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RESEARCH ARTICLE

Good days, bad days: Weather patterns driving bryophyte carbon-exchange dynamics in tropical rainforest canopies

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Abstract

1. The physiology of tropical mosses, liverworts and lichens may be challenged by the daily weather patterns in lowland rainforests. Since these poikilohydric organisms can only photosynthesize and respire when hydrated, unfavourable timing of light and water availability (i.e. desiccation during light hours and hydration during dark hours) may lead to small or negative diel (24-h) carbon budget, especially in the tree crowns, where desiccation frequently occurs.
2. Here, we tested this 'unfavourable timing' hypothesis that explains the low abundance of bryophytes and lichens in tropical lowland forests with a high frequency of weather patterns that limit carbon gain and increase carbon losses. By example of the forest surrounding the Yasuní Scientific Station (YSS) in the Ecuadorian Amazon, our approach consisted of three steps.
3. We used the carbon-exchange model for poikilohydric organisms PoiCarb (Version 1.1) to simulate diel carbon budgets at a 10-min temporal resolution for 290 days based on canopy climate data from inside a tree crown and species-specific physiological parameters. Our simulations explicitly included parameter uncertainty; hence, we were able to discriminate simulations based on their certainty.
4. We implemented a classification tree analysis of the modelled diel carbon budgets for *Neckeropsis undulata*, the most abundant bryophyte species in the studied canopies. This analysis indicated that limiting light intensities, night-time hydration and daytime desiccation caused net carbon losses on more than two-thirds of the modelled days, while net carbon gains occurred only on bright days with rain.
5. We validated these classification rules for an independent subset of days for the same species and for two companion species (*Plagiochila raddiana* and

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Symbiezidium transversale). Our validation indicates >70% accuracy in classifying diel carbon budgets.

6. Our findings show that tropical lowlands are a physiologically marginal environment for bryophytes, mainly due to their frequent low-light cloudy days and, secondarily, due to sunny days with no moisture availability, limiting carbon gain in the studied canopy bryophytes. Our threefold approach constitutes a tool for predicting bryophyte physiological performance under current and changing weather and climate patterns.

KEYWORDS
canopy bryophytes, carbon budget, epiphytes, photosynthesis, poikilohydry, respiration, tropical rainforest, weather patterns

1 | INTRODUCTION

Tropical forest canopies harbour an incredible biodiversity despite setting a stressful environment for plants (Hietz et al., 2022). Tropical lowland forests host a rich vascular epiphyte flora (Benzing, 2008; Gentry & Dodson, 1987; Zotz, 2016) and non-vascular epiphytes (mainly bryophytes and lichens) further expand the diversity of physiological strategies to cope with the stressful canopy conditions (Niinemets et al., 2015). Due to their poikilohydric nature, that is, their limited ability to maintain a constant water content, bryophytes and lichens differ in their carbon-exchange dynamics from typical vascular plants (Proctor, 1990; Schellenberger Costa et al., 2018). In poikilohydric organisms, carbon exchange is strongly modulated by thallus water content (Green & Lange, 1994), which can vary at a fast pace when equilibrating with moisture conditions in the environment (Morales-Sánchez et al., 2022). Apart from very frequent measurements (Bader et al., 2010; Lange, 2003), the only way to get a grip on these fast dynamics is by modelling carbon exchange through time based on high-resolution microclimate data (Ma et al., 2023; Nikolić et al., 2024). In the tropical lowlands, carbon-exchange patterns and their resulting diel carbon budgets have hardly been studied in bryophytes and lichens, with a few exceptions (Nikolić et al., 2026; Zotz & Winter, 1994; Zotz et al., 2003). For longer time spans, such as monthly, seasonal or yearly, no information about carbon budgets and their environmental drivers is available at all (Slate et al., 2024).

The low abundance (cover and biomass) of bryophytes and lichens in tropical lowland forests could emerge from frequent weather patterns that limit carbon gain and improve carbon losses in poikilohydric autotrophs: desiccant weather at times when light is suitable for carbon assimilation and moistening weather during dark hours, which leads to high respiration rates (Richards, 1984; Wagner et al., 2014). This *unfavourable timing* hypothesis poses that the high frequency of unfavourable daily (dial) weather patterns for bryophytes and lichens in tropical lowland forests drives the carbon budgets of these organisms. The hypothesis highlights the poikilohydric physiology of bryophytes and lichens, namely, carbon gain is possible only when a wet thallus coincides with a light intensity above the compensation point, while dark respiration occurs whenever the bryophyte or lichen thallus is wet, and respiration rates are higher at high (night) temperatures. However, elevation-adapted (or -acclimatized) respiration rates have been identified in tropical bryophytes (Wagner et al., 2013). This finding contradicts the hypothesis that high night temperatures drive poikilohydric carbon loss under current conditions, but it does not contradict that unfavourable timing of hydration restricts diel carbon gains and abundance in tropical lowland forest. In addition to being limited at low thallus water contents, net photosynthesis, but not respiration, is typically reduced at very high thallus water contents due to slower CO_2 diffusion into cells. Because the responses of photosynthesis and respiration to water content and other environmental variables vary among species (Grau-Andrés et al., 2022; Stanton & Coe, 2021; Violle et al., 2007; Wang & Bader, 2018), testing the *unfavourable timing* hypothesis demands: (i) profiling the physiology of species (Coe et al., 2019, 2024; Stanton & Coe, 2021; Wagner et al., 2014; Zotz & Bader, 2024) and (ii) assessing, modelling and validating diel and long-term carbon budgets of poikilohydric organisms based on weather conditions (Lange et al., 1993; Nikolić et al., 2024). Relevant physiological data, however, are still limited to a handful of tropical bryophyte species (Nikolić et al. 2026; Wang et al., 2022).

Models aimed at assessing the response of poikilohydric organisms to climate drivers differ in biological specificity and input demand. The LiBry model (Porada et al., 2013) simulates water content and carbon exchange in lichens and bryophytes based on theoretical combinations of physiological traits, selecting suitable traits during the modelling process. LiBry, originally designed for global studies (Porada et al., 2013), has also been adapted for use with real species and with microclimate data (Ma et al., 2023, 2024). Coe and Sparks (2014) developed a statistical model for dryland mosses that predicts carbon budgets as a function of rainfall regimes. This model is based on measured carbon exchange during discrete rainfall events and specific to desert conditions, where physiological activity between such events can be assumed to cease completely. Most recently, Nikolić et al. (2024) developed the more generally applicable model PoiCarb to simulate thallus water and carbon-exchange rates over time for poikilohydric organisms. This model uses climate data series and species-specific physiological response curves and is

therefore most suitable for assessing the effect of different tropical weather patterns on the carbon budget of bryophyte species found in particular microclimates, such as those found in rainforest canopies.

Here, we test the *unfavourable timing* hypothesis—the notion that frequent unfavourable weather patterns limit carbon gain and increase carbon loss in poikilohydric autotrophs in the tropical lowlands—by modelling carbon budgets for three epiphytic bryophytes from a long (290-day) data series of weather conditions in tree crowns in a tropical rainforest in Amazonian Ecuador (Berdugo, Heyer, et al., 2022). We aimed at identifying weather patterns associated with net carbon gain, that is, 'good days' for bryophyte carbon budgets and, ultimately, biomass development, as well as at predicting how global warming-induced changes in weather patterns will affect tropical bryophytes in the future (Zotz & Bader, 2009).

2 | MATERIALS AND METHODS

We implemented the PoiCarb model (Nikolić et al., 2024), with small adjustments, for the most frequent bryophyte species in the studied tree crowns, *Neckeropsis undulata* (Hedw.) Reichardt (Berdugo, Gradstein, et al., 2022a). By classifying diel weather patterns associated with diel carbon gain, carbon loss and neutral carbon exchange, we identified diel weather patterns and thresholds of climate parameters that discriminate carbon gain ('good') days from carbon loss ('bad') days for *N. undulata* and validated this classification for an independent subset of days for the same species and for *Plagiochila raddiana* Lindenb and *Symbiezidium transversale* (Sw.) Trevis, two co-occurring species in the rainforest of Yasuní National Park, Amazonian Ecuador.

2.1 | Study area and data collection

Canopy-climate input data and species-specific response curves were obtained from, respectively, microclimate records and bryophyte samples collected in the canopy (medium tree crown) of the forest surrounding the Yasuní Scientific Station (YSS) in the Ecuadorian Amazon, a well-preserved and iconic location of lowland tropical forest. These records and collections were granted by the Research Permit number 003-2019-IC-PNY-DPAO-PUCE, issued by the Ministry of the Environment of Ecuador.

The YSS, in the Orellana province (0°40′27″ S 76°23′50″ W, ~230 m a.s.l.) to the south of the Tiputini river, hosts a highly diverse terra-firme forest typical of the Yasuni National Park, renowned as one of the most diverse tropical forests on Earth (Bass et al., 2010). The YSS standard climate station (0°40′28″ S 76°23′52″ W, 230 m a.s.l.) registered 24.9°C of mean annual temperature and a mean of ca. 3300 mm (ranging between 2318 and 4347) of annual precipitation between 2013 and 2024. These values are consistent with the wet equatorial climate that is typical of tropical rainforests (Bailey, 2014). Although it rains frequently throughout the year (see climate diagram, figure 1b, in Berdugo, Gradstein, et al., 2022b), precipitation is higher than average between October and February and lower in March, August and September.

Canopy climate parameters were recorded for 290 days between May 2019 and February 2020. A climate station, powered by a solar panel, was installed within the crown of a 28-m tall *Byrsonima putumayensis* Cuatrec. (Malpigiaceae). This tree had a diameter at breast height of 55 cm, a crown radius of 8 m, a crown depth of 16 m and within the crown (where the sensors were installed and the bryophytes were collected), the overhead canopy cover was 80%. This climate station consisted of a datalogger and sensors that recorded photosynthetically active radiation (PAR), relative humidity (RH), air temperature (T), leaf wetness (LW) and precipitation (Prec). The sensors were installed in the medium crown on main branches (thick enough to hold the measurement devices) positioned between 18 and 22 m above the ground. Therefore, precipitation within the crown corresponds to throughfall, that is, the water remaining after subtracting interception from rainfall but adding dripping water from fog or dew combing by the canopy. For further details on climate sensors and parameters, see Berdugo, Heyer, et al. (2022).

We collected fresh bryophyte material from the inner crown of eight canopy trees, including the one with the climate station. These samples, consisting of dense green clusters of epiphytic bryophytes, were transported to the non-climatized YSS lab. There, humidity conditions are likely less desiccating than those in the tree crowns, given that the lab is closer to the ground and located close to the forest understorey. The samples were kept in the shade and sprayed with water to avoid dehydration until they were processed, within 5 days of collection. Sample processing included carefully separating colonies into species (see Supplementary Methods for details about species identification in the Supporting Information) and profiling the physiology per species. Thus, species-specific response and desiccation curves were based on two composite samples per species; composite samples corresponded to the aggregated material from several trees. This strategy allowed us to gather enough material to run the controlled essays to build the response curves and to account for within-species variability.

We used these bryophyte composite samples to describe how carbon assimilation varies in response to light intensity and how water content influences carbon exchange under both light and dark conditions. We measured the CO_2 exchange of monospecific layers of green bryophyte shoots in a 3.5-cm diameter cuvette with a portable gas exchange system (GFS-3000; Heinz Walz GmbH, Effeltrich, Germany). Measurements took place under constant CO_2 concentration (400 ppm) and temperature (26°C) within the cuvette; relative humidity entering the cuvette was set at 80%, but the relative humidity within the cuvette is not controlled by the gas exchange system (Walz, 2005) and will have been higher than the setting due to evaporation from the samples. The light intensity (PAR) was increased stepwise to build light response curves (0, 10, 25, 50, 100, 150, 200, 250, 300, 400, 500, 600, 800 and 1000 $\mu mol\, m^{-2} s^{-1}$, based on the protocol of Wang & Bader, 2018). To build water content response curves, PAR was kept constant at 0 $\mu mol\, m^{-2} s^{-1}$ for dark respiration or 300 $\mu mol\, m^{-2} s^{-1}$ for net assimilation and sample fresh weight was determined after each measurement to calculate the water content:

WC (%) = 100 × (weight$_{fresh}$ − weight$_{dry}$)/weight$_{dry}$. In addition, the drying speed of the samples was determined by weighing them hourly for up to 22 h, starting at the maximum water-holding capacity (WHC, determined after fully wetting and lightly shaking the samples). Samples were left outdoor near the YSS lab building between measurements.

For each set of measurements, we derived species-specific response curves (Figure S1) or drying curves (Figure S2) by fitting predefined nonlinear model types to the observations (Nikolić et al., 2024). These regression models provided us with estimates of species-specific parameters and their uncertainty (standard error) to simulate bryophyte carbon exchange (Table S1) and desiccation rate (Table S2). Bryophyte species for modelling were selected from those that were collected and measured, based on the fit of the response curves describing their physiology. Using this a posteriori selection method, we targeted the most frequent bryophyte species in the studied tree crowns, *Neckeropsis undulata* and two companion species, *P. raddiana* and *S. transversale* (Berdugo, Gradstein, et al., 2022a).

2.2 | Model description

To simulate bryophyte carbon exchange, we modified the mechanistic model PoiCarb 1.0 (Nikolić et al., 2024), creating PoiCarb 1.1. We preserved the essence of PoiCarb 1.0, that is, instant bryophyte water content and carbon exchange were computed for each time step in the climate input based on a set of physiological parameters, and the instant carbon exchange rates were integrated to estimate diel and longer term carbon budgets. However, we introduced six significant modifications:

1. We adjusted the integration method allowing the calculation of diel carbon budgets despite data gaps in the climate input.
2. We ignored the effect of temperature on carbon exchange rates, because seasonal temperature fluctuations in the humid tropics are very small and previous work suggests that temperature impacts on the carbon budget are small relative to the impacts of light and thallus water content (Nikolić et al., 2024). We acknowledge though that climate warming beyond the current range, and associated changes in humidity, may certainly affect future carbon budgets (Nikolić et al., 2026).
3. We incorporated a rehydration curve by implementing a Michaelis–Menten-shaped function (Figure S2; Table S2), as suggested by Morales-Sánchez et al. (2022). Rehydration curves increase thallus water content at a species-specific rate during slight precipitation events, defined here by events with <2 mm in 30 min (World Meteorological Organization, 2023). PoiCarb 1.0 used instantaneous rehydration.
4. During moderate and strong precipitation events, that is, those with ≥2 mm in 30 min (World Meteorological Organization, 2023), we set thallus water content to its maximum, whereas in PoiCarb 1.0, any precipitation event modified the thallus water content to 80% of the maximum water content.
5. We set a conservative thallus water content at equilibrium when the thallus is almost dry at a water potential equal to that of the air (Proctor et al., 1998). When canopy leaves were wet according to our leaf wetness records, we set the minimum thallus water content at 30% of the species dry weight, considering the range suggested by Dilks and Proctor (1979; 10% to 100% DW) and refined by Proctor et al. (1998; 28% to 38% DW). PoiCarb 1.0 did not consider leaf-wetness data.
6. We used the uncertainty associated with our desiccation parameter estimates (Table S2) to vary desiccation speed as a function of vapour pressure deficit (VPD). After calculating VPD in the canopy climate data series from relative humidity and temperature with the 'RHtoVPD' function of the R package 'plantecophys' (Duursma, 2015), we varied the desiccation coefficient (*k*), within the standard error of the species-specific desiccation curve (Figure S2; Table S2), as a linear function of VPD, within the range of VPD records. Thus, k decreases at higher VPD, resulting in faster desiccation. In PoiCarb1.0, desiccation measurements at different levels of VPD quantitatively determine the dependence of the drying speed on VPD, but such data were not available in our study.

In summary, PoiCarb 1.1 requires as input a climate data series with records for leaf wetness, PAR, precipitation, relative humidity and VPD, as well as a set of 14 species-specific physiological parameters that describe water dynamics and carbon exchange, based on the best fits for the desiccation, rehydration, light and water response curves (Table S3).

2.3 | Bryophyte diel carbon budget simulation

We ran PoiCarb 1.1 with 290 days of climate input data to calculate diel and overall net carbon assimilation for *N. undulata* with the best estimates of its physiological parameters. For the maximum assimilation rate (A_{max}) and the light compensation point (LCP), the ratio of maximum assimilation rate to dark respiration (A_{max}/R_d) = 6 for these best-fitting parameters (Table S4). As accounting for parameter uncertainty is essential in modelling (Yanai et al., 2012), we also simulated diel carbon budgets under alternative carbon assimilation scenarios defined in accordance with the alternative light-response curves (Figure 1; Table S4) within the standard error (SE) of the A_{max} and R_d estimates of this response curve (Table S1). Since A_{max} and LCP are the light response parameters that impact carbon assimilation the most (Table S1), we varied both parameters to obtain the most optimistic (highest A_{max} and lowest LCP, resulting in a higher ratio of maximum assimilation to dark respiration, $A_{max}/R_d = 12$) and most pessimistic (lowest A_{max} and highest LCP, resulting in $A_{max}/R_d = 3$) scenarios. The water-response curve modulated CO_2 exchange relative to the rate at the optimal water content, defined as the thallus water content at which the maximum assimilation is predicted in the water content response curve (Figure S1). The absolute values of the curve thus did not affect the rates, only the shape did, so we did not vary the parameters of this response curve.

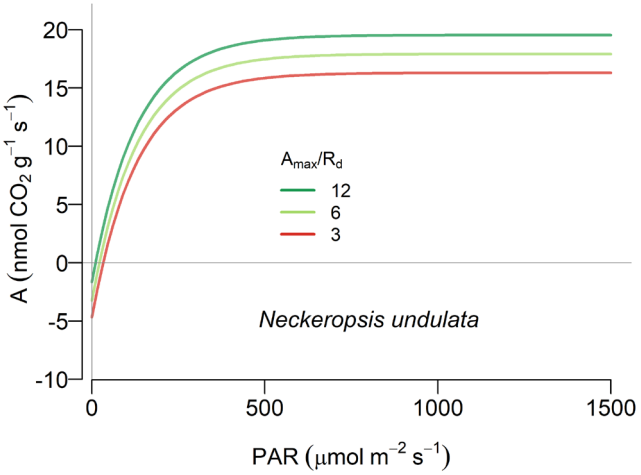


FIGURE 1 Alternative light-response curves for the epiphytic moss *Neckeropsis undulata* based on the best fit (medium) and different combinations of the physiological parameters: Maximum assimilation rate (A_{max}: ~the asymptote) and light compensation point (LCP: The photosynthetically active radiation—PAR—level at which assimilation (*A*, the *y*-axis) equals 0) plus or minus their standard errors (Tables S1 and S4), resulting in optimistic (higher) and pessimistic (lower) carbon assimilation rates, as summarized by the ratio between A_{max} and the dark respiration rate (R_d: Value on the *y*-axis at PAR = 0). These parameter estimates were derived from controlled observations on samples collected in tree crowns in the Yasuní Scientific Station in the Ecuadorian Amazon (Figure S1).

2.4 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Tropical lowland rainforest canopy climate	Rainforest canopy (medium tree crown)	Data from one climate station with long data series, representative according to comparison with seven other climate stations installed in medium tree crowns
Days (comparing days with different weather patterns)	Days	290 consecutive days
Bryophytes in general	Bryophytes	Three bryophyte species
Physiological profile of tropical epiphytic bryophytes	Bryophyte species	Two composite samples per species

2.5 | Data processing and hypothesis testing

With the output of these PoiCarb 1.1 runs, consisting of a diel course of carbon exchange and a net carbon budget for each of the 290 days, we used a three-step approach to test the 'unfavourable timing' hypothesis by relating the simulated diel carbon-exchange patterns and the diel budgets to the weather patterns of the respective days, based on the microclimatic data. First, we categorized dates according to the simulated bryophyte diel carbon budget and used plots of the carbon-exchange patterns and weather patterns on those dates to characterize the weather and thallus water content patterns of 'good' (carbon gain) and 'bad' (carbon loss) days. Then, we implemented and validated a classification tree to assess the importance of climate factors and weather patterns for bryophyte diel carbon budgets. Finally, we identified the frequency of the most relevant weather patterns driving bryophyte carbon budget.

To categorize the simulated dates according to the diel carbon budget of *N. undulata* (first step in our analytical approach), we evaluated the consistency of the diel carbon budgets among the three alternative carbon assimilation scenarios (Figure 1; Table S4). The dates when the carbon gain of the diel was consistently positive (>15 µmol CO_2 g^{-1} day^{-1}), negative (<−15 µmol CO_2 g^{-1} day^{-1}) or near-zero >−15 and <15 µmol CO_2 g^{-1} day^{-1} among scenarios were categorized as positive, negative or neutral, respectively. The remaining dates, that is, days on which a mix of positive, neutral and/or negative diel budgets were produced, depending on the scenarios, were categorized as non-consistent. A neutral range around absolute 0 was defined to acknowledge that not only absolute 0 but also budgets very close to 0 (here arbitrarily defined as 0% ± 2.5% of the total range of observed diel budgets within a scenario) can hardly be considered a gain or a loss for that day.

For the second step in our analytical approach, we fit classification trees (Breiman et al., 1984): (i) to assess whether individual climate factors and weather patterns were significant predictors of diel carbon budget categories, (ii) to evaluate the relative importance of these predictors in classifications using multiple predictors and (iii) to identify threshold values for the climate factors and weather patterns discriminating positive and negative diel carbon budgets. We prepared the predictor set in two steps. First, we aggregated climate parameters: air temperature, PAR during light hours, relative humidity and VPD were aggregated as daily averages, and leaf wetness duration and precipitation were aggregated as daily totals, interpolating across missing data. Second, we categorized diel weather patterns based on changing conditions throughout the day: as dry (no precipitation and no wet leaves), no precipitation (but wet leaves for at least a minute) or rainy (at least 0.2 mm of precipitation per day; note that we used precipitation data recorded inside the canopy, so our precipitation records already account for canopy interception) with no precipitation and rainy being further discriminated by moisture timing (Table S5).

We fit classification trees with the function 'rpart' of the R package with the same name (Therneau & Atkinson, 2022) to distinguish positive from negative diel carbon budgets (we did not consider neutral budgets, because they occurred on only 2% of the modelled dates), based on climate parameters and/or weather patterns. We identified the most informative predictors and their aggregation form (daily total, daily mean or daily pattern; Table S6) from simple classification trees (i.e. trees using a single predictor). Those predictions reached the minimum number of misclassifications (highest accuracy) and distributed the misclassifications more evenly among

diel budget categories (most balanced). To evaluate their relative importance and possible interactions, we fit a multiple classification tree with the most informative predictors identified and pruned it to a complexity factor of 0.1.

For the training tree, we used only the days when the three carbon assimilation scenarios (Figure 1; Table S4) consistently yielded either positive or negative diel budgets ($n = 118$). Out of the subset of non-consistent days for *N. undulata*, we used only those with either positive or negative diel budgets according to the medium carbon assimilation scenario ($n = 126$) to validate the accuracy of the classification rules. Furthermore, we validated our multiple classification rules on the output resulting from feeding the model with the same climate data and the medium carbon assimilation scenario identified for *P. raddiana* ($A_{max}/R_d = 1.7$, Table S4) and *S. transversale* ($A_{max}/R_d = 2.4$, Table S4) from their species-specific water response and drying curves (Figure S2). Consistent with the first validation, we used only those days with either positive or negative diel budgets according to the medium carbon assimilation scenario for each companion species ($n = 270$ for *P. raddiana* and $n = 269$ for *S. transversale*).

Finally, we illustrated the accuracy of the classification tree with Sankey diagrams using the function 'sankeyNetwork' of the R package networkD3 (Allaire et al., 2017), to implement the third step in our analytical approach. Data processing, modelling of physiological parameters and model runs, as well as classification analyses and data visualization were performed in R 4.2.2 (R Core Team, 2022).

3 | RESULTS

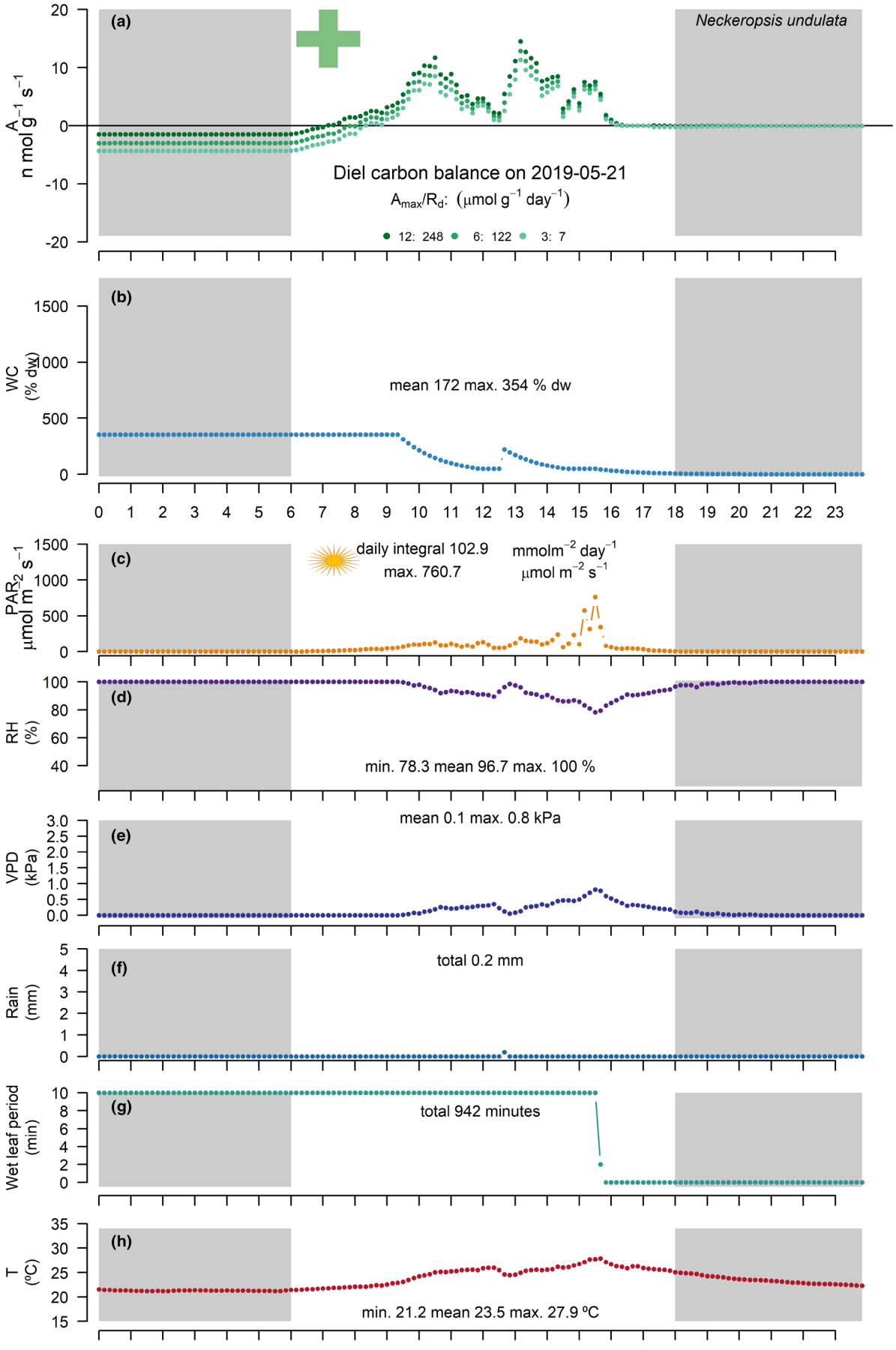
In the diel carbon-exchange patterns predicted by the model (Figures 2 and 3, and S3; see the entire simulated period in the Supporting Information, Dashboard), it could be observed that the carbon budget of *N. undulata* was consistently positive, that is, even under the most pessimistic scenario ($A_{max}/R_d = 3$), on days where light intensity was high or medium (maximum values equal or above 300 $\mu mol\, m^{-2}\, s^{-1}$) and some precipitation was recorded early in the day, so that thallus water content was sufficient but not too high during the day (Figure 2; Figure S3). Consistent diel net carbon losses occurred when light intensity was medium or low (maxim below 300 $\mu mol\, m^{-2}\, s^{-1}$), when thalli were wet during the night but mostly dry during the day (Figure 3), or thallus water content remained at very high values (Figure S1). The latter phenomenon was quite strong for this species, since our data suggest that it had a pronounced super-saturation depression of photosynthesis (Figure S1), although the respective species-specific parameters were highly uncertain. Neutral diel budgets were predicted when the thallus was dry all day so that carbon gains and losses were negligible, that is, within the neutral limits (>−15 and <15 $\mu mol\ CO_2\ g^{-1}\, day^{-1}$). Non-consistent days occurred under a range of weather patterns (SI dashboard).

For *N. undulata*, PoiCarb 1.1 predicted a consistently positive or negative diel carbon budget irrespective of the carbon assimilation scenario (Table S4) for 42% of the 290 simulated dates (Figure 4). Among consistently simulated dates, negative carbon budgets dominated over positive ones (71% against 29% of consistent days), and only five dates resulted in a consistently neutral carbon budget. For the remaining 167 'non-consistent' dates, 58% of the simulated period, the sign of the diel carbon budget depended on whether the most optimistic, $A_{max}/R_d = 12$ or the most pessimistic, $A_{max}/R_d = 3$ light response curve was used (Figure 5). Thereby the medium carbon assimilation scenario ($A_{max}/R_d = 6$) could be positive or negative but was positive only in about a fourth of the non-consistent days (Figure 5b). The diel budgets of non-consistent days ranged from −336 to 305 $\mu mol\ CO_2\ g^{-1}\, day^{-1}$ (Figure 5).

The diel budgets of consistently positive days had values up to 415 $\mu mol\ CO_2\ g^{-1}\, day^{-1}$ (264 for the medium scenario, Figure 5b), with a mean of 154 $\mu mol\ CO_2\ g^{-1}\, day^{-1}$ across all positive days. The most negative days reached −614 $\mu mol\, g^{-1}\, day^{-1}$ (−412 for the medium scenario, Figure 5b), with a mean of −128 $\mu mol\ CO_2\ g^{-1}\, day^{-1}$ across all negative days. The overall carbon budget over the 290 days was 15.4 $mmol\ CO_2\ g^{-1}$ for the optimistic, −9.9 $mmol\ CO_2\ g^{-1}$ for the medium and −32.8 $mmol\ CO_2\ g^{-1}$ for the pessimistic scenario for *N. undulata* (Figure 5). Because these absolute numbers should be taken with caution, we now turn our attention to the differences caused by different diel weather patterns.

The multiple classification tree attributed more importance to daily light intensity than to weather patterns (62% and 38%, respectively) and used a threshold of average daytime PAR (83 $\mu mol\, m^{-2}\, s^{-1}$) at its root (Figure 6; Table S7). Dates with daily light intensity below this threshold were classified as having negative diel carbon budgets with an accuracy of 97% (Table S7). Dates with diel light intensity above the PAR threshold were further classified based on diel weather patterns (Figure 6). High-PAR no-precipitation days (days without precipitation but with leaf wetness during discontinuous hour blocks along the 24-h period) were discriminated as having negative diel carbon budgets with 75% accuracy, and only two positive diel carbon budgets were mistakenly classified as negative (Table S7). In turn, high-PAR rainy days (with precipitations along the entire date, during light hours, until noon or during discontinuous hour blocks along the 24-h period) were classified as having positive diel carbon budgets with 81% accuracy, while seven negative diel carbon budgets were mistakenly classified as positive (Table S7). Two weather patterns did not appear in the rules of this classification tree: no precipitation with wet leaves all day and wet during

FIGURE 2 Example date (15 September 2019) with carbon exchange (a) and thallus water content (b) patterns resulting in a net diel carbon gain (indicated by the green + in (a)) for *Neckeropsis undulata* simulated by PoiCarb 1.1 based on 10-min resolution microclimate data (c–h). In (a), A_{max}/R_d annotations (12, 6 or 3) indicate diel carbon budgets calculated in alternative carbon assimilation scenarios (Table S4). The *x*-axis in (h) is common to all plots and indicates 24 h; shaded areas indicate night time before 6 AM and after 6 PM; sun in (c) indicates that this was a bright day.


(a)
Neckeropsis undulata
Diel carbon balance on 2019-05-21
Amax/Rd: (µmol g−1 day−1)
12: 248
6: 122
3: 7
An mol g−1 s−1
(b)
mean 172 max. 354 % dw
WC (% dw)
(c)
daily integral 102.9
max. 760.7
mmolm−2 day−1
µmol m−2 s−1
PAR µmol m−2 s−1
(d)
min. 78.3 mean 96.7 max. 100 %
RH (%)
mean 0.1 max. 0.8 kPa
(e)
VPD (kPa)
(f)
total 0.2 mm
Rain (mm)
(g)
total 942 minutes
Wet leaf period (min)
(h)
min. 21.2 mean 23.5 max. 27.9 ºC
T (ºC)

light hours, because they were among those below the PAR threshold and hence classified as negative. Overall, this multiple classification tree predicted diel carbon gains with 88% accuracy and diel carbon losses with 92% accuracy and reached a general accuracy of 91% (Figure 7a; Table S7). When applied to three validation data sets, the subset of non-consistent dates for *N. undulata* ($n = 126$) and the subsets of dates for *P. raddiana* (270) and *S. transversale* ($n = 269$) with either positive or negative diel budgets according to their medium carbon assimilation scenarios, these multiple classification rules reached a general accuracy of 74%–79% (Figure 7b–d).

For the other two species, the number of positive days was very low (4% for *P. raddiana* and 11% for *S. transversale*), while the decision trees expected the same days to be positive as in *N. undulata*, so that many days were misclassified as negative (Figure 7c,d). However, the dates of the few positive days for each species were recognized as such and were also very positive for *N. undulata*. This date matching for positive days for the three species indicates that, in general, the weather patterns leading to a diel net carbon gain for *N. undulata* also led to an improved diel net carbon gain for the two co-occurring species, *P. raddiana* and *S. transversale*.

4 | DISCUSSION

The most important driver of bryophyte carbon budgets in the studied rainforest tree crowns was light intensity, which was frequently insufficient for photosynthesis to compensate for respiratory losses. On days with higher light intensities, precipitation recorded within the canopy (excluding light rains fully intercepted but including dripping water from fog combing by the canopy) generally allowed bryophytes to obtain diel net carbon gains, while a lack of precipitation, even if bryophytes were wet during part of the day, led to negative carbon budgets on most days. Since bright rainy days were relatively rare, the modelled carbon budgets in the studied bryophytes were negative on most days, indicating a precarious ecophysiological situation. This may well explain their relatively low abundance in tropical lowland forests, even when allowing for the uncertainty of the physiological measurements to explicitly propagate through the model showed that alternative scenarios are also possible under current weather patterns.

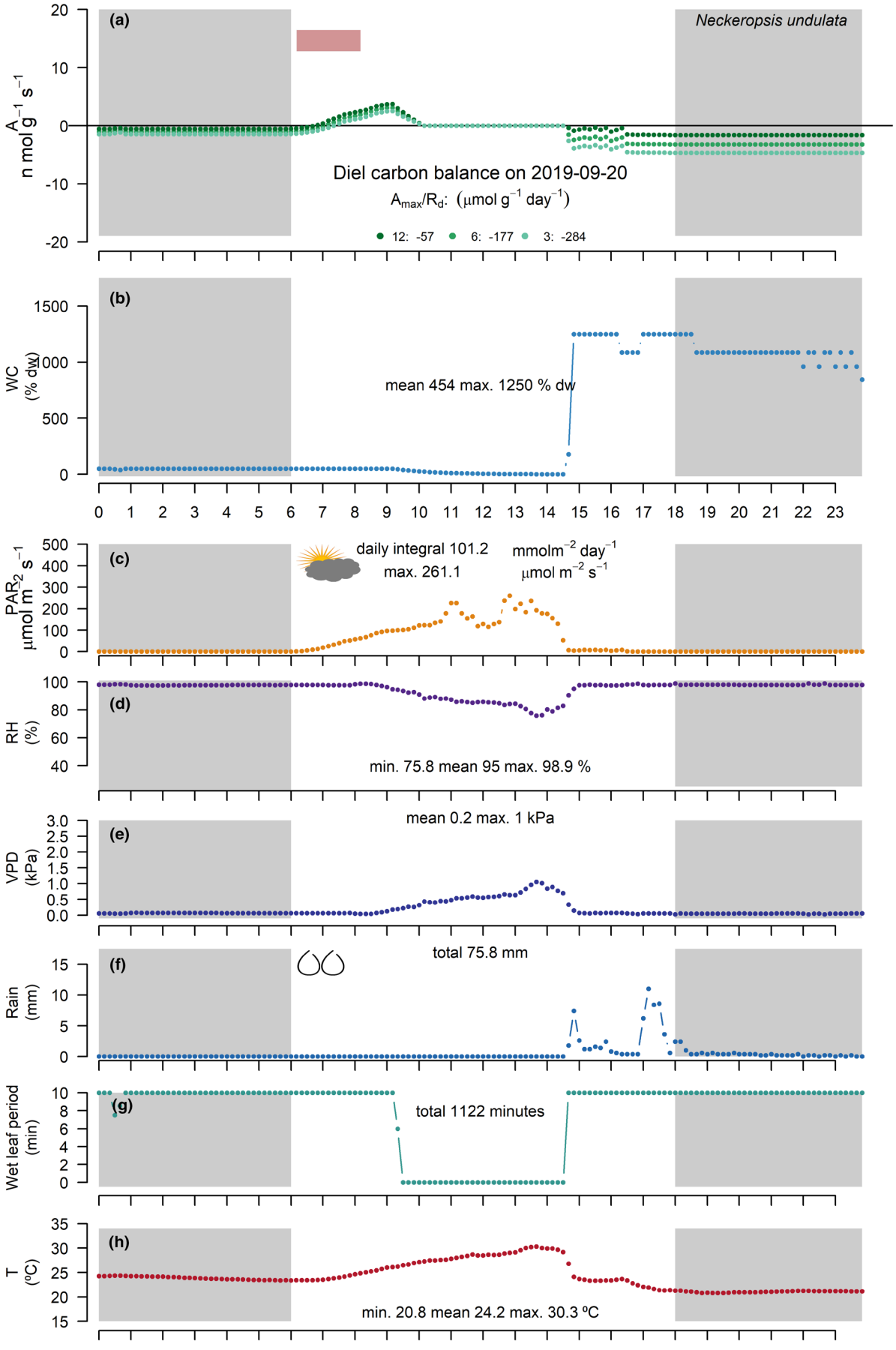
4.1 | Model performance

As already demonstrated by Nikolić et al. (2024, 2026), the use of PoiCarb can provide insights into both diel and long-term patterns of bryophyte carbon exchange. The propagation of parameter uncertainty in the model output confirmed that the quantitative output of PoiCarb 1.1 is very sensitive to the physiological parameters. Our parameter estimates resulted in a broad uncertainty range (Figure S1). This allowed us to study a range of scenarios that should cover other species similar to *N. undulata*, which according to our measurements has a ratio of maximum photosynthesis rate to dark respiration rate (A_{max}/R_d) between 3 and 12. The emergence of enough positive days from this A_{max}/R_d range allowed us to distinguish positive from negative daily carbon budgets. The best-fitting parameters estimated for *P. raddiana* and *S. transversale* (with $A_{max}/R_d = 1.7$ and 2.4, respectively; Table S4) led to more pessimistic medium carbon assimilation scenarios, suggesting that these species should not be able to survive under the climatic conditions in the studied tree crowns. Although this may be due to inaccuracy in the parameter estimates, reports of such unfavourable A_{max}/R_d ratios are, in fact, not uncommon for tropical bryophytes (Wagner et al., 2014) and bryophytes in other climate zones (Pannewitz et al., 2005). These low A_{max}/R_d ratios pose a problem for understanding how bryophytes manage to obtain positive carbon budgets (Zotz & Rottenberger, 2001). We based our models on almost the full range of A_{max}/R_d ratios observed in other tropical bryophytes (Wagner et al., 2014). Thus, in spite of uncertainties about the parameter values, explicitly including the uncertainty associated with the physiological parameters allowed us to assess weather effects on carbon budgets and to evaluate what weather conditions are 'good' or 'bad' for the carbon budget.

Treating carbon budgets as a categorical outcome (positive, neutral or negative) accounted for the inherent uncertainty associated with a modelling exercise and allowed us to use a decision tree for classifying the days with consistent results for alternative carbon assimilation scenarios (Table S4; Figures 4 and 5). We defined neutral days as days with a carbon budget consistently close to zero (~5% of the range of the modelled diel carbon budget). On such days (<2% of the studied period), carbon exchange was negligible, but budgets very close to zero may also emerge when photosynthesis and respiration are balanced. Using non-consistent days as a validation dataset allowed us to test the robustness of the classification criteria for predicting 'good' and 'bad' days, showing that even for less certain days, the weather type predicted carbon budgets with high accuracy (Figure 7b).

Moisture conditions directly determine the modelled thallus water content and, therefore, indirectly the modelled diel carbon budgets (Metcalfe & Ahlstrand, 2019; see the overall input and output in supplementary results in the Supporting Information; Figure S4). In our simulations, these direct effects on thallus water content and indirect effects on carbon exchange result in a dominance of negative over positive carbon budgets, which constitutes

FIGURE 3 Example date (20 September 2019) with carbon exchange (a) and thallus water-content (b) patterns resulting in a net diel carbon loss (indicated by the red—in (a)) for *Neckeropsis undulata* simulated by PoiCarb 1.1 based on 10-min resolution microclimate data (c–h). In (a), A_{max}/R_d annotations (12, 6, or 3) indicate diel carbon budgets calculated in alternative carbon assimilation scenarios (Table S4). The *x*-axis in (h) is common to all plots and indicates 24 h; shaded areas indicate night time before 6 AM and after 6 PM, the cloud over the sun in (c) indicates that this was cloudy day; drops in (f) indicate heavy rain, here occurring in the afternoon and sending the bryophyte well-hydrated (b) into the night.


(a)
Neckeropsis undulata
Diel carbon balance on 2019-09-20
A_{max}/R_d: (µmol g^{-1} day^{-1})
12: -57 6: -177 3: -284
A^{-1} n mol g^{-1} s^{-1}
(b)
mean 454 max. 1250 % dw
WC (% dw)
(c)
daily integral 101.2
max. 261.1
mmolm^{-2} day^{-1}
µmol m^{-2} s^{-1}
PAR µmol m^{-2} s^{-1}
(d)
min. 75.8 mean 95 max. 98.9 %
RH (%)
mean 0.2 max. 1 kPa
(e)
VPD (kPa)
total 75.8 mm
(f)
Rain (mm)
(g)
total 1122 minutes
Wet leaf period (min)
(h)
min. 20.8 mean 24.2 max. 30.3 ºC
T (ºC)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23

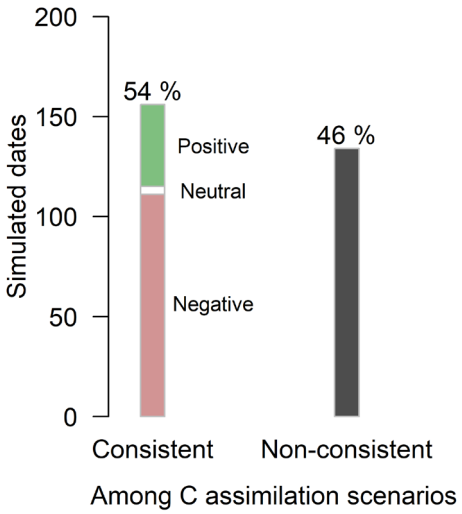


FIGURE 4 Count of dates according to the diel carbon budget of the tropical moss *Neckeropsis undulata* as calculated based on local microclimate data with the carbon-exchange model PoiCarb 1.1. Counts are categorized according to the consistency among 'optimistic' and 'pessimistic' carbon assimilation scenarios (Figure 1; Table S4) and coloured according to diel carbon gains and consistency.

a paradox: bryophytes are present in an environment where their simulated carbon budgets are mainly negative. Such a paradox has been highlighted to poikilohydric autotrophs in other world regions (Zotz & Rottenberger, 2001). The bryophyte colonies, although occurring along the branches, are more abundant towards the branch base, where they may have a thicker boundary layer than that of our climate sensors, located at least 2 m from the branch base. Furthermore, the water-holding capacity of the tree bark may extend the hydrated period for the epiphytic bryophytes in any branch section, while the climate sensors are isolated from the bark. Thus, the dominance of negative over positive carbon budgets appears to suggest that our simulations with PoiCarb 1.1 may have underestimated carbon gains and/or overestimated carbon losses.

The underestimation of carbon gains as well as the overestimate of carbon losses can be related to differences in the climate data recorded and the climate actually experienced by bryophytes. Reducing the differences between climate records and the climate within the bryophyte colonies may result in overall higher carbon assimilation and lower carbon losses because bryophytes regulate, to some extent, water loss (Perera-Castro et al., 2026). The water module in the current PoiCarb version, which was originally developed to study tropical rainforest understorey bryophytes, assumes that the water budget is minimally affected by wind and light (Nikolić et al., 2024). However, wind and solar radiation may be important drivers of drying speeds in tree crowns. On the other hand, the water-holding capacity of tree bark may be a factor extending hydrated periods for epiphytic bryophytes, and the boundary layer of the branches may provide a moister microclimate and slower drying under low-wind conditions. Future adjustments of the model processes determining drying speeds of bryophyte thalli are a clear priority in further model development.

4.2 | Effects of the weather pattern on bryophyte carbon exchange

A bright day with some moisture input was most likely to result in a positive diel carbon budget. Carbon budgets were highest when precipitation occurred early during the day and the bryophytes were dry by dusk, but to distinguish good from bad days in terms of positive and negative carbon budgets, it was sufficient to have rain at any time of the day, as long as there was also enough light during the day. Light levels and water input are usually negatively correlated, with precipitation coinciding with cloudy and hence darker conditions, which explains why the number of 'good days' was relatively low. Compared to vascular plants, bryophytes are considered shade-tolerant plants. However, bryophytes represent a wide spectrum of light affinity, ranging from shade tolerance to light preference (Hill et al., 2007). While *N. undulata* occurs from the understorey to the upper canopy in tropical forests, being a light generalist, other species in the tree crowns are usually light-loving bryophytes (Gradstein, 1992) and thus probably have high light compensation points and relatively low carbon gains under cloudy conditions.

In addition to unfavourable light and moisture conditions already challenging bryophytes in tropical lowland forests, air temperature could become important in pushing bryophytes towards their physiological limit if it increases beyond current ranges due to global warming (Nikolić et al. 2026; Zotz & Bader, 2024). This can lead to high respiration rates at high temperatures and fast drying, which shortens periods of photosynthetic activity. Temperature effects were not addressed directly in our study, but indirectly through drying rates depending on the VPD, which depends on temperature and the water content of the air (Anderson, 1936). Nikolić et al. (2026) found that faster drying is the most important driver of changes in carbon budgets at higher temperatures for rainforest understorey bryophytes. Whether temperature has the same effect on bryophytes in higher forest strata, including the upper canopy, is a relevant question for future research, but we do not expect any difference. The main driver of bryophyte performance is light, as long as the thallus water content allows for metabolic activity. Therefore, to understand climate-change effects on tropical bryophytes, particular attention should go to the climate change-induced increase in the frequency and severity of dry spells in the Amazon basin (Pohl et al., 2023). During such prolonged droughts, canopy and understory species may face limits not only in terms of their carbon budget but also even in terms of their desiccation tolerance (Pardow & Lakatos, 2013). The proposed refuge function of valleys with morning fog occurrence (Pohl et al., 2021, 2023) needs to be evaluated for poikilohydric organisms like bryophytes, accounting for the differences and interactions of fog- and rain-induced diel carbon-exchange patterns as well as for the nuances imposed by

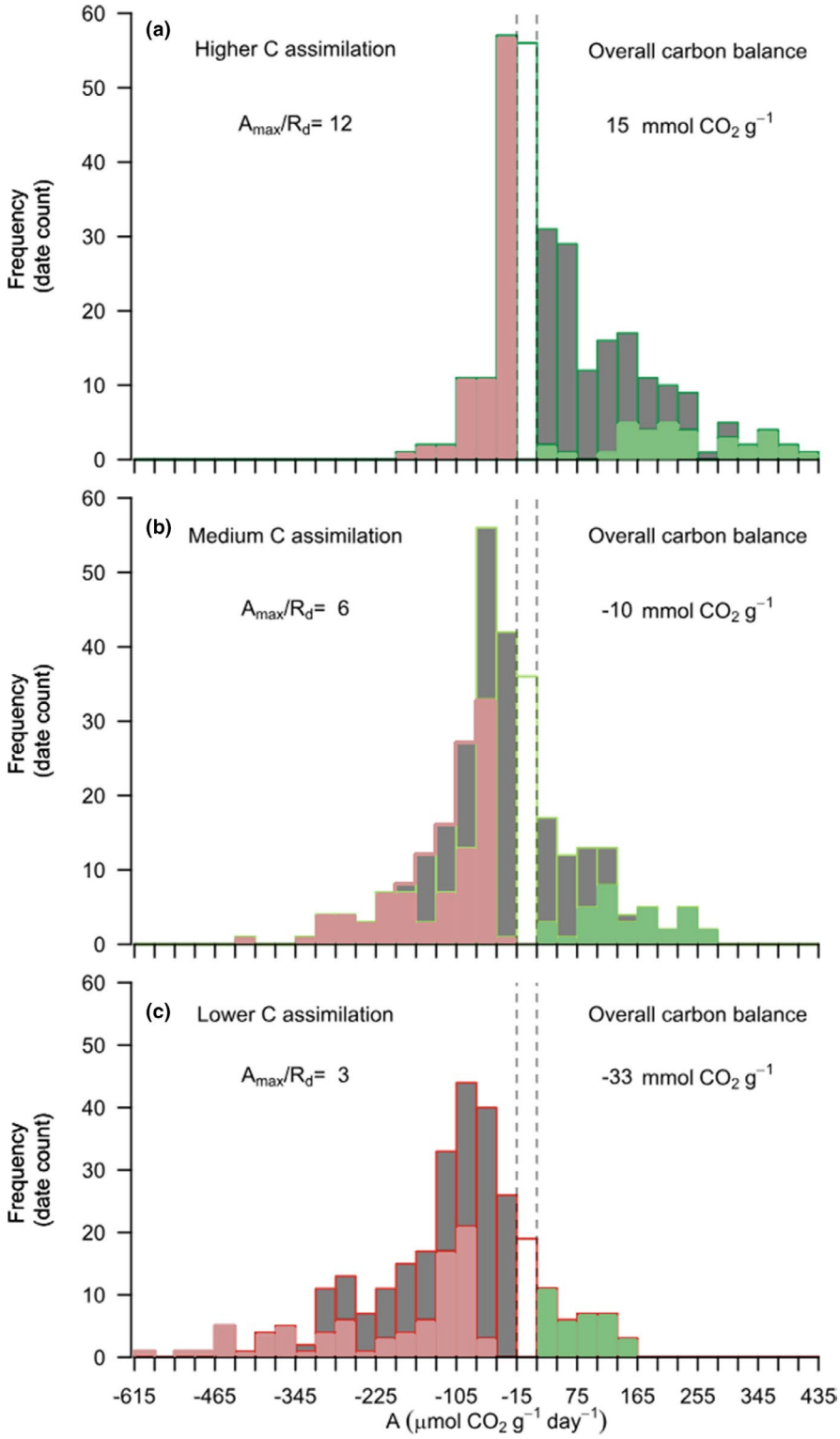
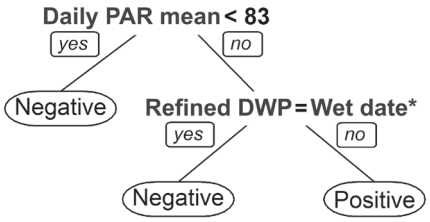


FIGURE 5 Frequency of dates under three carbon assimilation scenarios (a through c) for *Neckeropsis undulata*. Vertical dashed lines highlight the range of carbon budgets around zero (−15 to 15 μmol CO_2 g^{-1} day^{-1}) that we considered neutral, and separate carbon gains to the right from carbon losses to the left. In each scenario, counts of dates with consistent prediction are coloured (white for neutral dates) and the additional counts of non-consistent dates are grey.

each meso-environment, that is, canopy and understorey, and by the functional diversity of poikilohydric organisms.

Our analysis included two bryophyte life forms, a dendroid moss (*N. undulata*; Sreenath & Rao, 2021; WFO, 2026) and two leafy liverworts (*P. raddiana* and *S. transversale*). The substantial differences in their photosynthetic performance (Figure 7), modelled from their physiological profiles (Figures S1 and S2), could relate to their life forms, but systematic evaluations of physiological differences between life forms are surprisingly scarce. For several decades, the life form of poikilohydric organisms has been used as relevant descriptor (Mägdefrau, 1982; Untari, 2024) related to biomass estimates (Oishi, 2024) and to functional responses to environmental drivers (Hill et al., 2007). We suggest a systematic assessment of whether physiological profiles relate to life forms in poikilohydric organisms. Such an assessment would help to better understand how these organisms function and would further enhance our ability to

(a)



(b)

	Predicted				
	Negative		Positive		
Observed	Count	%	Count	%	Total
Negative	**77**	**92**	7	21	84
Positive	4	12	**30**	**88**	34
Total	81		37		118

FIGURE 6 Multiple classification tree (a) and its accuracy table (b) for 118 diel carbon budgets consistently simulated by PoiCarb 1.1 under three alternative carbon assimilation scenarios for the canopy moss *Neckeropsis undulata*. In a, daily PAR mean = average photosynthetically active radiation during light hours, with <83 indicating the classification threshold (in μmol $m^{-2}s^{-1}$), and DWP = Diel weather patterns, with Wet date* including two categories: No precipitation but wet leaves until noon and no precipitation but wet leaves during discontinuous hour blocks along the 24-h period. The classification outcome is binary: Negative = days with net carbon losses, and Positive = days with net carbon gains. In (b), bold numbers highlight accurate classifications.

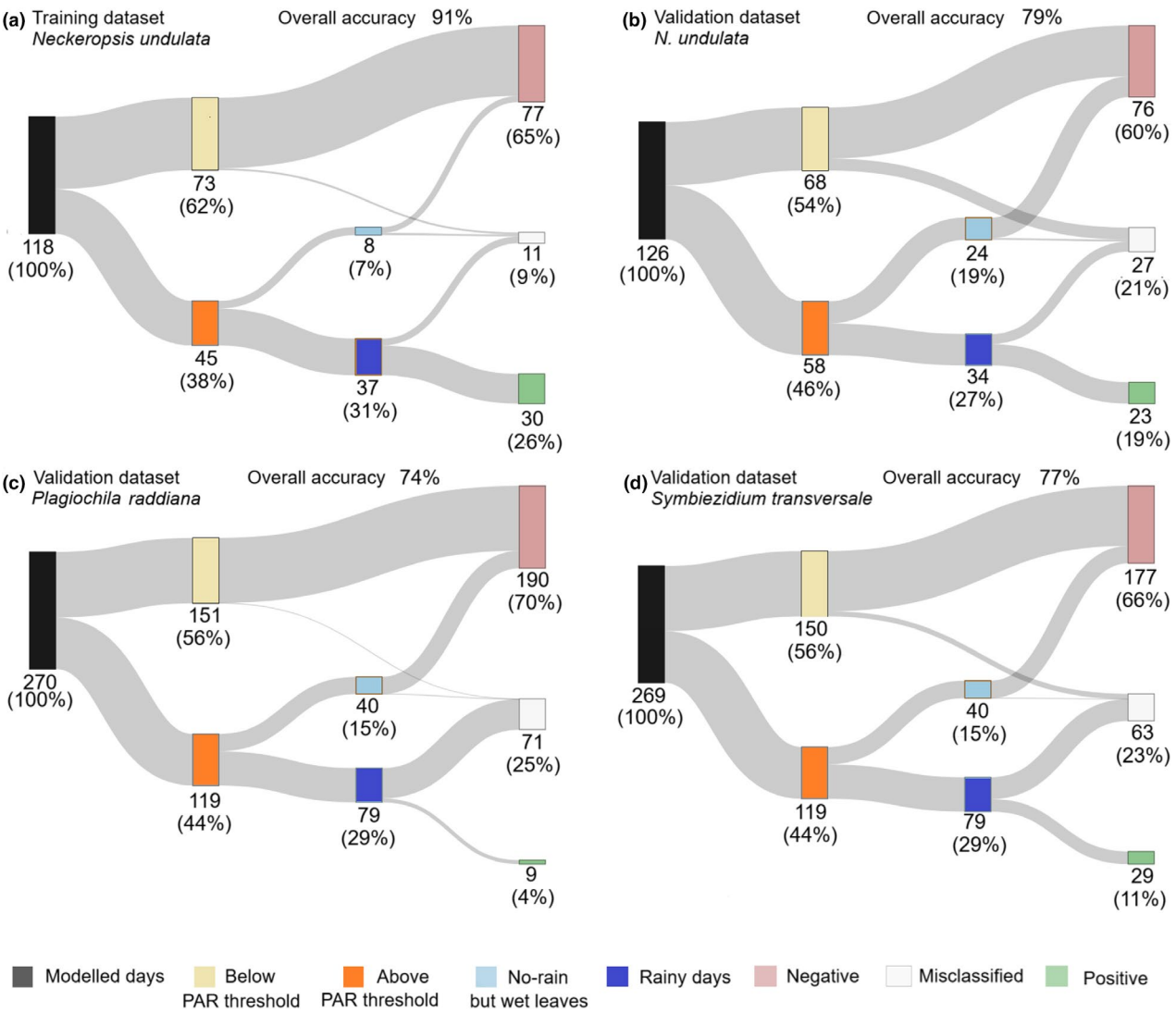


FIGURE 7 Sankey diagrams showing the multiple classification tree discriminating positive from negative diel carbon budget of bryophytes in tropical rainforest tree crowns based on weather conditions, for the training (a) and validation (b) data for *Neckeropsis undulata* and for two co-occurring bryophyte species (c and d). Shown are classifications applied to the outcome of simulations of diel carbon budget by PoiCarb 1.1 for (a) days on which the budget was consistently predicted to be positive or negative across three carbon assimilation scenarios assuming different A_{max}/R_d ratios, (b) the non-consistent (i.e. the sign of the budget depended on the scenario used) days for *N. undulata* according to the medium carbon assimilation scenario ($A_{max}/R_d = 6$), and the medium carbon assimilation scenario for two other bryophyte species (c, d). At each node, the count of days and, in parenthesis, its percentage relative to the modelled days classified are given.

model how entire communities respond to climate conditions within and across biomes.

5 | CONCLUSIONS

Assessing the frequency of dates with more favourable or less favourable weather patterns supported the *unfavourable-timing* hypothesis—that frequent weather patterns limit carbon gain and increase carbon loss in poikilohydric autotrophs in the tropical lowlands—because indeed unfavourable diel weather patterns appear to be more frequent than those allowing a positive carbon budget in the studied tropical lowland forest. This pessimistic conclusion, sensitive to physiological parameters, holds even with the most optimistic scenario, that is, for species with higher photosynthetic capacity relative to dark respiration (A_{max}/R_d). Our findings strongly suggest that tropical lowland climates can be indeed be considered marginal for bryophytes because gaining a positive long-term carbon budget is a challenge.

Although the biomass of tropical lowland bryophytes is generally low (Frahm, 1990; Horwath et al., 2019; Wolf, 1993), probably as a result of these limited carbon gains, their species richness can still be quite high (Gradstein, 2021; Berdugo, Gradstein, et al., 2022a; Berdugo, Gradstein, et al., 2022b). Global temperature increases will probably negatively affect this diversity by reducing the number of days with positive carbon budgets even further, thus imposing a more restrictive environmental filter.

By implementing PoiCarb 1.1, we showed that there are pronounced differences in the diel carbon budgets of bryophytes depending on the weather patterns, which implies that a change in these patterns will affect carbon gain and thereby the biomass and species composition of the tropical bryophyte communities. Our model also has a broad application potential to understand the effects of weather conditions on other tropical bryophyte and lichen species and in climatic contexts beyond the tropics. To reach this potential, three inputs are required: (i) high-resolution microclimate data series, (ii) well-replicated measurements of bryophyte carbon exchange and (iii) experiments to determine the drivers of poikilohydric hydration–dehydration dynamics; being the last input the one more urgently needed to improve the model accordingly. With this input and improvement, we may ultimately be able to use PoiCarb not only to determine what weather conditions are better or worse for the carbon balance of selected, arguably representative species, but also to help explain current and predict future distributions of poikilohydric autotrophs through an improved understanding of the strategies and functioning of these important and fascinating organisms.

AUTHOR CONTRIBUTIONS

Maaike Y. Bader and Monica B. Berdugo conceptualized the study and led the investigation. Louise Guérot collected the physiological data. Sarah Brach curated the physiological data. Nada Nikolić, Maaike Y. Bader and Gerhard Zotz developed PoiCarb. Monica B. Berdugo and Maaike Y. Bader modified it into PoiCarb 1.2. Maaike Y. Bader led funding acquisition with the support of Jörg Bendix. Monica B. Berdugo led data analysis and visualization as well as the manuscript writing with the support of Maaike Y. Bader and Philipp Porada. All authors contributed to the writing and editing of the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data, code and the dashboard with the high-resolution PoiCarb output are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2fqz6130f (Berdugo, 2026).

STATEMENT OF INCLUSION

The involvement of early career scientist of the region where the raw data were collected, via internships to support specialized field and monitoring techniques (see Acknowledgements), constitutes knowledge transfer. We are confident that this involvement will foster collaborations in future research projects. As a model-based work, the bulk of the study (data management, modelling and output analysis, writing and visualization) was conducted in Germany.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Gas exchange response curves for the three species.

Figure S2. Desiccation and rehydration curves for the three species.

Figure S3. Additional examples of positive days for *N. undulata*.

Table S1. Parameters describing the gas exchange response curves for the three species.

Table S2. Parameters describing the dehydration curves for the three species.

Table S3. Physiological parameters input.
Table S4. Alternative carbon assimilation scenarios.
Table S5. Periods set according to moisture timing.
Table S6. Comparison among simple classification trees.
Table S7. Summary of the multiple classification tree.
Data S1. Supplementary methods.
Data S2. Supplementary results: overall output and input.
Figure S4. Comparison between diel carbon-exchange patterns (left) and the climate variables (right) used to model them.
Data S3. Scripts Carbon-exchange patterns in canopy bryophytes (Inputs.Rmd, PoiCarb 1.1.Rmd). Dashboard Diel plots modelled for *N. undulata* (SI_Dashboard.html). *The scripts and the Dashboard are available on: Dryad: https://doi.org/10.5061/dryad.2fqz6130f and Zenodo: https://doi.org/10.5281/zenodo.14875786

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