

Epiphytes improve host plant water use by microenvironment modification

Daniel E. Stanton^{*,1,2,3}, Jackelyn Huallpa Chávez⁴, Luis Villegas⁴, Francisco Villasante^{4,5}, Juan Armesto^{6,7}, Lars O. Hedin¹ and Henry Horn¹

¹Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA; ²Plant Science Division, Research School of Biology, The Australian National University, Canberra, ACT 0200, Australia; ³Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108, USA; ⁴Instituto Regional de Ciencias Ambientales, Universidad Nacional San Agustín, Arequipa, Perú; ⁵Departamento de Ecología, Universidad Nacional San Agustín, Arequipa, Perú; ⁶Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago, Chile; and ⁷Institute of Ecology and Biodiversity (IEB), Santiago, Chile

Summary

1. Epiphytes have the potential to modify the canopy environments in which they grow. Accurately evaluating the impact of epiphytes can be challenging, since plants without epiphytes may also otherwise differ from host plants, and experimental removal is impractical and difficult to replicate in many forests.
2. We studied the impacts of epiphytes (primarily fruticose lichens and *Tillandsia* spp.) on host plants (*Eulychnia saint-pieana* and *Caesalpinia spinosa*) in two fog ecosystems in Chile (Pan de Azucar) and Peru (Atiquipa). These desert ecosystems sustain very high epiphyte loads and depend heavily on fog-water inputs. Using a combination of artificial substrates and epiphyte removals, we show significant impacts of epiphytes on their host plants.
3. The presence of epiphytes reduced throughfall volumes, reducing fog and rainfall inputs to the soil beneath host plant canopies.
4. Soil moisture loss rate was increased below cacti after removal of epiphytes from sun-facing but not shade-facing branches. This suggests epiphyte effects on hosts are microclimatic.
5. Epiphytes also buffered temperature fluctuations and reduced daytime vapour pressure deficit.
6. Epiphytes can have strong effects on host plant ecophysiology and forest ecosystem processes, making them an important component for models and studies of canopy environments.

Key-words: canopy, desert, epiphyte, fog, microclimate, VPD

Introduction

Epiphytes are a common occurrence in ecosystems with perennial plants. They are thought to have been a successful life strategy since the appearance of trees in the late Devonian and Carboniferous (Dilcher *et al.* 2004) and to have convergently evolved in a large number of lineages of vascular and non-vascular plants (Gentry & Dodson 1987). Despite their high abundance in many ecosystems, the effects of epiphytes on ecosystem processes are still poorly understood. Traditionally, epiphyte ecology has focused on the ecology of the epiphytes themselves, focusing on questions such as biodiversity patterns and microclimatic preferences (Johansson 1974; Benzing 1990; Hsu & Wolf 2009; Gehrig-Downie *et al.* 2011). However, the

considerable biomass and volume of epiphytes present in many forests is such that they are also of functional importance to the forest itself (e.g. Benzing 1990; Lowman & Rinker 2004; Nadkarni *et al.* 2004).

Epiphytes can influence the water economy of their host plants. In this study, we concentrate on the biophysical effects of epiphytes on whole host plant water relations. We can only fully account for epiphyte effects on host plants if we examine their impact not only on water input, but also on canopy microclimate, and thus on host plant transpiration and water use (Fig. 1). The net effect of epiphytes on the system is best understood as a water mass balance for individual trees that is influenced by epiphytes in terms of both inputs and outputs.

This mass balance differs from most plant ecophysiology models (e.g. Rodríguez-Iturbe & Porporato 2004) in the inclusion of a fog-water input. This inclusion is motivated

*Correspondence author. E-mail: stan0477@umn.edu

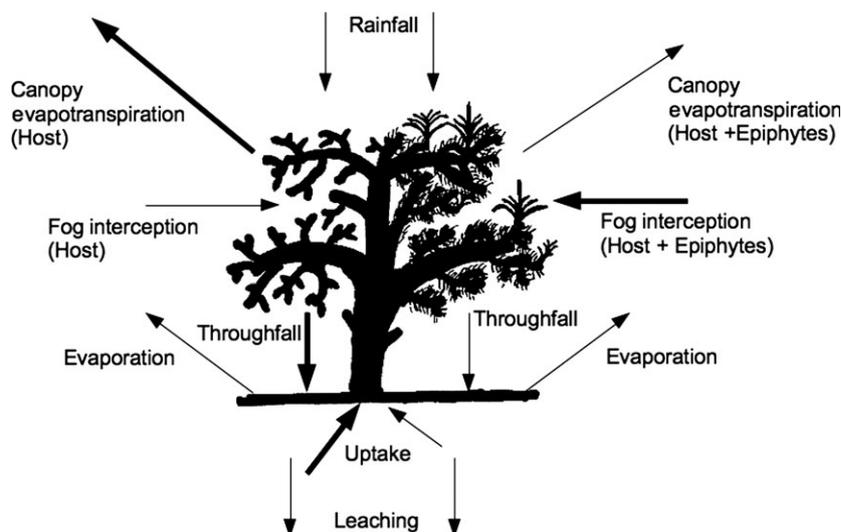


Fig. 1. Schematic of the water cycle through trees in the absence (left) or presence (right) of epiphytes. Epiphytes will directly affect fog interception by the canopy (by increasing surface area) and canopy evapotranspiration rates (by increasing boundary layer). Greater retention of water in the canopy by epiphytes results in reduced throughfall.

by the high prevalence of epiphytes in foggy ecosystems, where canopy surface area, a property directly impacted by epiphyte presence, drives water inputs.

Fog-water input differs from rainwater in its direct dependence on vegetation structure. At the local scale, rainfall is unaffected by the vegetation present, and water inputs to soil are negatively correlated with canopy retention. Fog, on the other hand, will not deposit any moisture unless a structure is present to intercept it. The presence of plant-like surfaces is sufficient to intercept fog water and increase nearby soil moisture (Stone 1957; Ellenberg 1959). Unlike atmospheric moisture absorption, fog-water collection is a physical process of interception (Villegas, Tobón & Breshears 2008), more comparable to filter-feeding by aquatic invertebrates than condensation (Larson 1981; Stanton & Horn 2013). As such, the surface area of the intercepting surface, as well as the boundary-layer conditions that it creates, will determine the amount of water intercepted. Interception is often used to describe rainfall retained by the canopy. We find that this commonly used terminology leads to potential confusion in the case of water and fog inputs, and so here we use the term interception exclusively to describe fog/rain harvesting by the canopy, in contrast to retention in the canopy (a storage process).

Large epiphyte loads constitute a significant modification of host branch surface area. Chang, Lai and Wu (2002) and Villegas, Tobón and Breshears (2008) found considerably greater amounts of fog water to be intercepted and retained in the presence of epiphytes. Several studies have found that epiphytes slow and retain throughfall and stemflow in forests (e.g. Veneklaas *et al.* 1990; Pypker, Unsworth & Bond 2006; McJannet, Wallace & Reddell 2007; García-Santos & Bruijnzeel 2010; Holwerda *et al.* 2010; Oyarzún *et al.* 2010). Retained water does not reach the soil and is unavailable to the roots of host plants. The net fog-water input will therefore be a balance of the increased inputs from surface area and the water retention by the corresponding epiphyte biomass.

The effects of epiphytes on host water relations may not be limited to inputs alone. Early work on epiphytes has suggested that wetted epiphytes may reduce transpiration by host branches (Rommel 1922; Phillips 1928). Alterations of canopy temperature (Freiberg 2001) and evaporative demand (Stuntz, Simon & Zotz 2002) have been shown in tropical forests. Water loss rates through transpiration are as important as input rates in the determination of water budget. Even the most efficient water-retaining epiphyte must transpire while photosynthetically active. This water vapour will contribute directly to the relative humidity of its immediate vicinity, in this case within the boundary layer of the canopy in which it is growing. As such, epiphytes do not contribute directly to water losses from the soil, but have the potential to modify canopy microclimate and thus influence losses by host plant transpiration.

The effects of a modified canopy microclimate on the host plant will translate into shifts in water use. More water-use-efficient host plants (as a result of reduced transpiration rates) will have decreased soil humidity draw-down rates. The net action of epiphytes can be interpreted as that of a capacitor, dampening the variance (particularly decreases in atmospheric humidity) in canopy microclimate ('canopy air conditioning' in Stuntz, Simon & Zotz 2002). A more stable, and most likely, moister canopy microclimate will favour host plants in all but frequently saturated conditions.

Given that local environment strongly influences epiphyte communities (Cornelissen & Steege 2009; Larrea & Werner 2010; Gehrig-Downie *et al.* 2011), the use of natural variability in epiphyte communities to determine epiphyte effects is suggestive but not definitive. In contrast, the experimental manipulation of epiphyte cover is logistically problematic given the considerable volume and biomass of epiphytes present in some forest systems. For example, Diaz *et al.* (2010) removed 134–144 kg per tree from three trees in dry mass of epiphytes in a Chilean temperate rain forest. Few replicated epiphyte removal

experiments have been conducted at the whole-plant scale, the notable exception being Knops, Nash and Schlesinger (1996), who conducted extensive epiphyte removal experiments in a California oak woodland and reported considerable changes in throughfall and litter chemistry. However, partial removal of epiphytes from only easily accessible portions of a plant may inaccurately represent the overall effect of epiphytes. An ideal experimental test of the effects of epiphytes requires host plants with non-overlapping canopies, abundant epiphytes and plants small enough for practical replication.

The desert fog oases or lomas of coastal Peru and Chile are striking for their rich plant biodiversity despite very low rainfall (0–200 mm per annum) and often no access to groundwater. The persistence of these diverse communities is attributed to frequent water inputs from coastal fog that far exceed rainfall (Rundel *et al.* 1991; del-Val *et al.* 2006). Less discussed is the presence of a considerable epiphyte biomass and diversity (Weberbauer 1945) in quantities proportionally analogous to cloud forest. The low stature of the vegetation (<10 m) and simplified ecohydrology (minimal run-off and leaching, discrete and rare rainfall events) make these ecosystems ideal for plant-scale experiments on the biophysical effects of epiphytes. We circumvented many of the difficulties associated with epiphyte removal by studying these ecosystems with relatively small mature woody plants and non-overlapping canopies, yet high epiphyte abundances. We recorded the effects of epiphyte removal on soil moisture and canopy microclimate dynamics, considering the following predictions: (i) epiphytes will retain water; however, where fog inputs are high, the increased volume intercepted by epiphytes will overcome retention by epiphytes, resulting in greater throughfall in the presence of epiphytes; (ii) increased water inputs will translate into longer periods of soil moisture availability under the host plants; (iii) presence of epiphytes will buffer host plant canopy microclimate, and hence (iv) plants with epiphytes will benefit from greater water-use efficiency and show greater growth and reproduction.

Materials and methods

STUDY SITES

Two field sites were chosen in coastal southern South America, reflecting different levels of fog-water dependence and dominant plant structural complexity. Pan de Azúcar National Park is a 25-year-old national park in the 3rd Region of northern Chile. Mean annual precipitation is recorded as 13 mm (Thompson *et al.* 2003), with considerable interannual variability and nearly all rainfall occurring during El Niño–Southern Oscillation (ENSO) events. The Lomitas sector of the park (S 26°00', W 070°36') sits atop a high coastal ridge facing the Pacific Ocean. Frequent (near-daily) fogs support a desert scrub community dominated by *Euphorbia lactiflora* (Euphorbiaceae) and *Eulychnia saint-pieana* (Cactaceae), a large (3–5 m) columnar cactus (Luebert & Pliscoff 2006). All cacti and shrubs are covered with epiphytic lichens (Fig. 2a).

The Lomas de Atiquipa are a section of the Comuna Campesina de las Lomas de Atiquipa y Taimara in the north of the Province

of Caravelí, Arequipa Department, south-central Peru. This communally managed area contains one of the few remaining lomas forests of coastal Peru (Rundel *et al.* 1991) and is historically known for its diversity and luxuriant vegetation (Macbride 1936; Weberbauer 1945; Raimondi 1948). Rainfall occurs annually; however, total precipitation is much greater during El Niño years and greatly influences vegetation cover (e.g. Rundel *et al.* 1991).

Experimental work was conducted in the Cerro Lloque sector, a 200-ha patch of forest within a grazing enclosure (S 15°14', W 074°22' 955 m). The dominant tree in this semi-open woodland is *Caesalpinia spinosa* (Fabaceae), with rare individuals of *Myrcianthes ferreyrae* (Myrtaceae) and *Carica candicans* (Caricaceae). Within the protected area, nearly all trees and shrubs bear heavy epiphyte loads, predominantly lichens and bromeliads (Fig. 2d).

EPIPHYTE REMOVALS

Epiphyte removals were conducted on dominant woody plant species at both study sites. At Lomitas, five sets of three mid-sized cacti (1–2 m) were chosen. Within each set, individuals were of similar stature, number of columns and landscape position. Due to concerns expressed by park officials that full epiphyte removal might have lethal effects on the cacti, epiphytes were stripped from only half of the columns of each treatment cactus (Fig. 2a). The removal treatments were the following: control (no epiphytes removed), sun removal (epiphytes removed from the north-facing half of the cactus) and shade removal (epiphytes removed from the south-facing half of the cactus). All epiphytes were picked off by hand, breaking off the lichens at the base of their holdfast to avoid damaging the spines on which they grow. Removals were conducted in March 2008, and all removed material was air-dried and weighed. Water saturation potential was estimated by wetting small (0.5–3 g) epiphyte samples and allowing them to dry until no dripping occurred before weighing.

In Atiquipa, three paired trees of 5 m 'tara' (*Caesalpinia spinosa*, Fabaceae) were chosen for epiphyte removals. Both individuals within each pair were of comparable height and landscape position. Treatments consisted in a control (no epiphytes removed, but tree repeatedly climbed to simulate disturbance during removal) and removal (all epiphytes accessible by climbing and ladders were removed). Lichens and moss were removed by hand, avoiding any damage to buds, while *Tillandsia* bromeliads were dislodged with poles. Removals were conducted in June 2009, removed lichens were dried and weighed, and bromeliads were weighed fresh.

ARTIFICIAL STRUCTURES

Artificial cacti were constructed by shaping chicken wire (1-cm mesh) into the shape of a 75-cm-tall individual of *Eulychnia saint-pieana* and covering the frame with tightly bound green plastic sheeting (Fig. 2b). Stainless steel nails were inserted to emulate large spines, and 10-cm pieces of two-mm wire used to imitate the longer thin spines on the crown. Three matched pairs (with or without side arms) of these '*Eulychnia plastica*' were installed near the cliff-edge at Lomitas in May 2008. Within each pair, one individual was covered with epiphytic lichens collected from nearby cacti, entwining the thalli on the nails to ensure they would not blow off (Fig. 2c). A 50-cm dowel was planted in a 15 cm deep hole to anchor the structures, and an identical hole dug and refilled as a control (to account for the impact of soil disturbance).

SOIL MOISTURE

Soil moisture below artificial cacti was recorded using a hand-held TDR probe (CS620; Hydrosense, Campbell Scientific Inc, Logan,

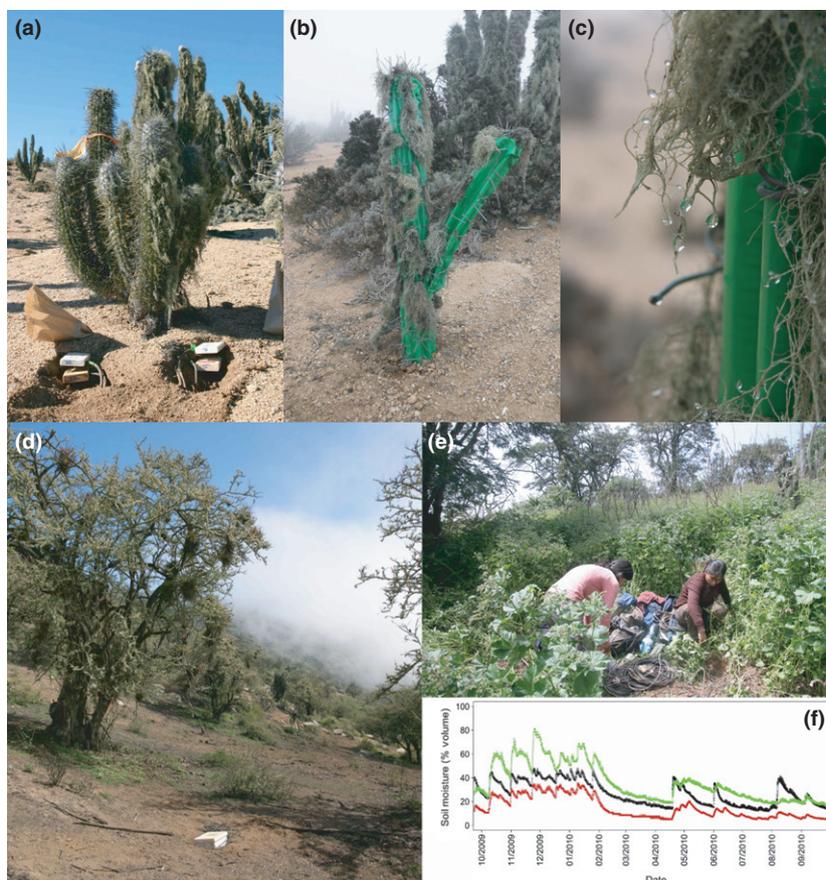


Fig. 2. Experimental manipulations of epiphytes. At Pan de Azúcar National Park (Sector Lomitas), northern Chile (a–c), we performed two parallel experiments. Epiphytes were removed from either the north-facing (a) or south-facing half of small individuals of *Eulychnia saint-pieana* (Cactaceae). Artificial cacti, constructed to resemble *E. saint-pieana* (b), were also placed in open sites, and epiphytes added to determine their impact on fog-water collection (c). At Atiquipa, southern Perú (d–f), soil moisture was measured below trees with and without epiphytes during dry (La Niña conditions, (d) and wet (El Niño conditions, (e). A representative soil moisture trace for trees with epiphytes (green), without epiphytes (red) and open ground (black) is also shown (f).

UT, USA) with 12 cm prongs. Five replicate readings were taken for each measurement. Treatment effects on soil moisture were analysed using linear mixed-effects models as implemented in R package nlme (Pinheiro and Bates). Treatment (open ground, epiphytes present or epiphytes absent) was applied as a fixed effect and cactus pair as a random effect.

Soil moisture below *Caesalpinia spinosa* with and without epiphytes ($n =$ three pairs) was also measured after epiphyte removals in August, October and November 2009. Because soil moisture below a tree canopy can be very heterogeneous, soil moisture was measured along transects in each cardinal direction from the base of the tree to the edge of the canopy. Five replicate readings using a hand-held TDR probe (CS620; Hydrosense, Campbell Scientific Inc) were made at 50-cm intervals along these transects. Treatment effects on soil moisture were analysed using linear mixed-effects models as implemented in R package nlme (Pinheiro *et al.* 2013). Treatment (epiphytes present or epiphytes absent) and sampling date (August, October or November 2009) were applied as a fixed effect and tree pair, distance from tree base and cardinal direction from base of the sampling point as random effects.

Hourly soil moisture dynamics were recorded using two dataloggers at Lomitas (CS10x; Campbell Scientific Inc) and one at Atiquipa (CS800; Campbell Scientific Inc). Each datalogger was supplemented with a 107 soil temperature probe and TE525 pluviometer. In Atiquipa, a second pluviometer with a modified Juvik fog collector was also installed, following the models used by del Val *et al.* (2006) in northern Chile. Each datalogger was equipped with an array of 30-cm TDR soil moisture probes (CS616; Campbell Scientific Inc). In Lomitas, one probe was placed 5 cm below the surface at the base of each treatment (open ground, without epiphytes, with epiphytes) of one set of artificial cacti (three probes total). A second array of probes was installed near a group of experimental cacti, 5 cm below the surface at the base of both north- and south-facing sides of each treatment (control, sun

removal and shade removal, for a total of nine probes). In Atiquipa, the datalogger was installed beneath a pair of experimental trees. Four soil moisture probes were placed in cardinal directions around the trees (control or removal), 5 cm below the soil surface at 1.5 m from the base of the tree (eight probes). An additional four probes were buried at 5 cm in open soil away from the influence of any tree canopy. All data were sampled at 30-s intervals and logged as hourly averages (hourly sums in the case of precipitation). Data from all dataloggers were downloaded regularly between July 2009 and November 2010.

Soil moisture probes were calibrated *in situ* to account for the considerable differences in soil density and organic matter content between sites, by comparison with water mass of known volumes of soil. The Atiquipa soils did not require correction from the manufacturer's settings, and although the Lomitas soils did, the extreme aridity of the site was such that no interpretable soil moisture traces were obtained during the study period. Temperature correction was performed according to a formula from Campbell Scientific technical support:

$$\begin{aligned} \text{VWC}_{\text{Corr}} = & \text{VWC} - 0.0044 \cdot T \cdot \text{VWC}^3 + 0.0014 \cdot T \cdot \text{VWC}^2 \\ & + 0.0029 \cdot T \cdot \text{VWC} - 0.0002 \cdot T + 2.4 \cdot \text{VWC}^3 \\ & - 1.6 \cdot \text{VWC}^2 + 0.32 \cdot \text{VWC} - 0.046 \end{aligned}$$

where VWC_{Corr} is the temperature-corrected volumetric water content (fractional), T is soil temperature in °C and VWC is the uncorrected water content value (fractional) at temperature T .

Soil moisture dynamics were considered in two manners: inputs from precipitation events (jumps) and subsequent soil moisture drawdown. Jumps were identified as large and rapid increases in soil moisture coincident with rainfall events. Soil moisture drawdown by vegetation and evaporation is well described by a

first-order decay function. The soil moisture drawdown decay constant (k) was calculated by identifying local maxima and minima within a 6-day window for each probe time series using R (R Development Core Team 2013) and measuring the loglinear slope between each maximum and the subsequent minimum (See Appendix S1, Supporting Information). Very small drops in soil moisture ($<0.025\%$) were excluded from further analysis. Because ground vegetation cover changed considerably over the course of the measurement period, data were divided into two time periods, El Niño (high ground cover of *Nicotiana* and *Loasa*; October 2009–March 2010; Fig. 2e) and La Niña/ENSO-neutral (minimal ground cover; July–September 2009 and April–November 2010; Fig. 2d). Treatment effects on log-transformed soil moisture jumps (Table S3) and drawdown rates (Table S5) were analysed using linear mixed-effects models as above. Treatment (epiphytes present or epiphytes absent) and season were applied as a fixed effect and probe identity (reflecting various probe positions about the base of trees) as a random effect.

AIR TEMPERATURE AND RELATIVE HUMIDITY

Air temperature and relative humidity were recorded using micro-dataloggers (Hygrochron iButtons, Embedded Data Systems, Lawrenceburg, KY, USA). The iButtons were placed at the surface of paired branches of *Caesalpinia spinosa* (Atiquipa, three pairs), columns of *Eulychnia saint-pieana* (Lomitas, four pairs) and artificial cacti (Lomitas, three pairs), lodged below the epiphyte layer when present, or exposed in the epiphyte removal treatments. Air temperature and relative humidity was logged at hourly intervals. Representative periods of 2–4 months are available for two wet (August–October 2009, July–October 2010) and one dry season (January–April 2010). Saturation vapour pressure was determined using the Tetens equation (Campbell & Norman 1998) to calculate vapour pressure deficit (VPD). Data were processed in R and are available from Dryad (Stanton *et al.* 2014).

Results

EPIPHYTE BIOMASS AND WATER RETENTION POTENTIAL

The mass of epiphyte loads varied with host plant size, from 31 g per plant for the smallest cacti to 270 g per plant for 2-m-tall cacti (mean = 111 g, SD = 79.6, $n = 10$) at Lomitas. All of the epiphytes removed were lichens, predominantly the fruticose genera *Ramalina usnea* and *Usnea* spp. Epiphyte loads were considerably greater at Atiquipa and consisted of lichens and mosses (mainly *Usnea* spp; 5 kg per tree, $n = 3$) and bromeliads (*Tillandsia* spp, 15 kg per tree, $n = 3$). Epiphyte water content at saturation was several times their dry mass (mean = 280%, SD = 56, $n = 10$). Even considering lichens alone, canopy epiphytes in *Caesalpinia spinosa* trees may be retaining approximately 10–15 L of water per fog or rainfall event.

EPIPHYTES REDUCE THROUGHFALL

Uptake and transpiration by plants will obscure the effects of epiphytes on soil water availability. The use of artificial cactus mimics at Lomitas excludes the effects of biotic losses, such that the influence of epiphytes on throughfall can be directly deduced from soil moisture. Although both artificial

cacti with epiphytes added (mean = 11.87, SE = 1.23, $n = 3$) and without epiphytes (mean = 16.07, SE = 1.23, $n = 3$) had significantly greater soil moisture than open disturbed ground (mean = 7.07, SE = 1.49, $n = 3$), they also differed significantly from each other, with epiphytes reducing soil moisture (Fig. 3, Table S1). As wind had a tendency to remove some of the epiphytes added to artificial cacti, this effect on soil moisture occurred despite epiphytes loads at time reaching as little as half that of natural cacti.

The impact of epiphytes on soil moisture below *Caesalpinia spinosa* was more mixed. In August 2009, before the annual rains, the removal of epiphytes significantly increased the soil moisture below tree canopies (Fig. 4a, Table S2). This period is characterized by heavy fog but no vertical precipitation, and the removal of epiphytes may have facilitated throughfall and stemflow of fog water. Alternatively, absence of epiphytes may have contributed to greater hydraulic redistribution and increased soil moisture in upper layer of the soil. During the subsequent rainy season (October and November 2009), the soil moisture was significantly greater below the trees with epiphytes intact (Fig. 4b, Table S2).

This seasonal difference in the effect of epiphytes is more clearly discernible from the continuous measurements of soil moisture (Fig. 5, Table S3). During the wet, El Niño, periods, there was a strong trend towards reduced water inputs from precipitation (measured as sudden jumps in soil moisture) under tree canopies, but no treatment effects (Fig. 5a, Table S3). In contrast, during drier, La Niña, periods, the inputs to soil water were fewer and most significantly reduced below the tree still retaining its epiphytes (Fig. 5b, Table S3).

HOST PLANTS TAKE UP LESS WATER IN THE PRESENCE OF EPIPHYTES

The dynamics of soil water content following identifiable precipitation events can reveal differences in water losses between treatments. No significant fluctuations or differences in soil water content were detectable at Lomitas due to the extreme aridity of the site. Only two rain events occurred during the study period (May 2010 and June 2011, the first significant rains in over a decade); however, the resulting surface run-off and flooding caused extensive damage to equipment and prevented the monitoring of post-rain soil moisture dynamics. Gravimetric measures of soil moisture were nonetheless possible during the week following the rains. These showed that the removal of epiphytes from cacti led to significantly greater rates of soil moisture decrease after the rain (Fig. 6, Table S4). Interestingly, as the epiphyte removals only affected half of each cactus, only cacti lacking epiphytes on their northern (equatorial) side differed significantly from controls, suggesting an insolation effect.

At Atiquipa, which receives several yearly rains and is less prone to flash-flooding, the drawdown of soil mois-

ture, as derived from post-rain soil moisture dynamics below trees (Fig. 7, Table S5), is consistently slower in the presence of epiphytes. This pattern was present during both dry (La Niña) and wet (El Niño) periods but only significant during the former. During the wet periods, the rates of soil moisture drawdown did not significantly differ between open areas and below canopies, perhaps due to the presence of a dense ground cover of annuals across the entire landscape (Fig. 7a, Table S5). During dry periods, when minimal ground cover is present, soil moisture drawdown was significantly greater below trees without epiphytes than in open ground (Fig. 7b, Table S5).

PRESENCE OF EPIPHYTES STABILIZES HOST MICROCLIMATE

The difference in water uptake rates may be attributable to an effect of epiphytes on evapotranspirative losses. *Eulychnia saint-pieana* with epiphytes were significantly cooler and more humid during the day, but slightly warmer at night (Table 1). These differences in mean daytime conditions of 2°C (5°C in daily maxima) and 0.3 kPa (0.8 kPa in daily maxima) are large enough to greatly change host evapotranspiration (see Appendix S1). A similar trend was observed in artificial cacti and *Caesalpinia*

branches, although the low replication makes strong statistical inference difficult (Table S6). In addition to the increased temperature and evaporative demand in the absence of epiphytes, the variance in daytime conditions was also significantly increased.

Discussion

Our results indicate that epiphytes had considerable effects on host plant water relations, primarily by directly retaining throughfall and stemflow water and indirectly buffering canopy microclimate. Although replication was low in many experiments, the differences were nonetheless marked enough to identify strong effects of epiphytes on host plants. The retention of water by epiphytes outweighed any increased water inputs from fog-water interception, although this effect may differ with fog frequency and density (Figs 4 and 5). The expected increase in water inputs from additional fog-harvesting ability was therefore not observed at the level of soil moisture dynamics, and the primary effect of epiphytes appears to be in reducing outputs rather than increasing inputs to these systems (Figs 6 and 7). Epiphytes had a considerable effect on microclimatic conditions in the host plant canopy (Tables 1 and S6).

Fig. 3. Volumetric soil moisture (a) and total soil nitrogen (b) below artificial cacti at Pan de Azúcar National Park. Soil moisture is increased by the presence of cacti-like structures, but this effect is reduced when the structure is covered in epiphytes (a). Adding epiphytes to artificial structures increased soil nitrogen content (b). Error bars show standard error about the mean, and letters denote significantly different groups ($P < 0.05$). The parameters of the linear mixed-effects models used to generate the data shown are given in Tables S1.

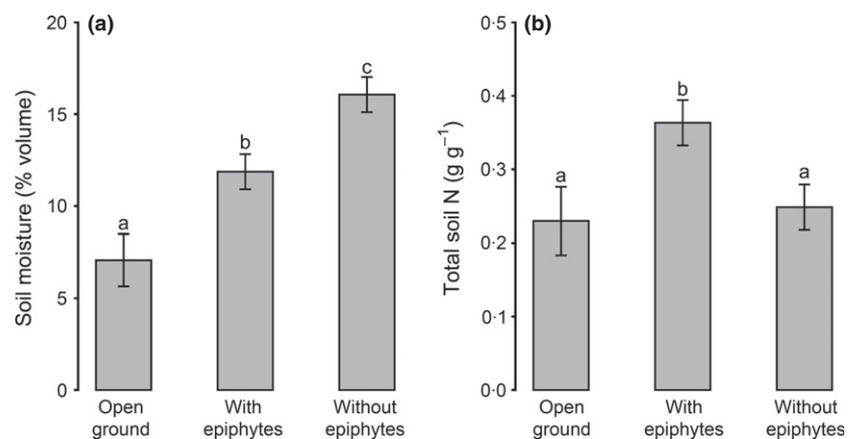
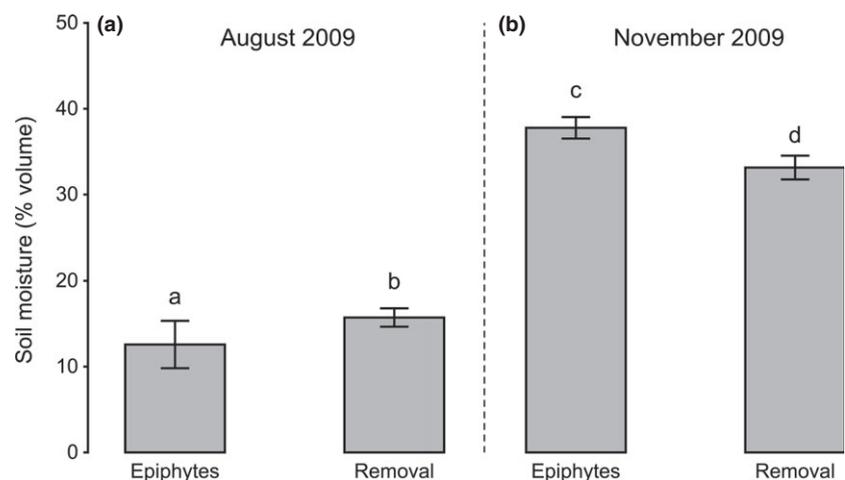


Fig. 4. Soil moisture below the canopy of *Caesalpinia spinosa* trees with or without epiphytes experimentally removed, during dry (a) and wet (b) months, at Atiquipa, southern Perú. The presence of epiphytes appears to decrease soil moisture when water inputs are primarily from fog (a), but contributes to greater soil water storage during rainy months (b). Error bars show standard error about the mean, and letters denote significantly different groups ($P < 0.05$). The parameters of the linear mixed-effects model used to generate the data shown are given in Table S2.



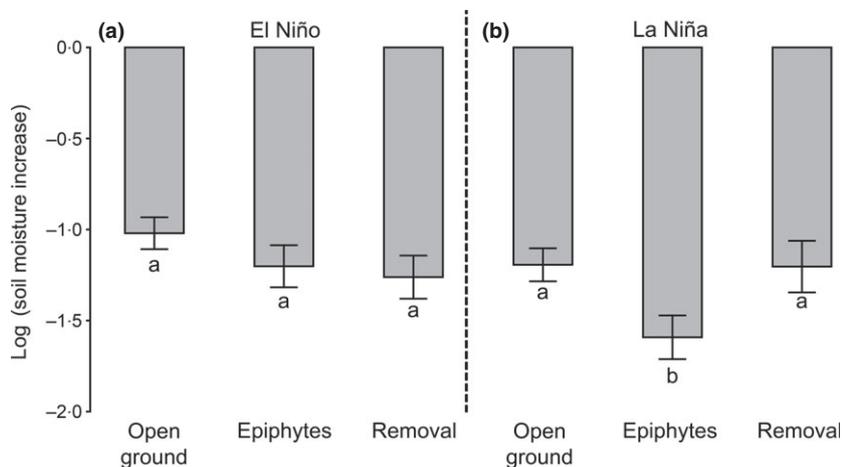


Fig. 5. Soil moisture increases in response to precipitation events in wet (a) and dry (b) conditions, as measured by TDR soil moisture probes buried in open spaces or below *Caesalpinia spinosa* trees with or without epiphytes in Atiquipa, Perú. There is a slight but non-significant trend towards decreased soil moisture increases below canopies during an El Niño season (a). In contrast, the inputs to soil water during dry periods are significantly reduced below the tree with epiphytes (b). Error bars show standard error about the mean, and letters denote significantly different groups ($P < 0.05$). The parameters of the linear mixed-effects models used to generate the data shown are given in Table S3.

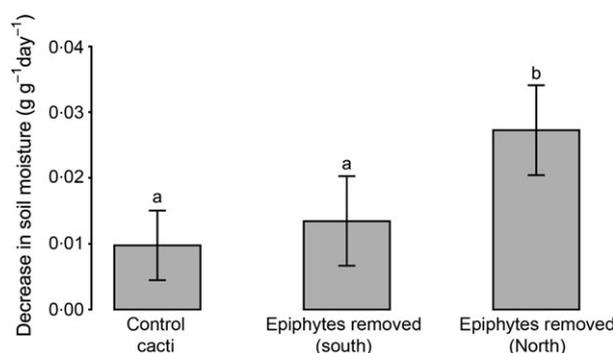


Fig. 6. Response of gravimetric soil moisture at the base of *Eulychnia saint-pieana* cacti following a rare rain event (May 2010) in Pan de Azúcar National Park, northern Chile. The soil moisture decreased significantly faster below cacti whose north-facing (equatorial) side had been stripped of epiphytes than similar sized unmanipulated cacti or south-facing epiphyte manipulations. Error bars show standard error about the mean, and letters denote significantly different groups ($P < 0.05$). The parameters of the linear mixed-effects models used to generate the data shown are given in Table S4.

Most previous evaluations of epiphyte effects on host plant water relations have either considered individual branches (Rommel 1922; Freiberg 2001; Villegas, Tobón & Breshears 2008) or compared plants with different epiphyte loads (Rommel 1922; Phillips 1928; Montaña, Dirzo & Flores 1997; Stuntz, Simon & Zotz 2002). The former approach may not provide insights into whole-plant effects of epiphytes, while the latter relies heavily on the assumption that the trees with and without epiphytes are otherwise identical. The validity of this assumption is cast into doubt by the parallel use by other researchers of epiphytes as indicators of microclimatic conditions (Cornelissen & Steege 2009; Larrea & Werner 2010; Gehrig-Downie *et al.* 2011). Unlike other manipulations of host plants, removal of many epiphytes can easily be performed without damaging the host plant. Not all epiphytes penetrate the host plant's bark, and even if they do, they can be trimmed until their physical presence is minimized. To further account for any damage to host plants, we also added

epiphytes to artificial plant mimics and found similar effects of epiphytes (Table S6), strongly suggesting that the changes are driven by the epiphytes rather than being side effects of manipulation. This result, as well as the persistence of epiphyte effects on cacti more than 2 years after their removal (Fig. 6), strongly indicates that the impacts associated with epiphyte removal are unlikely to have been caused by accidental direct damage to the host plant itself.

While our discussion and choice of field sites thus far emphasized fog-water inputs, the majority of effects of epiphytes reported here are unlikely to be restricted to interactions with fog. The effects of epiphytes on host plant water use (Appendix S1) and growth specifically examine responses to rainfall events, and the microclimatic effects of epiphytes will occur for both fog and rainwater inputs. The interception of additional fog water by epiphytes may help stabilize canopy microclimate between rainfall episodes in addition to the effects of epiphytes on canopy boundary-layer depth and moisture retention.

The presence of dense epiphyte cover significantly alters the microclimate at the surface of host plants. In the cases presented here, the dominant epiphytes were lichens (*Usnea* spp, *Ramalina usnea*) and bromeliads (*Tillandsia* spp); however, the effects are physical in nature and applicable to other epiphyte taxa equally well. The primary direct effects appear to be shading and the retention of atmospheric moisture. The former buffers diel cycles in temperature, lowering temperature spikes during the day and most likely decreasing daytime evaporation of water from the canopy. In concert, the presence of epiphytes slows airflow in the canopy and increases the depth of the boundary layer. As a result, the daytime atmospheric relative humidity below epiphytes is frequently more elevated (Table 1), indicating greater moisture retention within the boundary layer. Consequently, the vapour pressure differential in the vicinity of the host stomata is reduced. The effect of epiphytes on the microclimate of artificial substrates was not as strong (Table S6); however, it is unclear whether this is due to host plant contributions to microclimate or the lower density of epiphytes when manually suspended on the artificial spines.

Fig. 7. Decrease rate constants (k) of soil moisture after precipitation events in open ground or below *Caesalpinia spinosa* trees with or without epiphytes during wet (a) and dry (b) conditions in Atiquipa, Perú. Soil loss rates were slower below a tree with epiphytes than one without. Seasonal differences may be partly due changes in ground cover (see Fig. 2). Error bars show standard error about the mean, and letters denote significantly different groups ($P < 0.05$). The parameters of the linear mixed-effects models used to generate the data shown are given in Table S5.

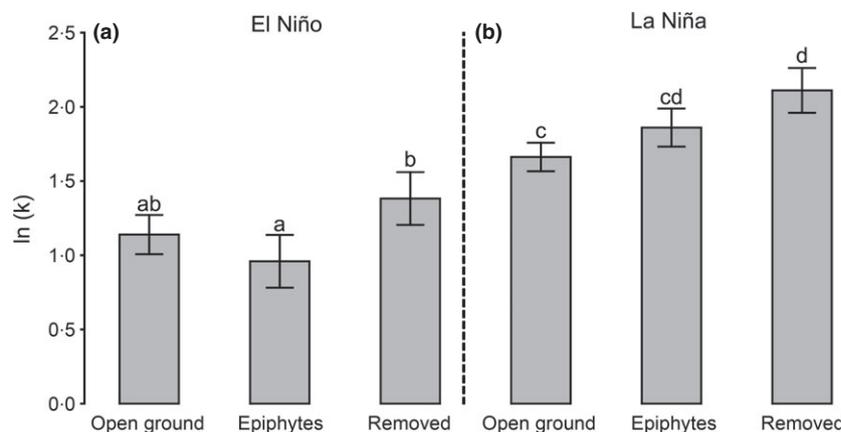


Table 1. Microclimate conditions [temperature (T) and vapour pressure deficit (VPD)] at the branch/column surface in the presence or absence of epiphytes on cacti (*Eulychnia saint-pieana*), (Pan de Azúcar National Park, Chile). Data were obtained from iButton dataloggers recording at hourly intervals, and then aggregated into daytime (7:00–19:00, subscript day) and night-time (19:00–7:00, subscript night) means (Mean), maxima (Max), minima (Min) and variances (Var). Summary statistics are given for the presence/absence of epiphytes [Mean, standard deviation (SD), number of replicate dataloggers (N)] and a pair-wise comparison of treatments (Student's t test and P -value)

Study Species	Variable	With Epiphytes			Without Epiphytes			Comparison	
		Mean	SD	N	Mean	SD	N	t	$P <$
<i>Eulychnia saint-pieana</i>	Mean T_{day} (°C)	15.1	1.2	4	17.3	0.7	4	3.69	0.035
	Max T_{day} (°C)	20.9	2.1	4	25.1	1.1	4	3.49	0.040
	Var T_{day} (°C)	17.0	6.8	4	29.0	4.9	4	3.41	0.042
	Mean T_{night} (°C)	10.4	0.2	4	10.3	0.2	4	-2.34	0.101
	Min T_{night} (°C)	8.6	0.2	4	8.3	0.2	4	-6.17	0.009
	Var T_{night} (°C)	3.2	0.2	4	3.4	0.1	4	2.08	0.129
	Mean VPD _{day} (kPa)	0.69	0.15	4	1.02	0.11	4	3.83	0.032
	Max VPD _{day} (kPa)	1.54	0.30	4	2.33	0.29	4	3.49	0.040
	Var VPD _{day} (kPa)	0.38	0.17	4	0.79	0.25	4	3.13	0.052
	Mean VPD _{night} (kPa)	0.28	0.02	4	0.29	0.03	4	1.38	0.260
	Var VPD _{night} (kPa)	0.07	0.01	4	0.07	0.01	4	-0.70	0.540

A qualitative analysis of the relative contributions of epiphytes on canopy evapotranspiration rates (Appendix S1) using a time-averaged form of the Penman equation (adapted from Eagleson 2002) suggests that changes in relative humidity are likely to have a greater influence than those of temperature, especially under arid conditions. Epiphytes can affect both the net radiation inputs and drying processes in the canopy, the former by changing albedo (and thus canopy temperature and back radiation) and the latter by increasing atmospheric relative humidity. Both effects are comparable in size, and the differences created by epiphytes in the data reported here translate into considerable decreases in canopy evapotranspiration (e.g. 10% increase in relative humidity leads to 12% decrease in evapotranspiration). These differences are great enough to have large effects on local climate at the stand or forest scale. This change may promote host plant photosynthetic activity during rainless periods, acting as a capacitor for canopy climates.

The contributions of vascular and non-vascular epiphytes are likely to differ slightly. Vascular epiphytes

are far less efficient at fog-water absorption than bryophytes and lichens, and likely to be slower at releasing captured water to the canopy. The contribution of vascular epiphytes to canopy microclimate buffering might be expected to therefore be more limited (but see Stuntz, Simon & Zott 2002), but still has the potential to be important. The transpiration of epiphyte water must occur and will occur directly into the canopy of the host plant. Non-vascular plants are common in most epiphytic floras, although they are traditionally under-represented in floristic surveys.

Shading by epiphytes has the potential to impede host plant photosynthesis. Although compelling in the understorey or similarly light-limited conditions, this is less likely to be of importance in open canopies or the upper reaches of closed-canopy forests. Although unable to accurately measure photosynthetic rates, Rommel (1922) suggested that nutrient and water limitation were more important than carbon limitation in determining the effects of epiphytic *Alectoria* on spruce trees. In the present study, there was no evidence of chlorosis of cacti below dense epi-

phyte cover, nor were there noticeable differences in cortex colour between epiphyte treatments. Any effect of shading in the high luminosity desert conditions may actually be one of photoprotection, representing another, albeit as yet untested, beneficial effect of epiphytes on host plants under certain conditions.

Epiphytes have occasionally been reported to physically damage host plants. Phillips (1928) reported damage to thin-barked *Podocarpus* trees by the holdfasts of *Usnea*, and Wang *et al.* (2008) showed that foliose lichens can inhibit leaf budding in commercial tea plants. Montaña, Dirzo and Flores (1997) applied the concept of 'structural parasitism' to bromeliads in a semi-arid ecosystem. In the absence of experimental work, the correlation between shoot mortality and epiphyte loads may simply reflect greater colonization of moribund branches and trees as suggested by Rommel (1922) and Benzing (1990). Preliminary detailed surveys of bud formation on epiphyte removals in Atiquipa and the greater floral production in the presence of epiphytes suggest that this effect is likely absent in the sites of the present study (J. Huallpa, unpublished data).

The impacts of epiphytes on their host plant water relations and, by extension, on whole ecosystem ecohydrology have been insufficiently accounted for in most conceptual models of ecosystem function. We have shown evidence for an important impact of epiphytes on their host plants in two dry ecosystems, and the conceptual model advanced may be broadly applicable. While epiphytes may occur in low abundances in the temperate forests that have shaped much of ecological theory, they are significantly more abundant in temperate rain forests and many tropical forests. The results presented here suggest that epiphytes need to be considered when scaling from plant physiology to ecosystem processes. Experimental removal of epiphytes is logistically challenging; however, the considerable impacts on host plants we observed suggest that more such experiments, in other ecosystems, may be necessary in studies of forest hydrology. The conceptual framework we present establishes a context for evaluating the relative positive and negative effects of epiphytes on hosts and shows that epiphytes are likely to have significant effects on host plants and ecosystems. This consideration is important to the accurate modelling of climate–vegetation feedbacks and ecohydrology of ecosystems with large epiphyte communities.

Acknowledgements

This research was funded by NSF DDIG award # 0909984 to L. Hedin and D. Stanton; Princeton Latin American Studies Travel Grants and a Princeton President's Award to D. Stanton. Research in Chile was conducted under CONAF research permit 06/08. We would like to extend special thanks to P. Jimenez, J. Molina, D. Heredia, the comuneros de Atiquipa and the UNSA Ecology Department staff for assistance in the field in Atiquipa. In Chile, special thanks are also due to The CONAF staff at Pan de Azúcar, including I. Páez, J. Mehler, N. Castillo and P. Salazar. J. Armesto, R. Vargas, G. Howe, D. Phillips and D. Lühr for help at Pan de Azúcar. C. Staver, S. Batterman, S. Bernal, other Hedin laboratory members and S. Córdoba, A. Wolf, J. C. Villegas and C. Jones gave helpful suggestions and feedback at various stages in the research. We would also like

to thank J. Dalling, J. Meyer, G. Zotz and an anonymous reviewer for contributions that greatly improved the manuscript. The authors declare no conflict of interests.

Data accessibility

Data deposited in the Dryad repository: <http://doi.org/10.5061/dryad.7gc7k> (Stanton *et al.* 2014).

References

- Benzing, D.H. (1990) *Vascular Epiphytes*. Cambridge University Press, Cambridge, UK.
- Campbell, G.S. & Norman, J.M. (1998) *An Introduction to Environmental Biophysics*, 2nd edn. Springer, New York, USA.
- Chang, S., Lai, I. & Wu, J. (2002) Estimation of fog deposition on epiphytic bryophytes in a subtropical montane forest ecosystem in north-eastern Taiwan. *Atmospheric Research*, **64**, 159–167.
- Cornelissen, J. & Steege, H. (2009) Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *Journal of Tropical Ecology*, **5**, 131–150.
- Díaz, I.A., Sieving, K.E., Pena-Foxon, M.E., Larrain, J. & Armesto, J.J. (2010) Epiphyte diversity and biomass loads of canopy emergent trees in Chilean temperate rain forests: a neglected functional component. *Forest Ecology and Management*, **259**, 1490–1501.
- Dilcher, D.L., Lott, T.A., Wang, X. & Wang, Q. (2004) A history of tree canopies. *Forest Canopies*, 2nd edn. (eds M. Lowman & H. Rinker), pp. 118–137. Elsevier Academic Press, Burlington, NY, USA.
- Eagleson, P.S. (2002) *Ecohydrology: Darwinian Expression of Vegetation Form and Function*. Cambridge University Press, Cambridge, UK.
- Ellenberg, H. (1959) Über den Wasserhaushalt tropischer Nebelosen in der Küstenwüste Perus. *Berichte der Geobotanischer Forschungsinstitut Rubel Zurich*, **1958**, 47–74.
- Freiberg, M. (2001) The influence of epiphyte cover on branch temperature in a tropical tree. *Plant Ecology*, **153**, 241–250.
- García-Santos, G. & Bruijnzeel, L.A. (2010) Rainfall, fog and throughfall dynamics in a subtropical ridge top cloud forest, National Park of Garajonay (La Gomera, Canary Islands, Spain). *Hydrological Processes*, **25**, 411–417.
- Gehrig-Downie, C., Obregón, A., Bendix, J. & Gradstein, S.R. (2011) Epiphyte biomass and canopy microclimate in the tropical lowland cloud forest of French Guiana. *Biotropica*, **43**, 591–596.
- Gentry, A. & Dodson, C. (1987) Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden*, **74**, 205–233.
- Holwerda, F., Bruijnzeel, L.A.S., Muñoz-Villers, L.E., Equihua, M. & Asbjornsen, H. (2010) Rainfall and cloud water interception in mature and secondary lower montane cloud forests of central Veracruz, Mexico. *Journal of Hydrology*, **384**, 84–96.
- Hsu, R. & Wolf, J.H.D. (2009) Diversity and phytoecology of vascular epiphytes in a tropical–subtropical transition island, Taiwan. *Flora*, **204**, 612–627.
- Johansson, D. (1974) Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeographica Suecica*, **59**, 1–136.
- Knops, J.M.H., Nash, T.H. & Schlesinger, W. (1996) The influence of epiphytic lichens on the nutrient cycling of an oak woodland. *Ecological Monographs*, **66**, 159–179.
- Larrea, M.L. & Werner, F.A. (2010) Response of vascular epiphyte diversity to different land-use intensities in a neotropical montane wet forest. *Forest Ecology and Management*, **260**, 1950–1955.
- Larson, D. (1981) Differential wetting in some lichens and mosses: the role of morphology. *The Bryologist*, **84**, 1–15.
- Lowman, M. & Rinker, H. (2004) *Forest Canopies*, 2nd edn. Elsevier Academic Press, Burlington, USA.
- Luebert, F. & Pliscoff, P. (2006) *Sinopsis Bioclimática y Vegetacional de Chile*. Editorial Universitaria, Santiago, Chile.
- Macbride, J.F. (1936) *Flora of Peru*. Field Museum Botanical Series XIII, Chicago, USA.
- McJannet, D., Wallace, J. & Reddell, P. (2007) Precipitation interception in Australian tropical rainforests: II. Altitudinal gradients of cloud interception, stemflow, throughfall and interception. *Hydrological Processes*, **21**, 1703–1718.
- Montaña, C., Dirzo, R. & Flores, A. (1997) Structural parasitism of an epiphytic bromeliad upon *Cecidium praecox* in an intertropical semiarid ecosystem. *Biotropica*, **29**, 517–521.

- Nadkarni, N.M., Schaefer, D., Matelson, T. & Solano, R. (2004) Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. *Forest Ecology and Management*, **198**, 223–236.
- Oyarzún, C.E., Godoy, R., Staelens, J., Donoso, P.J. & Verhoest, N.E.C. (2010) Seasonal and annual throughfall and stemflow in Andean temperate rainforests. *Hydrological Processes*, **25**, 623–633.
- Phillips, J. (1928) The influence of *Usnea* sp. on the supporting tree. *Transactions of the Royal Society of South Africa*, **17**, 101–107.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. and the R Development Core Team. (2013) *Nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-111.
- Pypker, T.G., Unsworth, M.H. & Bond, B.J. (2006) The role of epiphytes in rainfall interception by forests in the Pacific Northwest. I. Laboratory measurements of water storage. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **36**, 809–818.
- R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: <http://www.R-project.org/>.
- Raimondi, A. (1948) *Notas de Viajes Para su Obra 'EL PERU': Viaje de Ica a Arequipa, Visitando Nasca, San Juan de Lucanas, Puquio, Coracora, Chala, Caravelí y Ocoña 1863*. Torres Aguirre, Lima, Peru.
- Rodriguez-Iturbe, I. & Porporato, A. (2004) *Ecohydrology of Water-Controlled Ecosystems*. Cambridge University Press, Cambridge, UK.
- Rommel, L.G. (1922) Hänglavar och tillväxt hos norrländsk gran. *Meddelanden Fran Statens Skogsforsokanstalt*, **19**, 405–451.
- Rundel, P., Dillon, M., Palma, B., Mooney, H., Gulmon, S. & Ehleringer, J. (1991) Phytogeography and ecology of coastal Atacama and Peru. *Aliso*, **13**, 1–49.
- Stanton, D.E. & Horn, H.S. (2013) Epiphytes as 'filter-drinkers': life-form changes across a fog gradient. *The Bryologist*, **116**, 34–42.
- Stanton, D.E., Huallpa Chavez, J., Villegas, L., Villasante, F., Armesto, J., Hedin, L.O. *et al.* (2014) Data from: epiphytes improve host plant water use by microenvironment modification. *Dryad Digital Repository*, <http://doi.org/10.5061/dryad.7gc7k>
- Stone, E. (1957) Dew as an ecological factor: I. A review of the literature. *Ecology*, **38**, 407–413.
- Stuntz, S., Simon, U. & Zotz, G. (2002) Rainforest air-conditioning: the moderating influence of epiphytes on the microclimate in tropical tree crowns. *International Journal of Biometeorology*, **46**, 53–59.
- Thompson, M., Palma, B., Knowles, J. & Holbrook, N.M. (2003) Multi-annual climate in Parque Nacional Pan de Azúcar, Atacama Desert, Chile. *Revista Chilena de Historia Natural*, **76**, 235–254.
- del-Val, E., Armesto, J.J., Barbosa, O., Christie, D., Gutiérrez, A. & Jones, C. (2006) Rain forest islands in the Chilean semiarid region: fog-dependency, ecosystem persistence and tree regeneration. *Ecosystems*, **9**, 598–608.
- Veneklaas, E.J., Zagt, R., Leerdam, A., Ek, R., Broekhoven, A. & Genderen, M. (1990) Hydrological properties of the epiphyte mass of a montane tropical rain forest, Colombia. *Plant Ecology*, **89**, 183–192.
- Villegas, J.C., Tobón, C. & Breshears, D.D. (2008) Fog interception by non-vascular epiphytes in tropical montane cloud forests: dependencies on gauge type and meteorological conditions. *Hydrological Processes*, **22**, 2484–2492.
- Wang, L., Oh, S.-O., Niu, D.-L., Tan, Y.-H. & Hur, J.-S. (2008) Diversity of epiphytic lichens on tea trees in Yunnan, China. *Acta Botanica Yunnanica*, **30**, 533–539.
- Weberbauer, A. (1945) *El Mundo Vegetal de los Andes Peruanos*. Ministerio de Agricultura, Lima, Peru.

Received 25 July 2013; accepted 6 January 2014

Handling Editor: Jim Dalling

Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Effects of epiphytes on canopy evapotranspiration.

Table S1. Linear mixed-effects model of soil moisture below artificial cacti in Lomitas, grouped by treatment (open ground, epiphytes present or epiphytes absent), with experimental pair as a random effect.

Table S2. Linear mixed-effects model of log-transformed oil moisture below trees in Atiquipa, grouped by treatment (epiphytes present or epiphytes removed) and time of sampling (August, October or November 2009), with experimental pair and sampling point (direction and distance from base) as nested random effects.

Table S3. Linear mixed-effects model of the log-transformed increases in soil moisture associated with precipitation events (jumps) below trees in Atiquipa, grouped by treatment (epiphytes present or epiphytes removed) and ENSO season (El Niño or La Niña), with soil probe identity (different distances and directions from base of trees) as a random effect.

Table S4. Linear mixed-effects model of gravimetric soil moisture decrease rate ($\text{g g}^{-1} \text{day}^{-1}$) below cacti in Lomitas following an exceptional rain event, grouped by treatment (untouched cactus, epiphytes present or epiphytes absent), with location (north or south side of base) and depth (0–5 cm or 5–10 cm) of sampling as nested random effects.

Table S5. Linear mixed-effects model of the log-transformed slopes for post-rain soil moisture decreases below trees in Atiquipa, grouped by treatment (epiphytes present or epiphytes removed) and ENSO season (El Niño or La Niña), with soil probe identity (different distances and directions from base of trees) as a random effect.

Table S6. Microclimate conditions (temperature-T and vapour pressure deficit-VPD) at the branch/column surface in the presence or absence of epiphytes on artificial cactus mimics (Pan de Azúcar National Park, Chile) and trees (*Caesalpinia spinosa*, Atiquipa, Perú).