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Review

Forests and Their Canopies: Achievements and Horizons in Canopy Science

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Forest canopies are dynamic interfaces between organisms and atmosphere, providing buffered microclimates and complex microhabitats. Canopies form vertically stratified ecosystems interconnected with other strata. Some forest biodiversity patterns and food webs have been documented and measurements of ecophysiology and biogeochemical cycling have allowed analyses of large-scale transfer of CO_2, water, and trace gases between forests and the atmosphere. However, many knowledge gaps remain. With global research networks and databases, and new technologies and infrastructure, we envisage rapid advances in our understanding of the mechanisms that drive the spatial and temporal dynamics of forests and their canopies. Such understanding is vital for the successful management and conservation of global forests and the ecosystem services they provide to the world.

Trends

Microclimate and biodiversity changes are more marked vertically than horizontally. Canopy arthropods are significant globally. Other biotic elements remain less well known.

In the canopy environment, food webs are complex, specialisation is less common than expected, and herbivores and pathogens are important; microcosm studies flourish but larger, canopy-based webs are challenging.

Climate change has impacts on the canopy via ecosystem distributions, productivity, phenology, pollination, herbivory, and plant–atmosphere interactions. Plantations may be carbon sinks yet diminish air quality.

Loss of forest canopies undermines global water and carbon cycle security and leads to biodiversity loss. How ecophysiology and plant-emitted volatile organic compounds impact atmospheric composition is poorly known.

A global system of large-scale, versatile canopy access facilities is necessary and emerging.

Forests and Their Canopies at the Frontiers of Ecology and Conservation

Forest canopies (see Glossary) are hotspots of biological diversity, engines of global biochemical processes, and the dynamic interface between organic nature and the atmosphere [1]. Forest canopy science has been an active discipline since the 19th century but its progress has been slow due in part to the limited accessibility of canopies [2]. Despite considerable advances in our understanding of canopy ecology over the past 30 years, due in part to methodological improvements, many critical knowledge gaps remain [3]. The degradation of forests and their canopies leads to loss of carbon storage, biodiversity, macro- and microclimate regulation, and other ecosystem services, having significant implications for human livelihoods. For example, 43 million hectares of tropical forests were lost between 2000 and 2005, which not only removed carbon stored as live biomass but generated an estimated emission of 0.8 Gt of carbon from cleared forests per year, contributing to global climate change [4]. Maintaining current carbon uptake by forest canopies and avoiding emissions resulting from forest loss could deliver up to 50% of the carbon mitigation needed to stay below a 2 °C global temperature rise [5]. Loss of forests also reduces the interception, evaporation, and transpiration of moisture by the canopy, eventually leading to reduced precipitation and water availability [6].

In the face of severe anthropogenic pressures, the conservation of forests and their associated species and ecosystem functions has become a central focus of research and policy. Improved

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understanding of global change impacts on forest ecosystems is also fundamental [1]. To this end we first need to obtain a clear picture of biodiversity and forest ecosystem function, in which the canopy plays an essential role. Here we examine how progress (or lack thereof) in canopy-specific or canopy-inclusive studies will contribute to our understanding of the ecology and conservation of forests, with particular emphasis on forest microclimate, species biodiversity and interactions, and biogeochemical processes. We explore how the forest canopy, with the aid of new technologies, experimental approaches, and a global **canopy crane** network, can be integrated into forest ecology. We demonstrate that more multilateral and collaborative effort involving all stakeholders in forest research and management should be directed towards the canopy to understand the impacts of forest loss and degradation on the ecosystem services they provide.

Forest Climate

Some large-scale interactions between forest canopies and climate such as rainfall interception and evapotranspiration are relatively well understood. However, other key links between forests and climate remain poorly described, such as the link from evapotranspiration to cloud formation and resulting climate feedbacks [7]. Forest and climate interactions at smaller scales are also less understood. The forest canopy creates microclimates through attenuating and buffering variation in climatic conditions, creating vertical gradients of mean **photosynthetically active radiation**, temperature, and **vapour pressure deficit** [8]. Forest canopies also buffer the effects of precipitation by intercepting rainfall and snowfall [9]. The architecture and physiology of canopy trees and epiphytes drive variation in forest microclimates [10], forming a complex set of feedback loops with microclimate both determining and being determined by species identity, growth traits, and stand age composition [11]. Other dimensions of forest climate, including the temporal and spatial dynamics of key microclimatic variables, also remain understudied [12], particularly at global scales. This is partly due to the difficulty of collecting standardised data from a sufficient diversity of vertical structures within a study area and replicating this temporally and between study sites. Existing methods, such as towers, are insufficient as they are geographically sparse and are themselves large enough to alter the local microclimate. The formation of a canopy crane network will help alleviate these problems (Box 1) by enabling easy canopy access to establish and maintain high numbers of sampling points within a single area.

Vertical climatic gradients within forests are much steeper than those driven by elevation and latitude. In the dipterocarp and montane forest of the Philippines, for example, changes in both temperature and moisture regimes were much greater over the ~20 m between the forest canopy and the understorey than the changes over 200 m in elevation [13]. It becomes increasingly clear that arboreal biodiversity is structured by these vertical gradients across many different taxa, especially in tropical forests [12,13]. This has important implications under climate change because arboreal species might show resilience through an ability to shift their vertical locations to compensate for changes in temperature [14] or by seeking buffered conditions within particular microhabitats [13]. This scenario remains understudied in forest canopies [15] and might manifest only as a delay in the effects of climate change on community composition rather than allowing permanent persistence of species. Documenting the links between forest architecture, microclimate refugia, and species' distributions and dispersal abilities at fine scales within the canopy is therefore of vital importance [15,16]. In complex forests tackling these questions will be challenging and requires the implementation of long-term monitoring programmes that explicitly include vertically stratified surveys.

Species Diversity and Distributions

While our knowledge of the distribution patterns of canopy species is growing, it remains limited, particularly for invertebrates. Over the past three decades, speculation on the contribution of canopy fauna to global species richness has generated much interest. Early

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calculations assumed a distinct stratification between canopy and ground, with the canopy having high insect host specificity, greater species richness, and a unique set of species compared with the ground stratum [17]. In many cases the canopy does appear to hold the highest species richness, as shown in a study which collected an exceptionally large number of arthropods (113 952 individuals representing 5858 species) from multiple vertical strata (including a subterranean layer) [18]. Patterns in compositional stratification appear to be consistent across taxa; for example, recent work on moth communities has demonstrated that vertical stratification is almost universal across both elevation and latitude [19]. Similar vertical stratification was also found for beetles in the Australian tropics [20] and spiders in Japanese temperate forests [21]. However, these studies also demonstrated that the degrees of vertical stratification are less distinct than had been previously thought. The aforementioned study of beetles [20], for example, showed that only about 25% of all beetle species were restricted to either the canopy or ground while the remaining 50% occurred across both layers. These data and new approaches to analyses have produced more modest diversity estimates than suggested by earlier studies [22]. A comprehensive review of the field using four innovative analyses of the global beetle fauna produced estimates of global terrestrial arthropod richness of 5.9–7.8 million species [17] – considerably less than the earliest canopy-oriented authors' 30 million species [23]. We add the caveat that some potentially species-rich arthropod groups such as flies and mites are still so poorly known taxonomically that these extrapolated numbers could remain considerable under- (or over-) estimates. While the diversity of other prominent canopy biota such as epiphytes is well studied, the canopy microbiota is almost wholly unknown (Box 2).

Unlike vertical stratification (e.g., [18,20]), the horizontal distribution of species within canopy layers has received scant attention, with the exception of ants [24]. The concept of 'ant mosaics' has been used to describe the spatial structure of arboreal ant assemblages, which are driven by mutual exclusion or positive associations of two or more ant species [24]. However, patterns of ant mosaics were described primarily within plantations or simple forest systems. A more recent study in lowland tropical forests suggested that mutual exclusion of ant species is not as strong as previously thought and ant species appear to be distributed randomly [25]. Past work on epiphytes also indicated low species turnover across horizontal gradients in the canopy [26]. More recent work has shown that fruit-feeding nymphalid butterflies have greater spatial and temporal species turnover in the canopy than the understorey [27]. This variation between taxa might be due to differences in host specificity. However, in general, horizontal variation within canopy layers remains poorly understood.

The relative importance of different ecological processes driving species turnover, or **beta diversity**, shifts across spatial scales. The beta diversity of woody plants in subtropical eastern China at small scales (10 m) is primarily driven by 'neutral' processes, whereas environmental drivers become stronger at larger scales [28]. Similar stochastic and deterministic switching in relation to spatial scale can also explain turnover in moth species with distance in Bornean forests [29]. However, different ecological processes can operate at different latitudes even at the same scale. In both temperate and tropical forests, strong intraspecific aggregation can result in high beta diversity of woody plants [30]. In temperate forest, however, intraspecific aggregation is likely to be driven by environmental filtering, whereas the distribution of species in tropical forest is likely to be driven by dispersal limitation [30]. We note that beta diversity is often quantified using very small sample sizes relative to regional species pools. Incomplete sampling potentially leads to inaccurate measurement of species abundance distributions and inflated beta diversity estimates [31]. This problem is not alleviated by standardising sampling protocols or null-modelling approaches [31]. Due to limited accessibility, canopy studies present the same problem. Methodological studies with large-scale and spatially explicit data are required

Glossary

Beta diversity: a component of diversity defined as variation in the identities of taxonomic (e.g., species), functional (e.g., functional traits) or phylogenetic (e.g., sites) units among samples.

Biogenic non-methane volatile organic compounds (bVOCs): carbon-based volatile organic compounds released by plants for biochemical and physiological reasons that are not yet fully clear.

Canopy crane: a construction tower crane built in forested areas to gain access to the canopy stratum. A metal enclosure (gondola) is hoisted above the ground by the crane and lowered to research locations within the canopy.

Ecophysiology: the adaptation of an organism's physiology (e.g., growth and gas exchange in plants, thermoregulation and dispersal in animals) to its environment.

Ehrlich–Raven coevolutionary hypothesis: the hypothesis that the evolution of plant defences followed by adaptations in herbivores leads to adaptive radiation of both of the interacting lineages.

Forest canopy: the upper layers or aboveground zone of vegetation, generally formed by tree crowns. The forest canopy contains various other organisms (epiphytes, lianas, and other arboreal organisms) whose microhabitats are not necessarily restricted to the canopy.

Janzen–Connell hypothesis: the hypothesis that the lack of dominance in tropical vegetation is driven through negative density-dependent control of plants by pathogens or herbivores.

Metagenomics: a family of techniques that use DNA sequencing and bioinformatics to generate ecological information from a bulk environmental or community sample *en masse* without needing to separate individuals or use traditional morphological identification.

Photosynthetically active radiation: the spectral range of solar radiation that photosynthetic plants are able to use for photosynthesis.

Remote sensing: the detection of abiotic and biotic properties of a landscape from a vantage point outside said landscape.

Vapour pressure deficit: the difference between the actual humidity in the air and the maximum (e.g., the 24-ha stem-mapping plot [28]) but no such data are currently available from the canopy.

possible humidity at a given temperature.

Species Interactions

Species are linked in complex networks of interactions (e.g., predation, pollination, competition, mutualism) that span all forest strata. Understanding changes in the structure of species interactions across the vertical dimension under the influence of key environmental gradients including disturbance, latitude, and elevation is important in explaining global biodiversity patterns [32]. Studies on leaf miners in the understorey indicate a way forwards in this respect. The quantitative structure of a herbivore–parasitoid food web was investigated along elevational gradients of Australian subtropical rainforests [33], with the finding that the host specificity and parasitism intensity of herbivore–parasitoid food webs decreased with elevation while overall food web connectivity remained the same. A translocation experiment in the same system indicated that herbivores currently escaping parasitism at high elevations might not necessarily experience higher parasitism when parasite species at lower elevations move upwards in response to warmer temperature. Integrating vertical canopy components and additional herbivore guilds, such as leaf chewers, which are more environmentally exposed, into studies of this kind will provide a clearer picture of elevational patterns of species interactions and cross-stratum links.

Species richness generally increases with decreasing latitude, and the large numbers of coexisting species in tropical forests have been explained by their narrow specialisations in this 'stable' environment [34]. More critical analyses throw doubt on this commonly quoted generalisation, as some well-studied species interactions (*viz.* pollination and seed dispersal) among tropical species are less specialised than those at temperate latitudes where plant diversity is lower [35]. Little studied second-order interactions are also potentially important. Ants, for example, affect pollination-capable flower visitors negatively while maintaining mutualistic relationships with the plants themselves [36].

Interactions among many species in spatially complex canopies can be studied by documenting the full networks of species interactions or food webs – bottom-up surveys [37] – or by manipulating the particular web compartments, taxa, or trophic levels – a top-down approach (e.g., [38]) (Box 3). Data from bottom-up approaches become difficult to interpret (particularly in complex tropical forests) as the number of species and their interactions grow geometrically, whereas top-down approaches often lack species-level resolution for the manipulated food

Box 1. The Canopy Crane Network

Canopy cranes allow access to the upper canopy layer, covering 0.8–2.0 ha per crane [96]. They have been used in ecological research since 1990 and presently operate at 15 locations around the globe (Figure I), although large regional gaps remain (North America, Africa). Individually, cranes allow detailed and replicable sampling of and experimentation within a contiguous forest area but have limited options for replication over the wider region. Cranes are expensive and the only location at which multiple cranes that can be used as replicates exist is the Eucalyptus Free Air CO_2 Enrichment (EucFACE) experiment [94]. This is the major reason that canopy cranes have been underutilised, reflected in the decline of the number of research papers using canopy cranes since 2004 [80].

The 747 papers using canopy cranes listed on Google Scholar (1992–2016) include studies on: (i) tree ecophysiology, particularly photosynthesis and transpiration (36% of all papers); (ii) plant architecture and vegetation structure (21%); (iii) arthropod communities, particularly herbivores, pollinators, and ants (18%); (iv) epiphytes, epiphylls, and endophytes (10%); and (v) canopy access methods and reviews (10%). Manipulative experiments with arthropod communities (e.g., [82]) replicated across continents and latitudes are currently not represented but appear to be the most promising avenue for future research (Box 3).

There is a notable recent rise in the number of canopy cranes in China (Figure I) and the new Canopy Operating Permanent Access System (COPAS) provides canopy access similar to that of a crane in French Guiana. Many current and planned cranes form an underexploited latitudinal gradient in the Australia–East Asia region (Figure I). Research using this near-complete north–south transect could include comparative studies of diversity (of epiphytes, fauna, and microbiotas), food webs, and stratification. This has the potential to be a powerful tool for testing the impacts of environmental manipulations of local climate, water regime, and food web structure across spatial scales. Cranes remain a prime candidate for the underpinning of a global canopy research network [96], provided that well-established international cooperative networks can be developed.

Figure I. World Map Showing the Locations of Canopy Access Facilities. Areas with different tree densities (i.e., the ratio of the area covered with branches and leaves of trees to the ground surface seen from above) are indicated by cream (0–20%), light green (21–60%), and green (61–100%). Open-circle symbols are locations of canopy cranes or a Canopy Operation Permanent Access System (COPAS) established or currently being built, closed-circle symbols are disused or dismantled canopy cranes, and square symbols are planned cranes. (1) Solling, Germany; (2) Leipzig, Germany; (3) Kranzberg, Germany; (4) Basel, Switzerland; (5) Tomakomai, Japan; (6) Wind River, USA; (7) San Lorenzo, Panama; (8) Parque Metropolitano, Panama; (9) Surumoni, Venezuela; (10) COPAS, Nouragues, French Guiana; (11) Lambir Hills, Malaysia; (12) Baitabag, Papua New Guinea; (13) Daintree, Australia; (14) Eucalyptus Free Air CO_2 Enrichment (EucFACE), Richmond, Australia; (15) Changbai Mountain, China; (16) Gutian Mountain, China; (17) Badagong Mountain, China; (18) Liziping, China; (19) Lijiang, China; (20) Ailao Mountains, China; (21) Xishuangbanna, China; (22) Dinghu Mountain, China. Map drawn by Jia-qi Zhang and map information sourced from Global Map – Percent Tree Cover generated by the Geospatial Information Authority of Japan, Chiba University and collaborating organisations (http://www.iscgm.org/gm/glcnmo.html). Photographs: Quentin Martinez (10) David Ellsworth (14), and Yun Deng (21).

webs. The study of the relative importance of bottom-up and top-down controls in trophic cascades necessitates top-down manipulations of trophic levels including the removal of herbivores, predators, or pathogens [39]. The **Janzen–Connell hypothesis** has been a favoured explanation for diversity maintenance for over 40 years [40] yet has only recently been tested experimentally by demonstrating that plant diversity and species composition can indeed be driven by fungal pathogens and insect herbivores [38]. Epiphytes and canopy phytotelmata have been useful naturally replicated microcosms for food web studies, demonstrating the importance of habitat size, climate, and top-down influence in shaping food web structures and complexity (e.g., [32]), but lack the sheer complexity of the overall canopy food web [41].

No single forest food web covering all forest strata has been fully mapped. One of the most comprehensive assessments of plant–herbivore food webs documented that ~200 plant species can harbour an estimated ~9600 species of herbivorous insects in the highly complex lowland rainforest of New Guinea [37]. The number of herbivore species is at least matched by their parasitoids [42]. The number of host or prey species per consumer species (i.e., their generality) has been estimated at one to two for parasitoids and five for herbivores and can be more than ten for predators [43]. A plant-based rainforest canopy food web might thus comprise over 100 000 trophic links, making prediction of its dynamics challenging. Predictions of food web structure can be made from species traits [44] and food web responses to species' removal or insertion can be predicted on this basis, but the accuracy of these methods have not yet been tested. Progress in DNA sequencing is allowing tests of evolutionary signals in the assembly of large food webs as species-level phylogenies become more widely available (e.g., [45]). Furthermore, progress in **metagenomics** and low-cost parallel sequencing allows rapid elucidation of network links from bulk ecological samples [46]. As predictive power is added to canopy food web science [47], we can expect better tests of the **Ehrlich–Raven coevolutionary hypothesis** and other scenarios for plant–herbivore interactions [48].

Forests and Biogeochemical Cycles

We now have a good empirical understanding of spatial and seasonal patterns in canopy biogeochemical exchanges, including the transfer of carbon dioxide, water, and, to a lesser extent, trace gases between the land and the atmosphere. For example, using eddy covariance flux data and various diagnostic models, tropical forests have been found to account for the largest proportion (34%) of global terrestrial gross primary production (GPP) [49]. The temperature sensitivity of ecosystem respiration is independent of mean annual temperature among biomes, suggesting less pronounced climate–carbon cycle feedback than suggested by models [50]. The spatial variation of net canopy–atmosphere carbon and water fluxes is now routinely modelled given knowledge of meteorological conditions and basic canopy properties (e.g., leaf area index, relative angiosperm coverage) and validated against eddy covariance flux measurements.

Box 2. Epiphytes and Microbiotas

Here we highlight two groups of canopy taxa, both important for forest ecosystem function but one far more extensively studied than the other.

Epiphytes

Epiphytes (Figure I) are one of the relatively well-studied components of canopy biotas, the breadth of research contributing substantially to taxonomic inventory and ecological understanding. There are more than 27 000 species of vascular epiphytes, representing *ca* 9% of the extant global diversity of vascular plants. Orchids (*ca* 19 000 species), ferns and fern allies (*ca* 2700 species), and bromeliads (*ca* 1800 species) are most diverse in the tropics [86]. Herbivory was believed to be low in epiphytes, but a study using orchid, bromeliad, and fern species in Mexico showed that while leaf damage was low in epiphytic orchids and bromeliads, inconspicuous damage to reproductive organs and meristematic tissues negatively affected their fecundity and survival [81]. Orchids, even closely related species, have adapted to different pollinators (by placing pollinia on different parts of their bodies), contributing disproportionally to the diversity of pollinators [85].

There remain many gaps in our epiphyte knowledge; for example, the degree of host-tree specificity is highly variable. While many species of orchid are found to display high host-tree specificity, other vascular epiphytes generally display lower levels of host-tree specificity [87]. This might be explained by symbiotic relationships between orchids and their mycorrhizal fungi whose occurrence is likely to be related to host tree species. Alternatively, a tendency to preferentially study rare and endangered orchid species might have contributed to biased estimates of host specificity [87]. Additionally, much less taxonomic research has focused on non-vascular epiphytes [84] and these are unlikely to be biogeographically congruent with vascular species [83].

Microbiotas

Studies on the canopy microbiome have mainly focused on numerous microhabitats, including open water in plant containers, bryophytes, leaf surfaces (the phyllosphere), endophytes, and canopy-suspended soil. One study of bacteria on dry leaf surfaces in tropical canopies showed high diversity of bacteria and high community turnover across canopy tree species [89]. Fungal assemblages in temperate regions tend to be vertically stratified, with specific host, microhabitat and substrate preferences, although this is less studied in the tropics [90].

The importance of canopy microbes for plant health has not been thoroughly investigated and many canopy niches have not been sampled for their microbiomes (e.g., the leaves of the extremely exposed upper canopy). Much higher abundances of fungal spores have been observed at night [88], suggesting large diel variation in the canopy microbiota. Both the spatial and temporal distributions as well as the functional roles of canopy microbiotas need to be understood. New molecular technologies (e.g., metagenomics) that have been used in microbial ecology outside the canopy will facilitate studies of canopy microbial ecology [97].

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Figure I. Epiphytes on *Lithocarpus xylocarpus* Tree in Mixed Forest at Nat Ma Taung National Park, Myanmar (2700 m Above Sea Level). Photograph: L.S.

Meanwhile, our understanding of forest canopy **ecophysiology** has been substantially improved, not only by traditional *in situ* measurements and manipulative experiments but also by continuous automated observations from satellites and flux towers (Box 4). While satellites and flux towers provide estimates of spatially aggregated canopy fluxes, a deeper knowledge of the links between canopy plant diversity and function requires description and understanding of the variation of key plant functional and ecophysiological traits. Such understanding is essential for prediction of how changing species composition may lead to changes in canopy function. Efforts such as the Global Ecosystem Monitoring network (GEM-TRAITS; http://gem.tropicalforests.ox.ac.uk) are collecting such datasets for a wide range of tropical ecosystems and airborne and future satellite-borne hyperspectral **remote sensing** technologies offer the prospect of mapping canopy plant traits at landscape and regional scales [51]. These extensive data sets can lead to large-scale analyses of the environmental controls on plant functional traits that play key roles in global biogeography and biogeochemical cycles [52]. These insights have not yet been fully incorporated into global ecosystem models but are likely to reduce some of the persistent uncertainties in predictions of future feedbacks between climate and carbon [53].

Forests and plantations (e.g., oil palm, eucalyptus, poplar) are the largest global emitters of **biogenic volatile organic compounds (bVOCs)**, especially isoprene and monoterpenes [54]. Several effects of bVOCs in the atmosphere are known (formation of aerosol particles, mediating in the oxidative capacity of the atmosphere, influencing the formation of ground-level ozone) but their linked effects on the Earth system are poorly understood. Knowledge of the atmospheric chemistry of bVOCs is improving, but the recent discovery that there are massive emissions of benzenoids from forests, rivalling emission rates from anthropogenic pollutant sources [55], highlights remaining uncertainties. There are large gaps in our knowledge of the environmental effects of bVOC emissions and the roles that microbiotas and invertebrates play in these processes. New remote sensing technologies (Box 4) coupled with ground-truthing

Box 3. Experimental Approaches to Canopy Science

Much of canopy science to date has focussed on observation of patterns and inference of causation through correlations. This is often problematic and experiments are one approach to disentangling drivers and responses; for example, to test impacts of future climate warming on tree physiology [93] (Figure I). Manipulations in the forest canopy are particularly challenging because access is difficult, and experiments require repeated visits to multiple sites to collect pretreatment data as a baseline, to apply manipulations, and to collect post-treatment data to assess impacts. This can limit the number of replicates that are feasible for experiments. At the extreme, intensive manipulations with only a single experimental and a single control plot (e.g., [78]) can nonetheless yield useful information, providing results are interpreted with caution [98]. These limitations are overcome to some extent in manipulations of canopies that do not require access to the canopy itself – for example, experimental forest fragmentation [99], or drought and irrigation simulation (e.g., [95]) – hence allowing larger areas to be utilised in ways that more closely mimic landscape-scale drivers of change.

For those experiments in which access to the canopy is necessary, choice of access method is critical. If experiments can be meaningfully conducted over small spatial scales, canopy cranes represent a useful method of access to the canopy that allows multiple visits with the possibility of little disturbance (e.g., [92]; Figure I). However, the use of cranes can suffer from low spatial replication since the reach of any single crane is limited, thus reducing the utility of the resulting experimental data for extrapolation of broader patterns. This problem could be overcome by conducting experiments on the increasingly widespread global network of canopy cranes (Box 1), a tactic not yet fully utilised. A further limitation of the use of canopy cranes for experimental work is that if experimental manipulations have ecosystem-wide consequences, this can compromise the use of the crane site for further research. Alternative methods, such as rope access, allow sampling of a larger spatial area for experiments with a lower risk of compromising future work, with the limitation that not all parts of the canopy will be accessible. Similar issues relating to pseudoreplication and lack of access to some canopy strata (canopy walkways, towers) and lack of possible replication (canopy rafting) apply to other access methods. Use of non-experimental background data collected at larger spatial scales can help with these issues of pseudoreplication (for the tree warming example given above, comparison with atmospheric temperature [93]). Data gathered through remote sensing (Box 4) has the potential to inform experimental projects in a similar manner.

Despite all of these challenges, forest canopies can be more suitable for experiments than other habitats. For example, epiphytes represent replicated compartments, and hence ideal systems for experimental manipulation [41]. The same is true of isolated tree canopies, which can serve as replicates for the exclusion of particular canopy functional groups [79].

Figure I. Two Examples of Manipulative Experiments on Forest Trees. Left: Whole-tree warming experiment to measure carbon uptake and release in eastern Australia [93]. Photograph: Sebastian Pfautsch. Right: Experimental branch warming experiment to measure phenological responses at the Tomakomai canopy crane site, Japan [92]. Photograph: Masahiro Nakamura.

flux towers and approaches using large-scale manipulations and traits-based modelling and scaling are promising in this regard.

Anthropogenic Impacts on Forest Canopies

Forest fragmentation is a common consequence of human activities including road construction, selective logging, and clearing for agriculture, with impacts on habitat connectivity, tree dynamics, microhabitat conditions, and biodiversity [1,56]. It results in changes in surface

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Box 4. Remote Sensing

Large-scale remote sensing data have been extensively applied to improve our understanding of the structure, function, and phenology of the forest canopy, especially the long-term response to environmental change (e.g., [91]). More recently, high-resolution, near-surface, hyperspectral remote sensing even allows the monitoring of plant traits and functional biodiversity, filling the spatial resolution gap between traditional satellite-based remote sensing and ground-based *in situ* measurements [51]. Additionally, new satellite-derived products such as the ECOsystem Spaceborne Thermal Radiometer Experiment on Space Station (ECOSTRESS) offer new insights into ecosystem health and environmental stress at the canopy scale.

Over the past 5 years, there has been a surge in the use of remotely piloted remote sensing systems (or ‘drones’) for various applications, including the mapping of habitats and vegetation, detecting wildlife, monitoring of natural and anthropogenic disturbances (e.g., canopy gaps created by tree falls; Figure I), and surveillance of protected areas for illegal activities (e.g., animal poaching [100]). These tasks are typically performed by a semiautonomous drone programmed to track a series of waypoints during a mission while the on-board sensor collects data in the form of moving or still imagery. There are several factors driving the mainstreaming of this technology, including: (i) the cost savings from replacing humans with drones; (ii) the ability to acquire data from inaccessible environments such as tall forest canopies; and (iii) the higher spatial and temporal resolution of data. There are also several operating constraints: (i) the restricted payload capacity and flying time; (ii) the validation of data required by ground truthing; (iii) the training required to effectively pilot drones; and (iv) the risk of complete system loss when operating in high winds or complex terrain (e.g., forest valleys) [100].

In the case of a mapping application, the individual images would be stitched together to produce a geographically accurate 2D and 3D representation of the target area (i.e., an orthomosaic or digital surface model, respectively; Figure I). Depending on the spectral nature of the data, further analyses could be conducted to track temporal changes in the landscape or to reveal the spatial pattern of relative photosynthetic activity (i.e., plant health or vigour). The 3D model of the habitat could also be further analysed to derive estimates of vegetation volume and biomass (to the extent that a digital elevation model for the site is available).

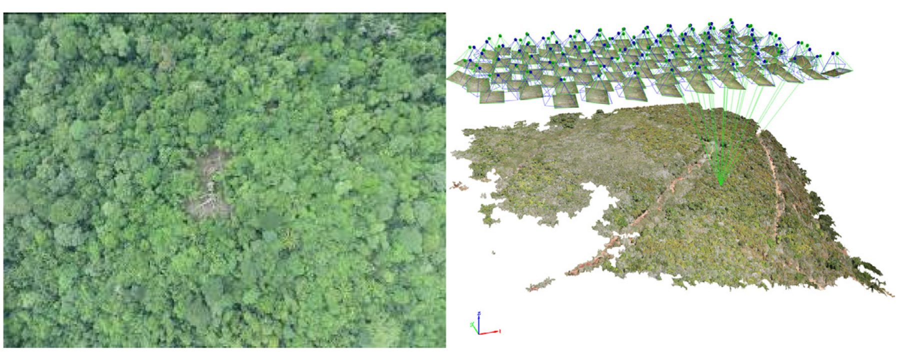

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Figure I. Two Examples of the Application of Drones in Studies of Canopy Ecology. Left: High-resolution and geotagged image of a canopy gap created by tree fall identified by a fixed-wing drone flying 300 m over Barro Colorado Island, Panama. Right: One-hectare dry forest habitat in New Caledonia showing detailed 3D canopy surface at a resolution of 5 cm per pixel mapped by a multirotor drone carrying a compact digital camera. Smaller images above the model indicate the location and orientation of individual still images captured by the drone. Photographs: L.P.K.

albedo, evapotranspiration, and cloud cover, affecting the regional and global climate [57]. Forest fragmentation also modifies canopy gap formation and dynamics. In tropical montane forest, for example, fragmentation and increased edge effects produced canopies with lower height and more spatially uniform surfaces [58].

Responses of canopy biodiversity to fragmentation and edge effects are highly variable: habitat specialist species with limited dispersal abilities are negatively affected, whereas other species benefit [59]. A recent synthesis of relevant experiments across multiple biomes suggested that habitat fragmentation resulted in 13–75% of biodiversity loss, affecting key ecosystem functions such as carbon and nutrient cycling, trophic interactions, and pollination [60]. In addition, forest loss disturbs multitrophic interactions through altered bottom-up (e.g., reduced plant antiherbivore defence mechanisms) and top-down (e.g., reduction in/of predators) controls [56]. However, we know little about the degree to which canopy biodiversity and trophic interactions are affected by anthropogenic disturbances at a global scale.

Conversion of forests to plantations has accelerated in the past 15 years, particularly in the tropics, further homogenising habitat and removing or simplifying canopy communities [29]. In addition, as natural forests or traditional crop lands are replaced by biofuel plantations of high isoprene emitters, interactions with NOx-rich air from urban areas will lead to enhanced ground-level ozone concentrations with potentially detrimental effects on human health and ecosystem functioning [61].

Climate change models estimate a global temperature increase of up to 5 °C by the end of this century [62] and the most recent reviews show that forests are already responding to elevated temperature with upwards or latitudinal movement of range margins and range contractions and expansions [63]. Phenological responses to temperature change (bud burst, flowering, and leaf fall) will result in changes in canopy composition and structure. These effects are likely to be reinforced by life-cycle shifts of invertebrate pollinators resulting in asynchrony with flowering patterns [64]. Downwards shifts in the body size of insect pollinators induced by warming might further disrupt pollinator relationships [64]. Canopy–atmosphere interactions involving bVOCs are also susceptible to change. Increasing atmospheric CO_2 concentrations have been shown to inhibit isoprene emissions, but recent studies suggest that this might not occur under warmer conditions [54].

Forest net primary productivity (in which the canopy plays a major role) has been predicted to increase up to 23% in response to increases in atmospheric CO_2 [65]. Consequential shifts in plant dominance and density will impact microclimate gradients [66]. However, more recent research shows that high temperatures might inhibit the increase in net primary productivity [67,68]. Consequently, large uncertainties persist in model predictions of future carbon and climate feedbacks, particularly in the responses of GPP to future climate change and atmospheric CO_2 elevation [53]. Despite model uncertainties, long-term growth rates are unlikely to increase substantially due to a combination of nutrient limitations, physiological variation, mycorrhizal relationships, temperature change, and water availability as well as interactions with animals, plants, and microbes [69]. Increased natural and anthropogenic canopy disturbance is likely to compound the effects of climate change [70]; indeed, the negative effect of forest insect outbreaks on uptake and storage of atmospheric carbon is so significant that it might need to be factored into climate change models [71].

For some anthropogenic disturbances (e.g., deforestation, logging), a space-for-time substitution is possible and changes in biodiversity and ecosystem processes can be examined over degraded landscapes and compared with intact forests. For others (e.g., climate warming, increasing atmospheric CO_2) this approach is not possible. Instead we must rely on large-scale monitoring (e.g., eddy flux, remote sensing) and more mechanistic, smaller-scale studies including direct measurements of canopy tree traits (GEM-TRAITs) and experimental approaches such as manipulating atmospheric CO_2 concentrations or temperature (e.g., FACE [72], BIFoR FACE [73], and TRACE experiments [74]; Box 3) or artificial drought and irrigation experiments [75]. Long-term forest inventories, ecophysiological studies, and a consideration of the atmospheric carbon budget suggest that intact forest canopies provide a carbon sink that is at least partially stimulated by increasing atmospheric CO_2 concentrations [72,76]. How long this buffering ability would persist in the face of climatic, ecophysiological, and ecological feedbacks is unknown.

Concluding Remarks

New avenues for exciting canopy research are opening up (Figure 1). Many of these research directions are urgent in light of current rates of forest loss and climate change. The forest canopy remains under threat from multiple human drivers, as does its resilience and resistance to change. The major impacts of anthropogenic change have shifted from local to global scales as a result of climate change and the growth in industrial agriculture [77]. The medium- and long-term implications of this shift for canopy biodiversity, ecosystem function, and resilience are little understood. With increased access through the expansion of infrastructure, and new technologies for the description and manipulation of diversity and function, the forest canopy is no longer 'the last biological frontier'. Despite limitations in current understanding, it is clear that forest canopies are unique zones of biodiversity, support the interface of a large part of the Earth's biogeochemical processes, and are critically sensitive to anthropogenic change.

This review demonstrates that our current knowledge of forest functioning is heavily biased towards the understorey and that more emphasis is needed on studying the canopy at fine

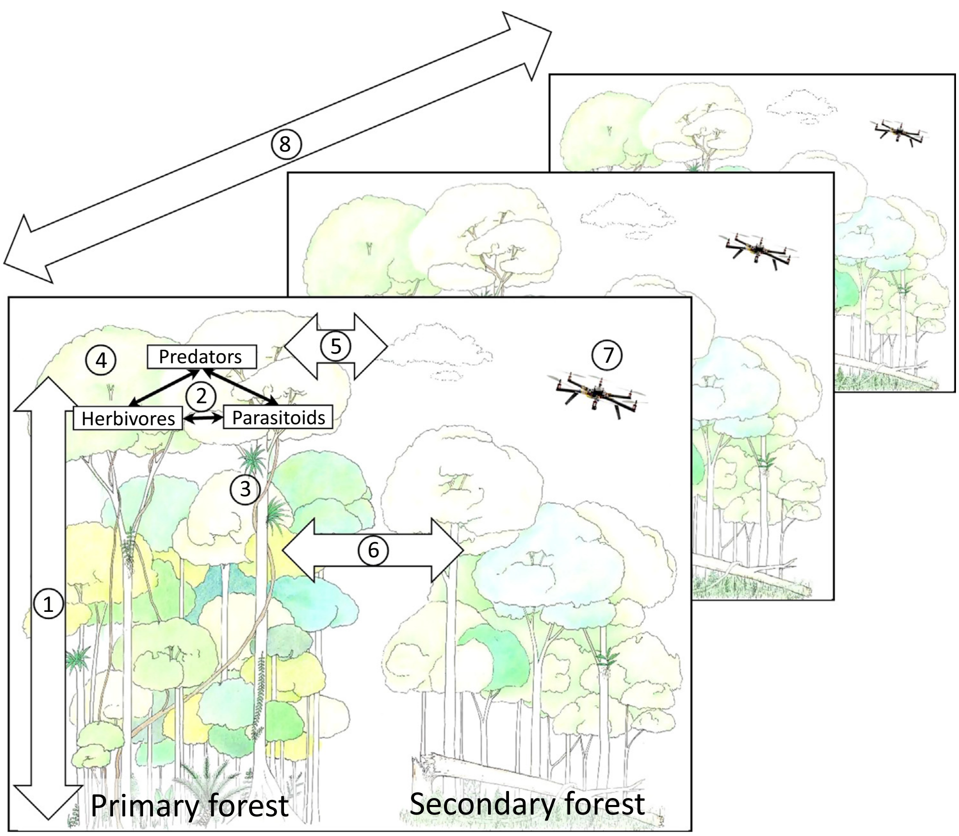

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Figure 1. Schematic Diagram of Primary and Secondary Forests Showing Key Thematic Areas of Canopy Studies and Examples of Studies Cited in this Review. (The same study is often included in more than one thematic area.) Only studies that included or focussed on forest canopies are included. (1) Vertical comparisons along canopy–understorey–ground gradients [19–21]. (2) Food webs and species interactions [12,36,37,42,44,56,78–82]. (3) Epiphyte [11,26,41,83–87] and canopy microbiology [88–90] studies (Box 2). (4) Canopy biodiversity [18,22,23,25,27,41,80], phenology [91,92], and microclimate [8–10,13–15,57,66]. (5) Biogeochemical [including biogenic volatile organic compound (bVOC) emissions] [4–6,49,54,55,61,65,67,68,71,74,76] and ecophysiological processes [50,65,93–95]. (6) Comparisons along gradients of forest degradation and fragmentation [6,29,58,59]. (7) Remote sensing [51]. (8) Inter-regional and continental comparisons [29]. Images: Yuan Liu.

Outstanding Questions

How do complex feedback loops create canopy microclimates and how do they buffer the effects of climate change on forest biodiversity?

How many animal, plant, and insect species are there and how specialised are species in the canopies of different forest types?

What are the patterns of canopy species diversity and food web interactions and how do these change across spatial scales and forest types?

What are the mechanisms shaping diversity and ecosystem structure in the canopy and how do they shift at different spatial scales?

What are the dynamics of forest primary production and associated food webs in response to climate change and atmospheric CO_2 elevation?

What is the role of forest canopies in the generation of bVOCs and what effects do these compounds have in the Earth system?

What are the impacts of anthropogenic disturbance (including pollution, fragmentation, and climate change) on forest canopy diversity?

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vertical resolution. It is clear that more multilateral and collaborative research effort should be directed towards forest canopies with the aid of new technologies, experimental approaches and a global canopy crane network. Acquiring this knowledge will improve our predictive abilities on how forest ecosystems will respond to human disturbances at multiple scales and improve management strategies in a rapidly changing world.

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