (Grossiord, 2020; Messier et al., 2021).

BOX: Open canopies, a potential blessing during drought?

Leaf wetness is a feature of potential ecological importance that is often overlooked (Dawson & Goldsmith, 2018). As a result of precipitation inputs (> 0.1 mm), leaves experience leaf wetting events on more than 141 days per year on average in temperate regions (Dawson & Goldsmith, 2018). While wet leaves can have some clear disadvantages, such as enhanced probabilities of fungal infections, a meta-analysis has indicated that about 93 % of investigated plant species are able to absorb water via their leaves (foliar water uptake) (Schreel & Steppe, 2020), a mechanism that increases a plant's water budget and might be aided by foliar fungal growth (Burgess & Dawson, 2004). Even though the amount of water absorbed by foliar water uptake is generally low and the absorption process is generally slow, its relative importance on a plant's water budget might be vital during dry conditions when precipitation is absent and leaf wetting events occur due to dew.

Because foliar water uptake is inherently slow, the duration of a leaf wetting event is more important than the amount of water supplied (Stone, 1963). Based on data from four temperate forests, we observed a significant increase in the duration per day that dew temperatures were reached below the canopy when forest canopy openness increased to 40-60 % (Fig. 2a). A similar increase is seen when leaf area index (LAI) decreased (Fig. 2b). These observations indicate that, while dense forest canopies buffer air temperature fluctuations, dew formation during dry conditions is more likely in open forests with a lower LAI due to the smaller temperature buffering at night. In other words, the potential benefits of foliar water uptake from dew formation during dry conditions on the water budget of a plant that is growing on the forest floor are more pronounced in open forests compared to closed canopy environments.

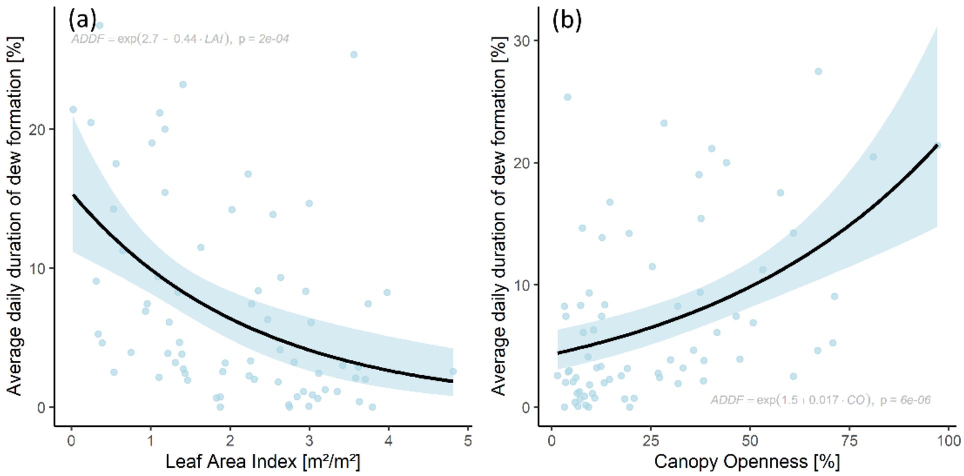

Figure 2: Average daily duration of dew formation, expressed in percentage per day (e.g., 50 % equals 12h per day, predominantly during nighttime) on severely dry days (Standardized Precipitation-Evapotranspiration Index (SPEI) <=-1.5) between 2020-08-18 and 2021-11-26 in four temperate forest sites (three experimental forest plantations: (https://treedivnet.ugent.be/ExpFORBIO.html and a network of semi-natural mature forests: https://treedivbelgium.ugent.be/pl_treeweb.html). Daily average duration of dew formation was modelled as a function of (a) Leaf Area Index and (b) Canopy Openness using generalized linear models with a log link function. Microclimate data to estimate the daily duration of dew formation were collected in 71 plots, distributed across the above-mentioned forest sites.

Mitigation of air pollution

Air pollution, including reactive nitrogen and particulate matter (PM), is affecting human (WHO, 2021) and environmental (Bobbink *et al.*, 2010) health globally. During the past century, air pollutant concentrations have increased drastically due to anthropogenic emissions, especially in industrialised regions (Holland *et al.*, 2005; Power *et al.*, 2023). While emission regulations have levelled off this increase in high-income countries - although emissions will most likely remain high for the coming decades (Fowler *et al.*, 2013; Engardt *et al.*, 2017) - air quality is still deteriorating in most low- and middle-income countries (WHO, 2021).

Forest canopies improve air quality at the landscape scale by acting as effective filters for air pollutants. In fact, trees and shrubs can take up gaseous pollutants through stomata and intercept airborne particles with their canopies via dry (particles in the atmosphere) and occult (particles in fog, mist and cloud water) deposition on the leaves (Schaubroeck *et al*., 2014). The deposited elements are subsequently washed off by precipitation and transported to the forest soil. As a result, forest canopies have the potential to enrich ion and PM concentrations in rainfall below-canopy, leading to elevated inputs of nutrients at the forest floor. Deposition velocities to forests have been found to be almost twice as high as those recorded for grasslands and other types of low green vegetation (Schrader & Brümmer, 2014). Especially in urban areas, where air pollution is often higher than in rural landscapes and affects many people, the removal of particulate matter and uptake of gaseous pollutants by trees is highly important (Sicard et al., 2021; Nowak et al., 2018). However, roadside tree rows in urban contexts, and especially street canyons, might in some cases lead to a local reduction in air quality, depending on their spatial configuration and canopy density (Buccolieri *et al*., 2018; but see Voordeckers *et al*., 2021 for contrasting empirical evidence).Furthermore, under heavy or long-lasting pollution or under drought stress stomata will close, which limits gas exchange at the leaf surface and therewith affects stomatal removal rates of gaseous pollutants (Nowak *et al.*, 2014; Samson *et al.*, 2017). Finally, trees also affect air quality through the production of pollen and emission of biogenic volatile organic compounds (BVOCs) that, as a result of their high chemical reactivity, promote the formation of secondary organic aerosols and PM (Laothawornkitkul *et al.*, 2009).

The amount of deposition in a forest is governed by (1) the level of atmospheric turbulence in the boundary layer between the canopy and the atmosphere, mainly generated by wind shear, and (2) the capacity of the receptor surface, i.e. the canopy foliage, to intercept aerosols or gasses (Erisman & Draaijers, 2003). High levels of turbulence, which promotes deposition, can be found in tall and heterogenous canopies (e.g. mixtures) with an intermediate openness and in the presence of forest edges. The receptor surface's capacity to intercept pollutants increases linearly with LAI (but may level off at high LAI values) and increases when leaf wetness is high and/or stomatal resistance is low, two factors that are mainly driven by micrometeorological conditions (Erisman & Draaijers, 2003). On the species level, main drivers include phenology (evergreen [+] versus deciduous [-]), leaf shape (needles [+] versus broadleaves [-]), leaf wettability [+], and species-specific BVOC emissions (Erisman & Draaijers, 2003; Steinparzer *et al.*, 2023). Although leaf wettability is often lower, coniferous species are able to intercept significantly more pollutants compared to broadleaved species due to their leaf shape and generally evergreen character: throughfall nitrogen has been found to be around 1.7 times higher in coniferous than broadleaved stands (De Schrijver *et al.*, 2007; Zhang *et al.*, 2022).

Mitigation of biological invasions

Biological invasions are expected to increase, presenting a pressing challenge to ecosystems worldwide. Here, we specifically focus on invasive plant species whose establishment and growth is impacted by the canopy above, rather than e.g. on invasive pests and diseases that may lead to canopy loss. In forests, invasive plant species often exhibit traits such as high growth rates, low shade tolerance, vegetative propagation, and the presence of multiple dispersal vectors (Hejda et al., 2009; Pyšek et al., 2009; Van Kleunen et al., 2010). Invasive plant species, and invasive shrubs and trees in particular, can outcompete native plants, leading to alterations in community composition, reduced biodiversity, shifts in primary production, and changes in nutrient cycles (Kohli et al., 2008; Laungani and Knops, 2009; Liao et al., 2008; Martin et al., 2009; Peebles-Spencer et al., 2017; Peltzer et al., 2010; Vilà et al., 2011). Biological invasions can have far-reaching ecological, economic, and societal consequences, underscoring the need for cost-effective, nature-based strategies to reduce the invasibility of forests.

Forest canopies have the capacity to reduce the success of invasive plant species, mainly through their effect on light availability (Petri & Ibanez, 2023). For instance, growth of the invasive tree *Prunus serotina* (American black cherry) was remarkably lower underneath a closed canopy, but benefited from gap formation (Closset-Kopp et al., 2007). The abundance of some invasive herbs (e.g. S*olidago gigantea*) was also substantially lower in closed-canopy conditions compared to open forests or clear-cuts (Vojík et al., 2018, Aszalós et al., 2023). Light availability is thus a main limiting resource controlling invasive plant performance in forests, likely because invasive plants are typically characterized by acquisitive traits (Martin et al. 2009). Native understorey plant communities, however, are generally well adapted to low-light environments and will therefore likely have a competitive advantage over invasive species under dense forest canopies (Sax & Brown, 2000) (especially regarding invasive species depending on disturbances, see below).

To reduce invader success, foresters should thus avoid management techniques that increase light levels at the forest floor. Actions such as clear-cuts and coppicing can favour the regeneration of invasive tree species (Vanhellemont et al. 2010), and herbs (Schnitzler & Muller 1998), and should thus keep in mind concomitant invasion risks. On the other hand, the governing role of light availability opens up an opportunity for managers to steer the canopy in such a manner that invader success is minimized. This can, for instance, be achieved by adopting selection systems in which a continuous tree cover is maintained (Sitzia et al., 2012). It should be noted, however, that some invasive plants are tolerant to high shade (e.g. *Microstegium vimineum*, *Lonicera tatarica,* and *Miconia calvescens*), and therefore particularly troublesome to forest management (Martin et al. 2009; Meyer & Florence 1996; Woods 1993; Heberling & Fridley, 2016; Heberling & Fridley, 2016). Moreover, in a few cases, invasive shrubs have been shown to maintain physiological advantages over co-occurring native species even in low-resource conditions (Heberling & Fridley, 2016). Maintaining or increasing canopy cover will thus not always be an effective solution, and sometimes direct control measures will be required to safeguard forest understoreys from invasive species.

Synthesis and outlook

Our review of the mitigating role of forest canopies on the impact of the four studied global change drivers shows that both the impact-magnitude and direction heavily depend on the canopy characteristics and the considered sub-canopy organism, as synthesized in Fig. 3.

The buffering of temperatures is increased in stands with a dense, high and structurally complex canopy, composed of species with a high shade casting ability. How this impacts understory vegetation, ground-dwelling fauna and humans is essentially similar: all will be sheltered from warmer temperatures outside forests. However, the optimal forest structure and composition is less unequivocal for the mitigation of extreme droughts. Whether or not a dense, structurally complex or a simple structured, more open canopy is most beneficial under those circumstances, depends on the relative importance of soil moisture deficit versus VPD causing drought stress. Understory vegetation may benefit from higher soil water availability and a higher potential for foliar water uptake (see BOX) in open forest stands, but the drier atmospheric conditions may conversely accelerate desiccation. Soil fauna, such as woodlice, may rather primarily depend more on soil moisture, though topsoil and litter layers will indirectly be affected by air humidity. The filtering role of forest canopies on air quality is even more ambiguous. For humans, a dense, complex canopy is more beneficial as more pollutants are filtered from the air. However, these filtered pollutants finally end up at the forest floor causing soil eutrophication and acidification, which in turn can be detrimental for below-canopy organisms, like understorey plants and soil fauna. Hence, for those organisms, more open, less complex canopies are preferred from an air pollution point of view. Finally, the presence of invasive trees and shrubs in the understorey affects the options for managers in a different way. Invasive trees and shrubs will typically benefit from open canopy conditions to spread and further increase in abundance, so that forest managers are inevitably directed towards a choice for dense, multi-layered canopies to limit the forest-floor light availability.

Although dense and structurally complex canopies are most effective in decoupling and sheltering the forest floor from most of the considered external influences, whether this is desirable is highly dependent on the context and target organism. Whereas closed, complex canopies may be advantageous for humans living in urban areas with poor air quality and hot summers, tree saplings may benefit most from a more open, simple canopy in areas that are particularly vulnerable to frequent droughts. Open canopies may also facilitate plant invasions, revealing co-occurring synergies and trade-offs.

This highly context-dependent effectiveness of forest canopies as nature-based solutions urges on the one hand for an integrated approach, encompassing multiple global drivers and a broad range of subcanopy organisms with contrasting requirements. On the other hand, it illustrates the need for more in-depth studies that allow quantifying the relative importance, trade-offs and synergies between the different canopy mitigation pathways for multiple global change drivers so that site-specific advice for the most effective local solution can be given. Indeed, whereas the knowledge base for the tempering effects of individual global change drivers has considerably grown during the last years – see earlier sections of this review – integrating knowledge across global change drivers remains challenging, among others, because of differences in research methodologies linked to the different research domains. The canopy's air pollution mitigation potential is, for example, often studied at the level of individual leaves and on individual trees in urban contexts, focusing on leaf traits, tree morphology and spatial tree configuration as key drivers. Temperature buffering, on the other hand, is mainly being studied by point measurements at the forest floor, using broader scale stand characteristics such as species composition, basal area or LAI as main predictors. The current mismatch between settings, scales and predictor variables hampers the quantification of trade-offs and synergies and urges for studies that investigate mitigating effects of the canopy on multiple global change drivers in an integrated way.

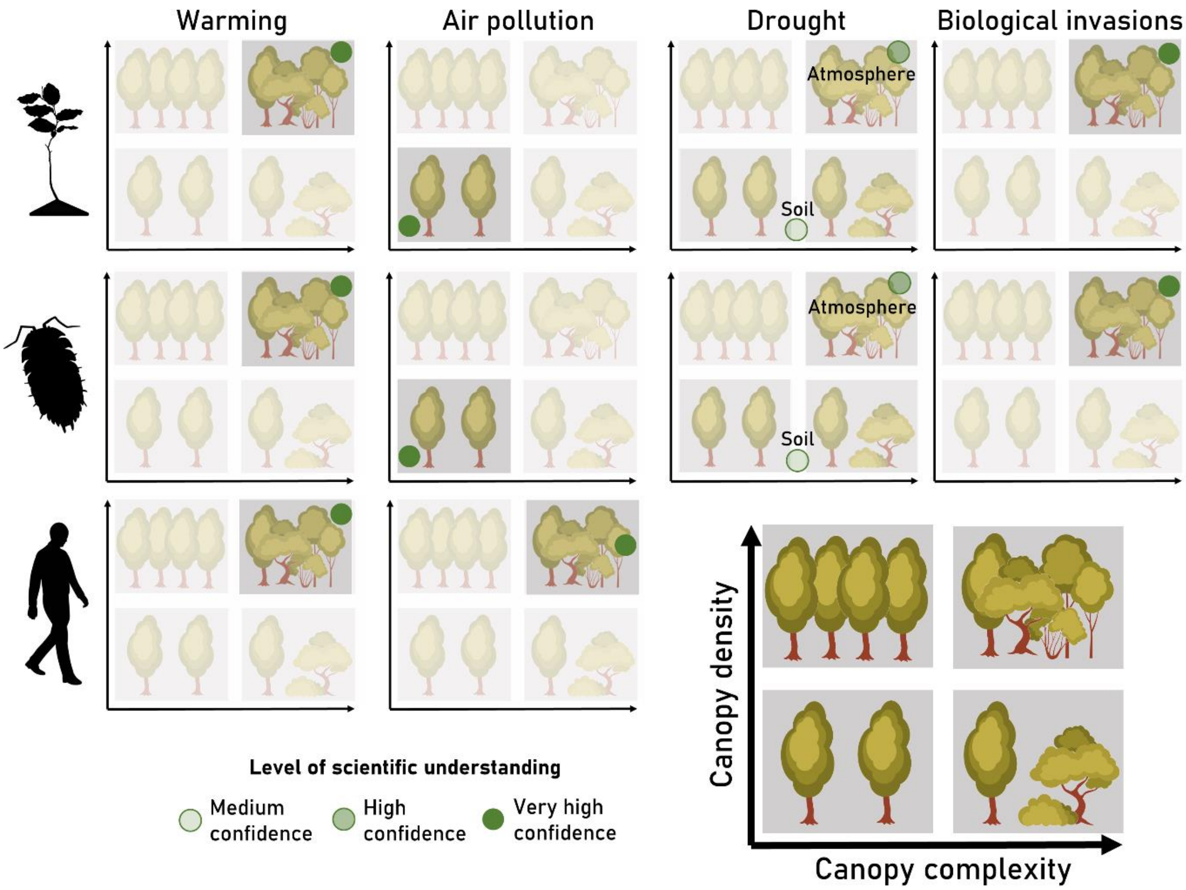

Figure 3: Synthesis of optimal canopy configurations to mitigate the effects of four global change drivers (warming, air pollution, drought and biological invasions) on three different species with contrasting ecological requirements (saplings of beech - Fagus sylvatica, a shade tolerant tree species; the drought-sensitive, forest-dwelling woodlice – e.g. Ligidium hypnorum; and humans – Homo sapiens). For each driver – species combination, we depict the most optimal position along gradients of canopy complexity (including - among others - the degree of vertical layering, the horizontal distribution of gaps and clearings, tree species richness) versus density. Biological invasions are here confined to shrub and tree invasions. The levels of understanding are shown in the transparency of dots and square panels and are based on the amount of evidence and degree of agreement found in literature. Forest elements by macrovector on Freepik.

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Conflict of interest statement

No conflicts of interest are present

Author contributions

All authors are linked to Ghent University's Forest & Nature Lab. An open call to all lab members, including junior and more senior researchers, to collaborate on this paper was launched. KV conceived the article, and all other persons who wanted to collaborate on this team-effort contributed to one or more sections of the manuscript. All authors have read and approved the final version of the manuscript.

Data availability statement

This review does not use data.

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