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Editorial: Understanding patterns and mechanisms of forest canopy diversity and ecosystem functions in a changing world

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Editorial on the Research Topic
Understanding patterns and mechanisms of forest canopy diversity and ecosystem functions in a changing world

Introduction

In this Editorial, we illustrate the ecological significance of the forest canopies and describe how a collection of papers in this Research Topic describes the importance of understanding forest canopy biodiversity and ecological processes in the age of the Anthropocene. We lastly address prospects and challenges in forest canopy ecology.

Forest canopies provide additional spatial dimensions

Traditionally, community assembly and ecosystem functions have been considered on a two-dimensional plane with reference points such as latitude, longitude, and elevation (or depth). Almost all terrestrial and aquatic habitats, however, include complex structures that create multiple, rather than just two, spatial dimensions (Basset et al., 2015; Oliveira and Scheffers, 2019). One of the most prominent multi-dimensional structures is found in forests (Ozanne et al., 2003), where the forest canopies function as climatic insulators that provide cool and moist climatic conditions in the understory compared with the hotter and drier climate of the more exposed upper canopy (Frenne et al., 2019; Figure 1). Despite their harsher and variable climatic conditions, forest canopies harbor high biodiversity by providing nesting and food resources and refugia to avoid predation and competition (Gámez and Harris, 2022). In addition, various microhabitats, such as bark, tree holes, lianas, fungi, and epiphytes, provide additional above-ground resources and thermal refugia (Frenne et al., 2021). Where each of these above-ground resources supports specialized consumers, then a whole dependent food web may be created (see, e.g., Kitching, 2000). Epiphytes, for example, provide unique microhabitats in the forest midstory and upper canopies, harboring a diverse array of trophic groups such as herbivores, detritivores, and predators (Stuntz et al., 2002b). Epiphytes also create microclimatic refugia with stratified climatic conditions from the epiphyte's core to their underlying substrates (Stuntz et al., 2002a). However, these patterns of microclimatic stratification may change depending on the vertical positions of the epiphytes and other microhabitats (Figure 1), causing complex interactions of vertical structures that occur at various spatial scales (Moffett, 2013).

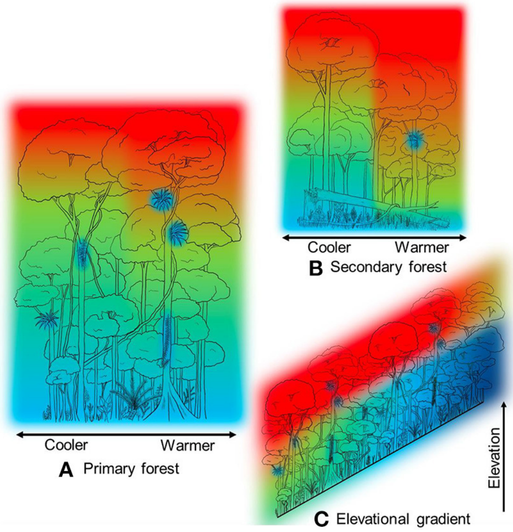

FIGURE 1
Hypothetical depictions of how vertical stratification created by forest canopies interact with anthropogenic disturbance and elevational patterns across time. Colors represent differences in microclimatic conditions (i.e., average and variability of temperature and humidity) and corresponding changes in biodiversity and ecosystem functions. In a primary forest **(A)**, canopies intercept a large amount of insolation, providing cool and stable microclimates in the understory. In addition, epiphytes in the canopy strata create and maintain cool and wet microhabitats. In a secondary forest **(B)**, the magnitude of thermal buffering is smaller than in primary forests due to more exposed canopy surfaces, creating hotter and more unstable conditions in the understory (Sagar and Devy). In addition, seasonal variations may be intensified in the secondary forest. Along an elevational gradient **(C)**, highly variable climatic conditions in the canopy may cause organisms to have greater elevational range distributions (analogous to Rapoport's rule), making elevational species' turnover smaller in the canopy than the understory (Leahy et al., 2021).

Forest canopy diversity and functions

Previous studies have demonstrated that forest biodiversity is stratified vertically (Stork and Grimbacher, 2006; Oguri et al., 2014). In many instances, forest canopies harbor high diversity, with many species only found in the upper strata (Basset et al., 2015). Although vertical stratification of diversity seems to be universal regardless of the latitude and elevation of the forest systems (Ashton et al., 2016), studies to date are limited geographically or taxonomically, and much more effort is required to fully understand the spatiotemporal distribution of forest organisms. In this Research Topic, research on forest canopy biodiversity and vertical stratification targets a variety of taxonomic groups, namely mammals (Haysom et al.), invertebrates (Kuchenbecker et al.; Nakamura et al.; Sallé et al.; Yoshida et al.; Gossner and Petermann; Sagar and Devy), epiphytes (Hu et al.; Seshadri et al.), and pathogens (Lan et al.). The studies represent a wide geographical coverage, including tropical and subtropical forests in Brazil, Borneo, Indo-Burma, and the Western Ghats, and temperate forests in Japan, western Oregon, and Germany. Some of these studies present wholly novel results and unique aspects of forest biodiversity and functions. Gossner and Petermann, for example, describe vertical stratification of aquatic communities in water-filled tree holes and suggest that not only tree hole microhabitat properties but also ecological traits of the invertebrate species that utilize them are determined by vertical position. Yoshida et al. focus on vertical stratification of "arthropod rain" (arthropods falling from above ground, providing important food resources for ground-dwelling predators) and address the importance of "wandering" detritivores and herbivores falling to the forest floor.

The exposed nature of the forest canopy surface also makes community assembly of canopy organisms more influenced by diel, seasonal, and annual variabilities in climatic conditions (Basham and Scheffers, 2020). Kuchenbecker et al., indeed, demonstrated that temporal beta diversity of herbivorous insects was much greater in the forest canopy than in the understory, implying that not only spatial but also temporal dimensions of forest structures must be considered to better understand community assembly and functions of forest ecosystems. Studies by Kuchenbecker et al. and Yoshida et al. both suggest weather conditions are a significant driver of temporal changes.

Anthropogenic impacts on forests and their canopies

Forest canopies are an interface between the land surface and the atmosphere (Ozanne et al., 2003); hence the organisms in the forest canopies are "at the forefront of major changes in response to both direct and indirect effects of climate change" (Sallé et al.). Impacts of climate change are likely to interact with other anthropogenic disturbances (e.g., selective logging and biological invasions, Sallé et al.) that impact forest canopy communities (Haysom et al., Seshadri et al.). Sagar and Devy show that canopies are more exposed and experience higher temperatures in secondary compared with primary forests (Figures 1A,B). This implies that forest disturbance may intensify the impacts of climate change on forest canopy diversity and ecological processes, as predicted by Frenne et al. (2021).

Arboreality, elevation, and latitude

Elevation and latitude are proxies for environmental conditions where temperature and other climatic conditions change spatially along with diversity and ecosystem processes. Nakamura et al. show a decrease in canopy leaf herbivory and an associated increase in tannins and phenolics (plants' defense against herbivores) with increasing elevation. Similarly, forest organisms show elevational stratifications of diversity (e.g., Wang et al., 2012) and ecosystem processes (e.g., Roslin et al., 2017). However, it should not be assumed that elevational or latitudinal patterns in diversity and ecological processes will be the same across forest canopies and the understory (Scheffers and Williams, 2018). Forest canopies present highly variable microclimatic conditions (Frenne et al., 2019, 2021). One recent study found that arboreal ants were indeed exposed to highly variable climatic conditions and presented their elevational range sizes greater than those found in the ground stratum (Leahy et al., 2021; Figure 1C). This suggests that the elevational Rapoport's rule (i.e., organisms present larger elevational range sizes with increasing elevation, Macek et al., 2021) may operate differently between the forest canopy and understory.

Current and future perspectives on forest canopy ecology

The papers published in this Research Topic add information and new insights to the body of work on the ecology of forest canopies. Clearly, however, further study is needed at multiple spatial and temporal scales to understand community assembly and the functioning of forest ecosystems in order to predict the impacts of climate change and other anthropogenic disturbances. As has long been pointed out, forest canopies pose challenging technical obstacles as accessibility to high canopy strata is often limited, making it difficult to produce much needed data (Cannon et al.). Current technological advances and infrastructure development have assisted the acquisition of data from forest canopies. The recent development of canopy cranes across the globe (Nakamura et al., 2017), for example, makes it possible to carry out spatially replicated intensive surveys and manipulative experiments that were not hitherto possible using conventional techniques such as single rope climbing and scaffolding. The development of mobile aerial platforms combined with advanced robotics (Cannon et al.) and next-generation sequencing, such as barcoding mass samples and environmental DNA (Ji et al., 2013; Ladin et al., 2021), provide additional research power that extends the capabilities of conventional surveys. Last, the establishment of multidisciplinary communication platforms (e.g., the Canopy Science Community Forum https://groups.google.com/g/canopy-science) and canopy-oriented conferences (e.g., the 8th International Canopy Conference in Xishuangbanna, China, October 2023) provide opportunities to share information and to collaborate with multidisciplinary communities for studying arboreality and vertical dynamics of forest ecosystems (Cannon et al.).

Author contributions

AN drafted the manuscript. LA, BS, and RK provided extensive edits and additional ideas. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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