

The functional roles of epiphytes and arboreal soils in tropical montane cloud forests

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(Received 1 March 2015; revised 14 June 2016; accepted 14 June 2016; first published online 13 July 2016)

Abstract: Epiphytes and their associated decomposing litter and arboreal soils (herein, epiphytic material, EM) are ubiquitous features of tropical montane cloud forests (TMCF) and play important roles in ecosystem function. EM intercepts water and nutrients from the atmosphere and from intercepted host tree sources, and may contribute significant inputs of these resources to the forest floor. Despite the importance of EM in the TMCF, a systematic review of the ecosystem roles of EM has not been compiled before. We have synthesized the literature that documents functions of EM in undisturbed TMCFs and discuss how these roles may be affected by disturbances, including changes in climate and land use. The range of EM biomass and water storage in the TMCF varies greatly across sites, with different amounts associated with stand age and microclimate. EM is important as habitat and food for birds and mammals, with over 200 species of birds documented as using EM in the Neotropics. Given its sensitivity to moisture, projected shifts in cloud base heights or precipitation due to changes in climate will likely have a large impact on this community and changes in EM diversity or abundance may have cascading impacts on the ecosystem function of the TMCF.

Key Words: biomass, dispersal, hydrology, interception, nutrient cycling, pollination, reproductive biology, water storage

INTRODUCTION

Tropical montane cloud forests (TMCF) are among the most structurally complex of all terrestrial ecosystems, due in part to the abundance and diversity of epiphytes (Vareschi 1986). Epiphytes contribute to complex arboreal communities, which consist of vascular and non-vascular plants, decomposing litter from the host tree and epiphytes, and canopy soil, which we refer to as epiphytic material (hereafter, EM) (Nadkarni *et al.* 2004). These canopy communities have attracted the attention of tropical botanists and ecologists for over 125 y (Schimper 1888). Vascular epiphytes can account for up to one-third of the species and one-half of the individual plants at the stand level in TMCFs (Gentry & Dodson 1987a). Because epiphytes are limited in their ability to gain access to terrestrial soil resources, many of them rely on morphological and physiological adaptations and biotic interactions to

acquire nutrients and water, including litter-impounding pools, foliar trichomes, foliar water storage, foliar uptake capacity, insectivory, myrmechocory and poikilohydric foliage (Benzing 1990, Gotsch *et al.* 2015). The species composition, physiology, distribution and conservation of EM in TMCF pools have been summarized elsewhere (Bruijnzeel *et al.* 2010, Coxson & Nadkarni 1995, Gentry & Dodson 1987b, Ingram & Nadkarni 1993, Sugden & Robins 1979, Zotz & Hietz 2001), but we lack a comprehensive understanding of the ecosystem roles played by EM.

Many studies in TMCFs have suggested that EM contributes to ecosystem function by increasing cloud water and nutrient interception and retention in the canopy, affecting the amounts and dynamics of inputs of resources to the forest floor, and creating or enhancing habitat for animals (Figure 1). In some TMCFs, epiphytic foliage provides a large fraction of the leaf area and foliar biomass of tree crowns (Hofstede *et al.* 1993), which enhances wet and dry deposition by increasing the total physical area of canopy surfaces (Nadkarni 1984a). The

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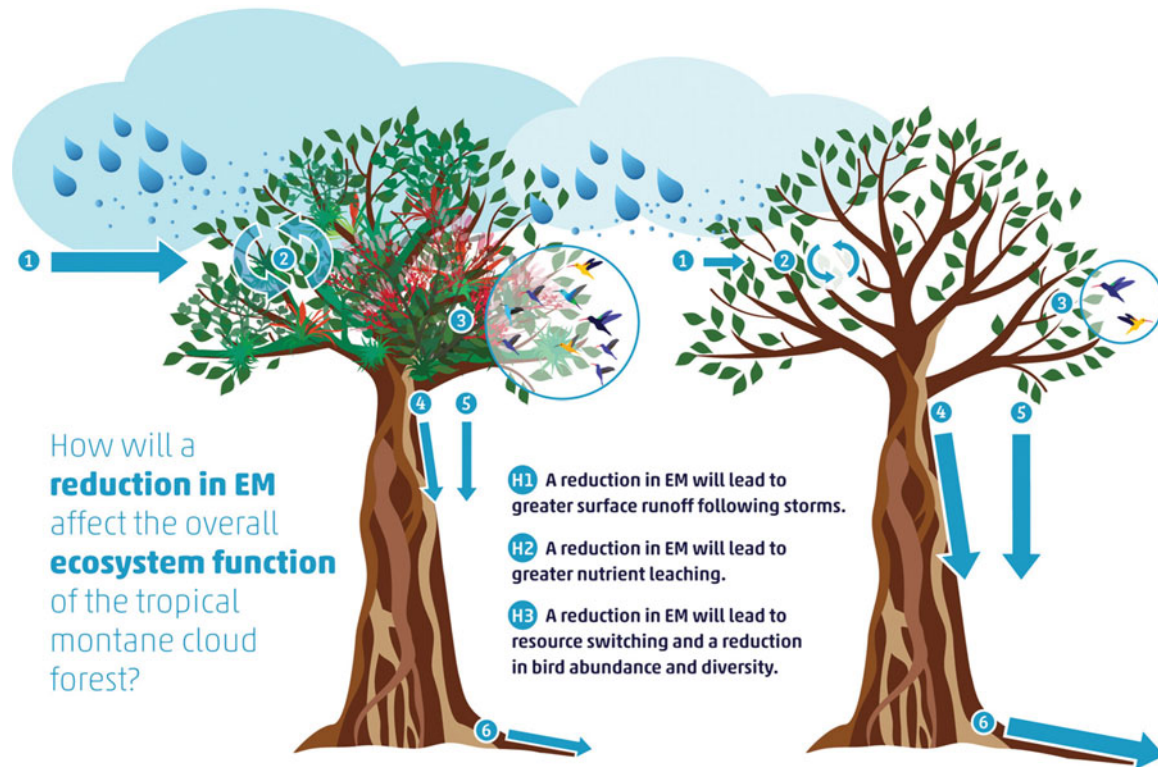


Figure 1. Ecosystem roles of epiphytic materials (EM, left tree) and the hypothesized reduction in ecosystem services due to a loss of EM (right tree). Water and nutrient deposition (1), water cycling and nutrient retention (2), and food resources and habitat are all reduced in the absence of EM. Decreases in interception and cycling due to a loss of EM will lead to an increase in stem flow (4, right) and throughfall (5, right) in disturbed EM communities and eventually lead to increases in surface run-off (6, right). These changes in ecosystem function can have large-scale impacts on the tropical montane cloud forest ecosystem.

dynamic nature of EM – which turns over rapidly due to short life spans relative to trees – allows it to move the allochthonous nutrients (ions derived from outside the ecosystem, e.g. in rain or mist) it impounds from the canopy to ground-dwelling members of the ecosystem via throughfall, stemflow and litterfall (Figure 2; Nadkarni & Matelson 1991). EM components – particularly non-vascular epiphytes and canopy soils – have a high water-storage capacity and can retain water intercepted by vascular plants in the canopy (Hölscher *et al.* 2004, Köhler *et al.* 2007). EM also supports organisms that fix nitrogen (N) (Forman 1975), which enhances the total nutrient pool available to components of EM and to the forest as a whole. The micro-environment of canopy soils in TMCFs can be highly acidic, which suppresses microbially mediated activities such as nitrification, creating less mobile forms of ions, and thus a more nitrogen-retentive environment (Vance & Nadkarni 1990). Both live and dead EM components provide food and habitat resources for a great number of birds and arboreal mammals (Nadkarni & Matelson 1989, Remsen & Parker 1984). All of these elements, then, create a canopy subsystem that is independent but related to the forest as a whole (Carroll 1980).

TMCFs are dynamic habitats that are subject to natural disturbances such as wind and hurricanes (Gannon & Martin 2014, Lawton *et al.* 2001, Pounds *et al.* 1999). Increasingly, disturbance is caused by human activities, such as harvesting of trees and secondary forest products, conversion to agriculture and climate change. These activities can also cause a reduction in or loss of the important ecosystem functions that the EM provide to the TMCF ecosystem. The rate of recovery of diversity and biomass of epiphytes following clearing on canopy-level branches is very slow. A study in Monteverde, Costa Rica documented that recovery of the EM community took on the order of two to three decades, indicating that even though canopy plant communities appear to be lush and resilient, physical disturbance can have extremely long-term impacts (Nadkarni 2000). Without healthy communities of EM, or with reduced EM vitality, these inputs and resources could be lost or reduced, resulting in less productive and efficient systems that are biologically less active and resilient (Figure 1).

Epiphytic communities in old-growth forests also tend to be far more abundant and diverse than those in recovering or secondary forests following disturbance. One study that directly compared epiphytic communities

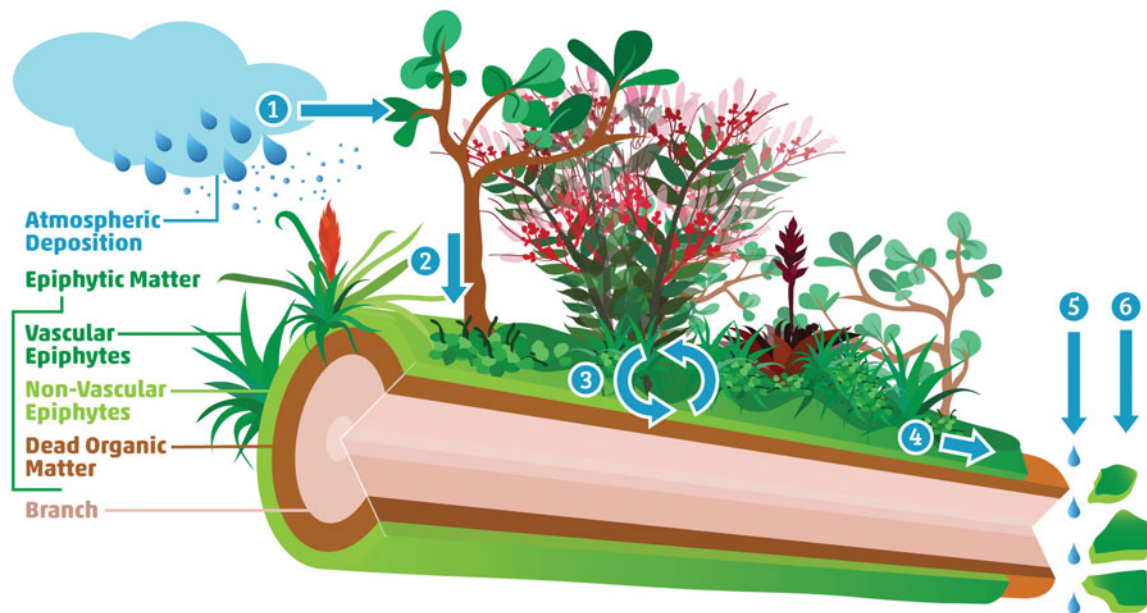


Figure 2. Pathways of water and nutrients through EM. Water and nutrients enter EM largely through the interception of wet deposition of water and nutrients (1). Intercepted moisture and nutrients enter EM via epiphytic throughfall and stemflow of vascular epiphytes (2), which can then be immobilized or recycled within the dead components of EM or taken up and stored in live EM components (3) or travel over or within the EM substrate as stemflow of host trees (4). Intercepted materials can also be moved to other ecosystem components via host tree throughfall (5) or through litter fall of EM that falls on its own or rides down on falling branches and trunks (6).

in old growth and 40-y-old secondary forests in the Dominican Republic found epiphyte life-form diversity, species richness, and abundance were strikingly higher in old-growth forests (e.g. arborescent ferns, palms, epiphytic bromeliads, orchids and bryophytes) (Martin *et al.* 2004).

EM and the functions they provide are likely to be vulnerable to projected changes in climate, as they are largely disassociated from resources on the ground. Nadkarni & Solano (2002) used experimental transplants of upper cloud-forest epiphyte mats to tree canopies at slightly lower altitudes that experience longer dry-season conditions, and documented that vascular epiphytes exposed to drier conditions experienced greater mortality and lower leaf production than control conspecifics exposed to moister conditions. Other researchers have found that epiphytes, despite adaptations to store water and nutrients, are not particularly resistant to the leaf water potentials associated with extended dry periods (Gotsch *et al.* 2015, S. Gotsch, unpubl. data). As the global atmosphere continues to change and as human activities continue to negatively affect epiphytes, EM may be the first biotic indicators of change.

In this paper, we review the literature on the ecological significance of EM in TMCFs. We also include studies from subtropical and temperate forests that receive significant inputs of low-lying clouds or fog as a point of comparison (herein, cloud-affected forests, Mulligan 2010). We focus on three main ecosystem functions: water interception and storage, nutrient interception and storage, and food,

and habitat use by animals (Figure 1). We synthesize our current understanding of the importance of EM to ecosystem function and place that in the context of possible outcomes of changes in EM ecosystem function due to changes in land use and climate.

BIOMASS OF EM

Quantifying the total amount of EM biomass is critical to understanding its role in ecosystem processes. In most mature TMCFs where EM loads are high, canopy soils constitute a large proportion of the dead biomass and nutrient capital that accumulates on nearly all stem surfaces held within the canopy (Hofstede *et al.* 1993, Nadkarni 1984a, Nadkarni *et al.* 2004). In the Monteverde TMCF, canopy soils constituted 63% of total EM biomass in the primary forest, and 3% of EM biomass in the secondary forest.

The biomass of epiphytes and their associated organic matter varies greatly across sites. The lowest estimate of EM (0.5 kg ha^{-1}) was documented for an 8-y-old regeneration site in subtropical cloud forest in the Canary Islands; the greatest EM biomass ($44\,000 \text{ kg ha}^{-1}$) was recorded for a TMCF in Colombia (Hofstede *et al.* 1993, Patiño *et al.* 2009). TMCF old-growth forest sites generally had the highest biomass (mean \pm SE = $25\,670 \pm 5\,730 \text{ kg ha}^{-1}$, $n = 7$) although there was an order of magnitude of variation across the sites (Table 1). Studies that determine biomass per hectare do so by measuring biomass on a

Table 1. Biomass estimates (kg ha^{-1}) of epiphyte communities in cloud-affected forests. Biomass was measured on dried subsamples from dominant canopy trees in the study sites and these values were then scaled up to the stand level (numbers of samples per tree and trees varied across sites). In most cases, all dominant plant functional groups (vascular plants, bryophytes, ferns) were considered as well as dead organic matter or DOM (canopy litter, detritus and arboreal soil). In two cases, only bryophyte groups were considered. In these cases (McCune 1993, Patiño *et al.* 2009) the dominant members of the canopy are bryophytes. The extent to which canopy soil is present in these systems was not reported. We limit our synthesis to those studies that quantify biomass at the stand level.

Biomass (kg ha^{-1})	Altitude (m asl)	Precip. (mm y^{-1})	Temp ($^{\circ}\text{C}$)	Location	Notes	Components considered	Study
0.5	1260	960.2	13.6	Canary Islands	Subtropical cloud forest	Bryophytes only (organic debris removed)	Patiño <i>et al.</i> 2009 (8 y)
7.1	1260	960.2	13.6	Canary Islands	Subtropical cloud forest	Bryophytes only (organic debris removed)	Patiño <i>et al.</i> 2009 (15 y)
200	1480	2970	NA	Costa Rica	Tropical montane cloud forest	Vascular and non-vascular epiphytes, roots and dead organic matter	Nadkarni <i>et al.</i> 2004 (secondary forest)
205	1260	960.2	13.6	Canary Islands	Subtropical cloud forest	Bryophytes only (organic debris removed)	Patiño <i>et al.</i> 2009 (25 y)
1000	725	2450	8.8–9.5	Cascades USA	Temperate rain forest	Different bryophyte groups. No mention of dead organic matter	McCune 1993
1035	1620	4385	16.6	Costa Rica	Tropical montane cloud forest	Bryophyte groups, ferns, bromeliads and other vascular epiphytes, canopy humus (partially or highly decomposed material)	Köhler <i>et al.</i> 2007 (secondary forest)
1253	1260	960.2	13.6	Canary Islands	Subtropical cloud forest	Bryophytes only (organic debris removed)	Patiño <i>et al.</i> 2009 (60 y)
1400	NA	NA	NA	Panama	Premontane	Live and dead epiphytes (in Nadkarni 1984a)	Golley <i>et al.</i> 1971
2130	1415	2860	NA	Tanzania	Submontane rainforest	Leaves of vascular and not vascular epiphytes, stems, alive and dead roots, leaf litter	Pócs 1980
2261	2600	1931	11.3	China	Montane cloud forest	All components of the mat including bryophytes, ferns, lichens, litterfall and canopy humus	Chen <i>et al.</i> 2010
2600	2475	2080	15.5	Ecuador	Lowland montane forest	Bryophytes, macrolichens, pteridophytes, angiosperms and dead organic material (canopy humus and epiphyte litter)	Werner <i>et al.</i> 2012 (ravine)
2600	2900	2812	10.9	Costa Rica	Montane oak forest (Talamanca)	Vascular epiphytes, mosses, liverworts, lichens and humus	Hölscher <i>et al.</i> 2004
2600	725	2450	8.8–9.5	Cascades USA	Temperate rain forest	Different bryophyte groups. No mention of dead organic matter.	McCune 1993
2870	2900	2812	10.9	Costa Rica	Montane oak forest (Talamanca)	Vascular epiphytes, mosses, liverworts, lichens and humus	Hölscher <i>et al.</i> 2004
3360	900	3600	18.2	North-east Taiwan	Moist evergreen subtropical forest	Bryophytes, filmy ferns, bird's nest ferns, all other ferns, epiphytic vines, hemi-epiphytic vines, angiosperms, accumulated detritus and suspended soil	Hsu <i>et al.</i> 2002

Table 1. Continued.

Biomass (kg ha ⁻¹)	Altitude (m asl)	Precip. (mm y ⁻¹)	Temp (°C)	Location	Notes	Components considered	Study
3400	2900	NA	NA	Costa Rica	Tropical montane cloud forest	Total epiphyte mass and canopy humus	Köhler <i>et al.</i> 2007
4350	972	NA	NA	Puerto Rico	Elfin cloud forest	Total epiphyte mass and canopy humus (from Köhler <i>et al.</i> 2007)	Weaver 1972 (ridgetop)
4400	2475	2080	15.5	Ecuador	Lowland montane forest	Bryophytes, macrolichens, pteridophytes, angiosperms and dead organic material (canopy humus and epiphyte litter)	Werner <i>et al.</i> 2012 (forest)
4730	1700	3100	NA	Costa Rica	Elfin cloud forest	Bryophytes, vascular plants, ferns and organic material	Nadkarni 1984a
4750	972	NA	NA	Puerto Rico	Elfin cloud forest	Total epiphyte mass and canopy humus (from Köhler <i>et al.</i> 2007)	Weaver 1972 (leeward)
6300	2475	2080	15.5	Ecuador	Lowland montane forest	Bryophytes, macrolichens, pteridophytes, angiosperms and dead organic material (canopy humus and epiphyte litter)	Werner <i>et al.</i> 2012 (slope)
6900	NA	3550	NA	Olympic National Park	Temperate rain forest	Bryophytes, vascular plants, ferns and organic material	Nadkarni 1984b
7360	972	NA	NA	Puerto Rico	Elfin cloud forest	Total epiphyte mass and canopy humus (from Köhler <i>et al.</i> 2007)	Weaver 1972 (windward)
12,000	3370	1453	NA	Colombia	Tropical montane cloud forest	Bryophytes, dead organic matter and lichens	Veneklaas 1990
14,000	2120	NA	NA	Tanzania	Elfin cloud forest	Leaves of vascular and not vascular epiphytes, stems, alive and dead roots, leaf litter	Pócs 1980
16,215	1490	6000	17	Costa Rica	Tropical montane cloud forest	Bryophyte groups, ferns, bromeliads and other vascular epiphytes, canopy humus (partially or highly decomposed material)	Köhler <i>et al.</i> 2007 (old-growth forest)
32,000	1200	3690	15	Costa Rica	Tropical montane cloud forest	Bryophytes, ferns, herbs, bromeliads, woody plants, lianas or hemiepiphytes and canopy humus.	Hager & Dohrenbush 2011 (1200 m asl)
33,100	1480	2970	NA	Costa Rica	Tropical montane cloud forest	Bryophytes, vascular plants (stems, leaves, reproductive parts, roots), ferns and dead organic matter	Nadkarni <i>et al.</i> 2004 (primary forest)
39,000	1450	6390	16.2	Costa Rica	Tropical montane cloud forest	Bryophytes, ferns, herbs, bromeliads, woody plants, lianas or hemiepiphytes and canopy humus.	Hager & Dohrenbush 2011 (1450 m)
44,000	3700	1250	2-6	Colombia	Tropical montane cloud forest	Living green epiphytic matter (bryophytes, lichens, ferns, angiosperms), living non-green matter (shoots, roots) and dead material (litter, canopy humus and plant organs)	Hofstede <i>et al.</i> 1993

number of branches or trees and then scale up values based on stand basal area. Such scaling may introduce potentially large errors into these estimates.

This synthesis also indicates that the EM takes decades to accumulate after disturbance and that the forests with higher EM biomass are likely to take even longer to reach such levels. For example, in the Canary Islands, only 0.5 kg ha⁻¹ of EM accumulated after 8 y of recovery and that number rose to 205 kg ha⁻¹ after 25 y. In the span between 25–60 y of regeneration, EM biomass accumulated exponentially (from 205 to 1253 kg ha⁻¹, Patiño *et al.* 2009). In the wetter TCMF of Monteverde Costa Rica, EM biomass in a ~40-y secondary forest was 200 kg ha⁻¹, whereas EM in the old-growth forest was over two orders of magnitude greater (Table 1, Nadkarni *et al.* 2004).

WATER-HOLDING CAPACITY OF EM

The large surface area of canopy epiphytes and the high water-storage capacity of bryophytes and canopy soils in the TCMF can lead to overall high canopy water storage. For example, in Costa Rica, mosses in the TCMF have been documented to have a water-holding capacity of over 400% of their dry weight (Hölscher *et al.* 2004, Köhler *et al.* 2007). In an extreme case, a tropical cushion moss species, *Octoblepharum pulvinatum*, has a water-holding capacity of ~7000% its dry weight (Wagner *et al.* 2014). At the stand level, the average of point estimates of water-storage capacity across all studies is 2.2 ± 0.8 mm. The maximum water-storage capacity of EM varies from 0.81 mm in a tropical montane rain forest in the Talamanca Mountains of Costa Rica, to 5.0 mm in a mossy elfin forest in Tanzania (Hölscher *et al.* 2004, Pócs 1980) (Table 2).

The importance of EM to total canopy interception is likely to vary greatly depending on the dominant components of EM (bryophytes versus vascular epiphytes) and rainfall patterns (Hölscher *et al.* 2004, Pócs 1980). Only one study quantified the water-storage capacity of vascular and non-vascular components of the EM (Pócs 1980). Water-storage capacity was within the range of that documented in bryophyte-dominated systems (Table 2). Future work is needed to quantify the water storage of different components of the EM, especially in wetter TCMFs, which have high biodiversity and biomass. These sites tend to have vascular epiphytes with specialized leaf and stem adaptations for water storage, which may play an important role in canopy water storage (Gotsch *et al.* 2015, Ogburn & Edwards 2010).

Although the capacity for water storage by EM may be high, the realized water storage will depend on rainfall dynamics and canopy microclimate at each site. If the EM remains close to saturation at the time of a rainfall event, then little to no additional water storage will be

realized. In the Talamanca region of Costa Rica, Hölscher *et al.* (2004) found that despite a considerable maximum storage capacity, modelling results suggest that mosses contribute just 6% of total interception due to their generally high saturation. While consistent rainfall inputs may be the case in some sites, microclimate in the TCMF is often variable (Holwerda *et al.* 2010, Ritter *et al.* 2009). Köhler and colleagues found that during a 3-d period without rainfall, maximum water loss was 251% of dry weight for bryophytes and 117% for canopy humus (Köhler *et al.* 2007). In TCMFs with more variability and seasonality in precipitation, EM will have a larger role in forest water-holding capacity.

Changes in climate such as increases in cloud-base heights and precipitation patterns may increase dry periods and thereby alter water storage dynamics of EM. In the TCMF of Monteverde, Costa Rica, over the last 40 y, researchers have documented changes in climate that include increased variability in annual precipitation and total rainfall and an increase in the number of days without rain on an annual basis, and the number of 3–5-d periods without precipitation (Pounds *et al.* 1999, A. Pounds, unpubl. data). In this region, storm size is increasing. Large rain events may quickly saturate the EM and terrestrial soils and less of the total water in each event will be available to the forest as a whole since more will be lost as run-off. Increases in drought events may also lead to water stress in EM, leading to changes in species composition and biomass, which will in turn also affect water-storage capacity.

NUTRIENT POOLS AND FLUXES OF EM

Nutrient pools

Nutrients within the EM have only rarely been quantified, due to difficulties with canopy access and because the spatial complexity (three-dimensional irregular topography of tree surfaces) of EM makes statistical analysis difficult (Affeld *et al.* 2008, Gradstein *et al.* 2003). Several studies have compared nutrient content of terrestrial and epiphytic vegetation (Cardelús & Mack 2010, Hietz *et al.* 2002, Nadkarni *et al.* 2004). One study assessed the biomass and nutrient capital of EM and terrestrially rooted components of a primary and an adjacent secondary montane forest in Monteverde, Costa Rica (Nadkarni *et al.* 2004, Table 3). The latter study also compared the nutrient capital held in labile portions (i.e. those elements that are rapidly decomposed, including foliage and small stems) vs. non-labile elements (large stems, bark, trunk) of the EM vs. the terrestrially rooted material in the primary and secondary forest. The ratios were 4.4:1 in the primary forest and 0.05:1 in the secondary forest, indicating a much larger proportion of

Table 2. Water retention and maximum water content of epiphyte communities in cloud-affected forests. In the Pócs (1980), Zotz *et al.* (1997), Wagner *et al.* (2014) and Pypker *et al.* (2006) studies, maximum water content was determined as the difference between the saturated epiphyte mat weight and the fresh weight of the mat. In the Hölscher *et al.* (2004) and Köhler *et al.* (2007) experiments, the fresh and dry weight of moss mats were determined at different times of the year. In these two cases, the maximum water content was the greatest percentage of fresh to dry weight measured throughout the year.

Stand-level Water Retention (mm)	Maximum Water Content	Altitude (m asl)	Location	Components Measured	Notes	Study
1.5	NA	1415	Tanzania	all epiphytes and humus	submontane rainforest	Pócs 1980
5	NA	2120	Tanzania	all epiphytes and humus	mossy elfin forest	Pócs 1980
NA	4000%	1100	Panama	pendant moss	lower montane rainforest	Zotz <i>et al.</i> 1997
NA	2500%	1100	Panama	cushion moss	lower montane rainforest	Zotz <i>et al.</i> 1997
NA	~7,000%	NA	NA	cushion moss	Unpubl. data	Wagner <i>et al.</i> 2014
0.81	406%	2900	Talamanca Costa Rica	bryophytes and humus only	tropical montane cloud forest	Hölscher <i>et al.</i> 2004
1.2	NA	NA	Oregon, USA	bryophytes and humus only	temperate cloud forest	Pypker <i>et al.</i> 2006
4.4	418%	1490	Monteverde Costa Rica	bryophytes and humus only	tropical montane cloud forest	Köhler <i>et al.</i> 2007 (old-growth forest)
0.36	NA	1620	Monteverde Costa Rica	bryophytes and humus only	tropical montane cloud forest	Köhler <i>et al.</i> 2007 (secondary forest)

Table 3. Nutrient capital of epiphytes in TMCFs. Amounts of mineral capital in epiphytes in proportion to ecosystem components of cloud forest ecosystems. Amounts of mineral capital of total above ground and of foliar components are given in kg ha⁻¹. Proportions of stand-level epiphyte mineral capital estimates (in parentheses) are expressed as a percentage of ecosystem components.

Forest type and component	N	P	K	Ca	Mg
New Guinea upper montane					
Total above-ground mineral capital	770.0 (0.08)	46.5 (0.03)	682.0 (0.02)	713.0 (0.04)	192.2 (0.01)
Foliar mineral capital	117.5 (0.49)	7.4 (0.22)	80.9 (0.15)	105.7 (0.08)	25.8 (0.08)
Jamaica Lower montane					
Total above-ground mineral capital	432.0 (0.13)	25.9 (0.06)	259.2 (0.05)	432.0 (0.02)	159.0 (0.01)
Foliar mineral capital	78.7 (0.73)	4.2 (0.38)	41.1 (0.30)	46.5 (0.19)	24.8 (0.08)

available nutrients are held in the primary-forest EM than in the secondary-forest EM.

Canopy soil in TMCFs is of special interest in assessing the functional roles of EM because of its capacity to capture incoming nutrients by storing them on its negatively charged sites and its large pool of organically bound nutrients (Lesica & Antibus 1991, Nadkarni & Longino 1990, Vance & Nadkarni 1990, Veneklaas 1992). These arboreal soils are histosols (dominated by organic materials, Bohlman *et al.* 1995, Nadkarni *et al.* 2002) and are derived from decomposing live epiphytes and canopy biota and ions intercepted from wet and dry deposition and throughfall (Coxson & Nadkarni 1995).

Intercanopy nutrient fluxes

Nutrient inputs for EM may be autochthonous (intercepted host tree litter, throughfall and stemflow) or allochthonous (ions derived from outside the ecosystem, e.g. in rain or mist). From the standpoint of ecosystem function, it is important to distinguish between those two source types. If epiphytes obtain all of their nutrients from autochthonous sources, then they would simply be diverting nutrients from the tree to the ground flux pathway for some length of time and not increasing the total nutrient pool. Alternatively, if they were to sequester nutrients from outside the system, this would potentially

increase the total nutrient input to the ecosystem in addition to altering the form and location of these new nutrients (Nadkarni & Matelson 1991, Figure 2). However, we have found no studies that have documented the degree to which nutrient input to EM derives from these two sources.

However, atmospheric deposition has been documented as one of the major avenues for input of new nutrients in TMCF ecosystems (Clark *et al.* 1998a, Stewart *et al.* 1995). Tobón *et al.* (2010) noted relatively long residence times of ions in cloud water and mist captured by epiphytic bryophyte mats, facilitating nutrient retention. In the TMCF of Monteverde Costa Rica, per cent net retention of nitrate and ammonium by the canopy was 80% and 61%, respectively, indicating that a large majority of the inorganic N in atmospheric deposition was retained by the canopy for some length of time, although the intervals of this dynamic have not been measured (Clark *et al.* 1998b). Clark *et al.* (2005) developed a canopy model driven with hourly meteorological and event-based atmospheric deposition data to estimate inorganic N retention from atmospheric deposition by canopy components. They estimated net retention of inorganic N by samples of four components of canopy communities: (1) epiphytic bryophytes, (2) epiphyte assemblages (small vascular epiphytes, intercepted litter and canopy soils), (3) large vascular epiphyte foliage and (4) host-tree foliage. Samples of each component were exposed in situ to artificial cloud water and precipitation solutions that mimicked field concentrations. Leaching experiments indicated that NO_3^- was strongly retained by and incorporated into epiphytic bryophytes, but not by the foliage of large vascular plants. Net retention of NH_4^+ by epiphytic bryophytes and epiphyte assemblages was somewhat lower, and reflected the internal cycling of NH_4^+ in canopy soils. With a multi-layered model of the canopy, they determined epiphytic assemblages retained 33–67% of the inorganic N deposited in cloud water and precipitation (annually, $3.4 \text{ kg N ha}^{-1} \text{ y}^{-1}$, c. 50% of the inorganic N in atmospheric deposition, $6.8 \text{ kg N ha}^{-1} \text{ y}^{-1}$). Thus, in this TMCF, epiphytic bryophytes play a major role in N retention and cycling in the canopy by transforming highly mobile inorganic N (c. 50% of atmospheric deposition is NO_3^-) to less mobile (exchangeable NH_4^+) and recalcitrant forms in biomass and remaining litter and canopy humus. Nitrogen fixation may be an important allochthonous source of N for TMCF epiphytes, either by above-ground adventitious roots (e.g. *Alnus* sp.) (Murcia 1997) or, more commonly, by symbiotic and lichenized N fixation (Forman 1975).

A potential autochthonous source to epiphyte communities is abscised plant litter that is intercepted within the tree canopy by inner branches and their epiphytes. The decomposition and mineralization of nutrients from abscised canopy foliage may differ from

that on the forest floor. For example, in the Monteverde TMCF, Nadkarni & Matelson (1991) quantified the amounts of nutrients in litterfall that are stored within the canopy and then released via decomposition and mineralization. Decomposition rates of tethered leaves within the canopy were half that of leaves on the forest floor (turnover time in the canopy = 2.7 y vs. 1.7 y on the forest floor). Inputs from intercepted host-tree litterfall appeared to be small relative to the productivity of epiphytes, which suggested that epiphytes rely on other sources of nutrients.

Nutrient release and uptake

Nutrients from live and dead EM are released into the nutrient cycles of whole forests when: (1) EM falls to the forest floor (via senescence, wind, disruption by birds and mammals), dies and decomposes; (2) EM is leached by precipitation and moved via stemflow and throughfall; and (3) epiphyte and host tree canopy roots take up nutrients within the canopy (Figure 2). Nearly all litterfall studies have focused on the biomass and nutrient composition of fine litter derived from terrestrially rooted plants, but in TMCFs, EM litterfall can constitute a potentially significant nutrient transfer pathway (Songwe *et al.* 1988, Tanner 1980). In Monteverde, for example, EM input constituted c. 15% of total litterfall biomass and nutrient input to the forest floor, but it was deposited more sporadically in time and less regularly in space than terrestrially rooted litterfall (Nadkarni & Matelson 1992). Major disturbance events such as hurricanes (which occur in some TMCFs) may be critical. Future research should differentiate the sources of litterfall (epiphytic vs. host tree foliage) in TMCFs that are affected by hurricanes and other major storms.

Direct uptake of nutrients can also occur from adventitious roots from dead organic matter in the canopy. Canopy rooting is a widespread phenomenon in diverse taxa, including common neotropical TMCF families Lauraceae, Flacourtiaceae and Cunoniaceae (Herwitz 1986, Nadkarni 1981). In the Monteverde Cloud Forest, fine-root biomass in canopy soils of canopy branch junctions was 20% higher than comparable organic soil horizons on the forest floor, although the amount of host tree canopy roots relative to epiphytic roots was not reported (Vance & Nadkarni 1992). The importance of mycorrhizal fungi to plant nutrition and seedling establishment in low-nutrient environments has been demonstrated in TMCF canopy environments (Maffia *et al.* 1993, Rains *et al.* 2003). Hertel *et al.* (2011) suggested that canopy roots of trees in an upper TMCF oak forest, though common and showing an abundance of endophytic fungi, lacked mycorrhizal colonization. These canopy roots appeared not to be important, as they

showed a reduced ability for nutrient acquisition relative to terrestrial roots. Surveys of canopy plants are needed to ascertain the extent of mycorrhizas and other symbionts in canopy microhabitats.

Epiphytes move physically from the canopy to the forest floor when they are dislodged by wind or animals, or because their associated branches break and fall (Strong 1977). Some epiphytes die, decompose and vanish quickly, while others can survive for months or even years (Matelson *et al.* 1993). Implications for nutrient cycling are that before nutrients can be released, the live plants must die, so fallen EM affects nutrient cycling differently than tree and shrub litterfall, which has already senesced (and has often undergone retranslocation) before arriving to the forest floor, ready for nutrient release. Little has been quantified concerning epiphyte decomposition, but results from one study indicate that certain components of EM decompose very rapidly (e.g. bryophytes, turnover = 0.23 y), while others decompose very slowly (e.g. canopy soils, turnover = 3.6 y) (Nadkarni & Matelson 1991).

Leaching and throughfall

An extensive literature on nutrient transfer via crown-wash in whole forests exists (reviews in Bruijnzeel & Proctor 1995, Cavelier *et al.* 1997). For canopies where vascular plants dominate, nutrient loss from the canopy is largely due to the re-suspension of surface-deposited nutrients (dry deposition) and from exchange processes between surface water films and mesophyll cells (Scott & Hutchinson 1987). In TMCF, where non-vascular and vascular epiphytes co-occur, both processes may be co-occurring, but more research is needed on these processes (Figure 2).

EM RESOURCES FOR ANIMALS

The Food and Agriculture Organization of the UN describes TMCFs as comprising only a portion of the 1.6% of the world's closed tropical forests, yet they provide habitat for numerous vertebrate and invertebrate species, many of which are endemic (Aldrich *et al.* 2000, <https://portals.iucn.org/library/node/7809>). EM facilitates the existence of animal diversity because it provides food, water and habitat resources (Ackerman 1986, Céréghino *et al.* 2010, Hietz & Winkler 2006, Wilson 1988). With the increasing pressure of land-use and changes in climate, it is critical to identify the relationships between EM and the animals that interact with them. Little research on invertebrate use of EM in TMCFs exists, with some exceptions (Nadkarni & Longino 1990). We focus here on the interactions of birds and mammals with EM in the TMCFs of Costa Rica to illustrate

the significance of EM for animals, which provide the most complete set of relevant data (Nadkarni & Matelson 1989, Nadkarni & Wheelwright 2000, Sillett 1994).

Epiphyte foraging and fruit dispersal

Research on bird use of EM has been studied by Nadkarni & Matelson (1989) and Sillett (1994), and provides the most complete studies exploring the importance of EM for survival of animal populations. In Monteverde, of the 33 bird species studied, 59% used epiphyte food resources, which were primarily hummingbirds, tanagers and flycatchers (Nadkarni & Matelson 1989). In the Talamanca Mountains, birds used EM and epiphytes by foraging on the undersides of branches, probing epiphytes and bark surfaces, and feeding on epiphytic fruits (Sillett 1994). Many bird species were documented as epiphyte-specialists, species using epiphytes for at least 75% of their foraging time (Sillett 1994). For example, the buffy tuftedcheek (*Pseudocolaptes lawrencii*) spent 74% of its time foraging in bromeliads, often pulling out and tossing leaf litter to reveal food items. For birds foraging in flowers, epiphytic flowers were used more frequently than flowers of the host trees (Nadkarni & Matelson 1989). Because of this frequent use of epiphyte resources by birds, the resource pool available to birds in tropical systems might be underestimated. Further studies are needed to estimate the resource pool for birds in TMCF ecosystems (Nadkarni & Matelson 1989).

In a Costa Rican TMCF, pollinating and dispersing animals appear to provide critically important vectors for epiphyte pollen and seed dispersal accounting for 62% of the epiphyte species studied (Figure 3), thereby contributing to sustaining healthy epiphyte populations. While these species do not take into account abundant species such as ferns and orchids, which do not use animal dispersers, fruiting species are also common and abundant and clearly provide an important resource to animals in the TMCF. Many epiphyte species and their pollinators and dispersers have highly specific relationships with animal dispersers (Fontoura *et al.* 2010). Additionally, epiphytes and EM provide critically important habitat and food resources, which are especially important during times of the year when trees and shrubs are not flowering and fruiting. Research in other TMCFs on the relationships between EM and vertebrates are needed to understand the impacts and importance of EM.

PRIORITIES FOR FUTURE RESEARCH

We suggest six areas for future research on EM in TMCF which include: (1) more process-oriented studies,

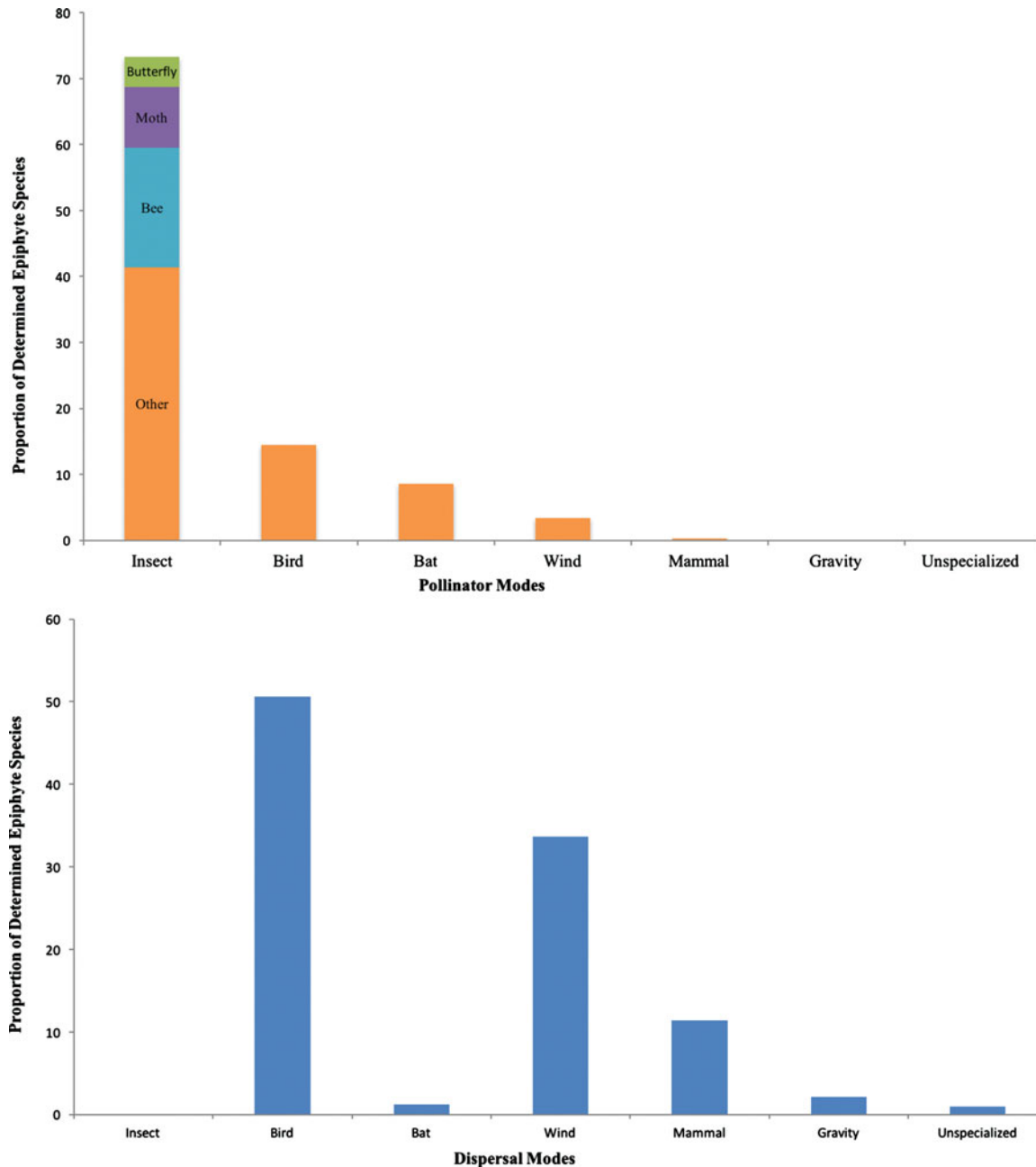


Figure 3. Proportion of determined epiphyte species and their vertebrate and invertebrate pollinators and dispersers studied in TMCF of Costa Rica. The upper graph represents pollinator modes and the lower graph represents fruit and seed disperser modes. Insects, birds and bats were the three most important pollinator modes, whereas, birds, wind and mammals were found to be the three most important dispersal modes. Sample sizes (number of epiphyte species) for each pollinator and dispersal mode are shown in the graph. While these species do not take into account abundant species such as ferns and orchids, which do not use animal dispersers, fruiting species are also common and abundant and clearly provide an important resource to animals in the TMCF. This data was drawn from three publications, including Cascante-Marín *et al.* (2005), Appendix 1 (Haber) in Nadkarni & Wheelwright (2000), and Bush & Beach (1995).

particularly with respect to water interception and uptake by epiphytes, and retention by canopy soils; (2) the development of standardized measurements of canopy nutrient and water cycling so that measurements can be compared between sites and studies; (3) define the

limits of scaling from within-tree to ecosystem- and landscape-level spatial scales, using statistically sound techniques and an understanding of the distribution of variability within and across sites; (4) additional experimental work (drought experiments, fertilization studies,

removal experiments) to determine water and nutrient limitation as well as vulnerability to projected changes in climate; (5) establish long-term studies to quantify epiphyte growth, disturbance, death and recolonization rates; and (6) initiate simultaneous studies in a wide range of TMCF to generate a broadly based and comparable pool of data on EM and its effects in TMCF systems.

CONCLUSIONS

Epiphytes flourish in TMCFs. In the past three decades, exciting changes in canopy research approaches have informed our knowledge of canopy communities and their roles in ecosystem function. Research has shifted from autecological studies on individual organisms to ecosystem-level studies on the complex ways by which the canopy influences the processing of nutrients, water and light, enhancing our understanding of dynamics in primary forests and identifying potential effects of canopy disturbance or removal due to natural and human activities.

EM derives a significant fraction of water and nutrition from atmospheric sources, and provides animals with considerable resources including food, water, nesting materials and habitat. Evidence has demonstrated that the presence of EM can result in the interception and retention of atmospheric nutrients, which are subsequently cycled to other ecosystem members via multiple dynamic pathways. This enhancement of allochthonous water and nutrients may more speedily swell and maintain nutrient reserves of the ecosystem as a whole than if the epiphytes were absent or reduced in abundance.

An emerging concept from this and other reviews is that EM contributes significantly to ecosystem function. EM may even play keystone roles (*sensu* Terborgh 1986) providing critical plant resources during lean times of the year that maintain the carrying capacity of bird frugivores and foragers. Although EM makes up a small or unapparent portion relative to the total biomass of the forest, the resources they produce augment those of host trees, and their dependent organisms appear to depend upon these resources in other systems (Boucher & Nash 1990, Knops *et al.* 1991). Although EM is clearly an important component of the TMCF ecosystem function, future research is needed to determine the vulnerability of the EM to changes in precipitation patterns and cloud base heights as well as the effects that any changes in EM communities will have on TMCF ecosystem function.

ACKNOWLEDGEMENTS

We acknowledge financial support from the National Science Foundation to the CloudNet Research Coordin-

ation Network (PIs Patrick Martin, Heidi Asbjornsen, Thomas Giambelluca, and Kenneth Young) who helped to guide the direction of this review. We acknowledge financial support from Franklin and Marshall College and the University of Utah. We are grateful for insightful comments from associate editor, Patrick Martin and two anonymous reviewers.

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