Journal of Tropical Ecology (2018) **34**:308–315. © Cambridge University Press 2018
doi:10.1017/S0266467418000275

The long-term effect of typhoons on vascular epiphytes in Taiwan

Rebecca C.-C. Hsu[1,*], Jan H.D. Wolf[2], Jer-Min Tsai[3] and Yi-Chin Lin[4]

[1] Taiwan Forestry Research Institute, No. 67, SanYuan Street, 10079 Taipei, Taiwan
[2] University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics (IBED), PO Box 94248, 1090 GE Amsterdam, the Netherlands
[3] Department of Information Communication, Kun Shan University, No. 195, Kunda Rd., 710 Tainan, Taiwan
[4] Department of Life Science, Tunghai University, 1727, Taiwan Blvd. Sec. 4, Taichung, Taiwan

(*Received 12 January 2018; revised 2 July 2018; accepted 2 July 2018; first published online 26 July 2018*)

Abstract: We used all 167 typhoon warnings issued by the Taiwanese Central Weather Bureau from 1958–2006 to assess the long-term effect of cyclone disturbance on vascular epiphytes. Tracks and eyes of past typhoons were plotted as circles with radii of Beaufort scale 7 and 10, and the frequency of each cohort in 1-km^2 grid cells was calculated. The presence of vascular epiphytes in the same grid cells was predicted using species distribution models (SDMs). First, we used herbarium specimens and other sources to compile a comprehensive georeferenced vascular epiphyte database that contained 39 084 records in 331 species. Next, we assigned each epiphyte record to a cell in the same 1-km^2 grid as above. Finally, we used SDMs (MaXent), based on 30 environmental variables except typhoon frequency, to predict the potential presence of each species in the grid cells. For our analysis we only considered cells east of the central mountain ridge where typhoons hit with full force. After elimination of rare species and species that could not be validated in the SDMs, we were left with 156 epiphyte species in 10 725 1-km^2 cells. The number of projected species in the cells was 36.5 on average, varying between two and 82 species. Correlation analyses showed that, over time, typhoons led to a decrease in epiphyte richness at Beaufort scale 7 and 10 (Pearson's $r = -0.07$ and -0.08 respectively). Ferns, orchids, hemiepiphytes and dicotyledons generally showed the same pattern, except hemiepiphytes that showed a positive correlation at B7 (Pearson's $r = 0.15$). A partial canonical correspondence ordination analysis showed that, independent of temperature- and rainfall-related variables, Beaufort scale 7 and 10 typhoons also had significant influence on the species composition of the vascular epiphyte communities in the landscape. We recommend *in situ* monitoring of epiphytes over a long period to corroborate the suggestion from this indirect study that typhoons have a long-term effect on the distribution of epiphytes in Taiwan.

Key Words: disturbance, hurricane, island, Pacific Asia, species distribution models

INTRODUCTION

Tropical cyclones often have an immediate effect on forest structure and associated microclimate (Basnet *et al.* 1992, Chazdon 2003, Mabry *et al.* 1998). For instance, understorey light levels may increase by 30% from canopy defoliation (Lin *et al.* 2003). Despite extensive short-term damage, recovery of forest structure and composition may be relatively rapid following tropical cyclones when only the forest canopy is affected (Chazdon 2003, Kang *et al.* 2005). However, forests that are repeatedly disturbed by cyclones, called typhoons in the western Pacific, show long-term changes in forest structure, such as a lower tree height and a decrease in tree diversity (Chang 2001, Chuang 2005, Goode & Allen 2008, Kang *et al.* 2005, Lee *et al.* 2008, Lin *et al.* 2011, Lugo 2008). In particular when the cyclone triggers large-scale landslides in primary forest, such as during typhoon Morakot when in Taiwan a record-breaking 2777 mm rainfall fell in 72 h, the forest is unlikely to recover in the near future (Chu 2014, Hilton *et al.* 2008, Tsai *et al.* 2010).

Whereas the devastating impact of a tropical cyclone on forest trees has been relatively well studied, far less is known about the effect of typhoons on other components of the forest (Lugo 2008). Canopy epiphytes may be severely impacted by cyclones, because they are subject to the full force of the winds and are especially vulnerable to changes in the microclimate associated with alteration of the forest structure (Benzing 1998). Immediate observations in Florida have shown that a single hurricane may have a devastating effect on the population density of epiphytic bromeliads, resulting

---

* Corresponding author. Email: ecogarden@tfri.gov.tw

in a reduction by 12–43% (Oberbauer *et al.* 1996). Representatives, but not all, of other epiphyte groups may be better attached and/or less sensitive to desiccation after impact, resulting in local changes in community assemblages. For example, orchids in Florida were less sensitive than bromeliads and in Honduras orchids were not as much affected as ferns (Batke & Kelly 2015, Oberbauer *et al.* 1996).

Several studies suggest that the immediate impact of cyclones on epiphytes persists in the long term (Batke & Kelly 2015, Mújica *et al.* 2013). One reason for the slow recovery of the epiphyte vegetation may be that long-distance colonization by epiphytes of large depleted patches of forest is a slow process. In apparent agreement, epiphyte populations are shown to possess a clear spatial genetic structure in the landscape (Cascante-Marín *et al.* 2014). Slow colonization is especially to be expected if source populations are small and at a large distance, as is often the case on isolated tropical islands. On tropical islands in the Caribbean, the low richness of epiphytes has indeed been attributed to geographic isolation and large-scale disturbances of tropical cyclones (Migenis & Ackerman 1993). Whereas the above-mentioned studies report shifts in epiphyte community structure near the vortex of the cyclone, it is less clear what happens in its periphery where associated increased precipitation may even benefit canopy epiphytes.

In this study, we addressed the hypothesis that in Taiwan typhoons have a long-term effect on epiphytic vegetation. Our specific hypotheses were as follows: (1) Repeated historical typhoons decrease local epiphyte species richness and (2) have an effect on the composition of epiphyte assemblages; (3) the effect near the vortex of the typhoon differs from that in its periphery.

Study area

Taiwan is an island located in the western Pacific (21°–25°N, 119°–122°E; Figure 1) and tropical cyclones are an important aspect of the regional climate (Lin *et al.* 2011). On average, 3.7 typhoons hit Taiwan every year, mostly from June to October. About 80% of all typhoons land on the island's east coast (Chu *et al.* 2012, Wu & Kuo 1999; Figure 1). The central mountain range generally decreases the intensity of typhoons by more than 40% within 12 h after the eye of the cyclone reaches the island (Wu & Kuo 1999). Therefore, typhoon impact in the western leeward side of the central range is relatively mild.

Despite its relatively small area (36 000 km^2), Taiwan is exceptionally rich in vascular plants (*c.* 4000 species) compared with other (sub-)tropical islands such as Hawaii (*c.* 2700 species), the Canary Islands (*c.* 1600 species) and New Caledonia (*c.* 1500 species) (Creese *et al.* 2011, Dawson 1963, Reyes-Betancort *et al.* 2008). The presence of an extensive mountain system accounts for a high diversity of vegetation types on the island, ranging from alpine tundra to tropical rain forest, which partly explains the high species richness. In sharp contrast, but not unlike the Caribbean islands, Taiwan must be considered relatively poor in epiphytes. There have been *c.* 350 species of vascular epiphytes reported for Taiwan, comprising only 8% of the total vascular flora (Hsu & Wolf 2009). Worldwide, vascular epiphytes contribute approximately 9% to vascular plant diversity (Zotz 2013) and especially in wet tropical ecosystems epiphytes often contribute significantly more (Gentry & Dodson 1987), sometimes up to 52% (Kelly *et al.* 2004).

METHODS

We aimed to explore the long-term effect of past typhoons on the vascular epiphyte diversity of Taiwan. Epiphyte distribution is estimated from species distribution models. In our analyses, we separate the effect of lower wind speeds (Beaufort scale 7) enveloping the eye of typhoon from the effect of stronger winds (> Beaufort 10).

Epiphyte distribution

We first compiled occurrences of epiphytic species from herbarium records, published plant inventories and our own botanical observations into a comprehensive georeferenced epiphyte database. Epiphyte records included both true and hemiepiphytes (definitions following Kress, 1986). The final database contained 39 084 records comprised of 331 species (24 families, 105 genera). Ferns and lycophytes contributed most species (171), followed by orchids (120). The epiphyte species in the database were divided into four subcategories, based on life form and taxonomy: hemiepiphytes (abbreviation hemis, e.g. Moraceae, Araceae), ferns and lycophytes (ferns), orchids (orchids) and dicotyledons (dicots). For more detailed information on the species in the database, see Hsu & Wolf (2009).

Next, we allocated each of the 39 084 plotless epiphyte occurrences in the database to grid cells with a spatial resolution of 1 km^2, 35 928 cells in total for the entire island. Multiple occurrences of a species in a grid cell were considered a single record, which reduced the total number of records to 29 087. Whereas over the entire island the average number of documented species in the cells was thus less than one, in 252 cells at least 20 species were recorded with a maximum of 106 species.

It is well known that botanical collections are biased for certain accessible localities as well as taxonomic groups and the absence of species in cells is likely due to

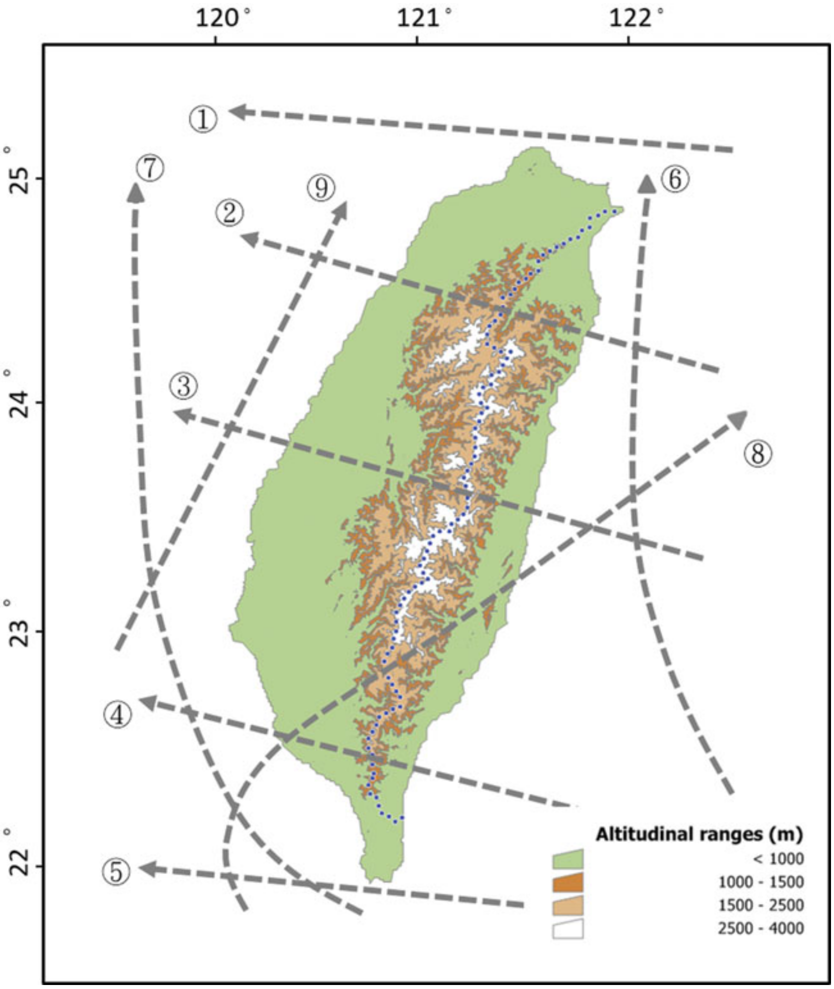

Figure 1. Historical typhoon tracks in the island of Taiwan (21°–25°N, 119°–122°E). The Central Weather Bureau categorizes typhoons with warning records (for the period 1897 to 2014 there were 452 records) into nine trajectories (indicated as dashed lines) as follows: trajectory (1) 13%, (2) 12%, (3) 11%, (4) 10%, (5) 19%, (6) 15%, (7) 7%, (8) 4%, (9) 7%; about 2% were typhoons with singular trajectories. The blue dotted line indicates the highest point in the central mountain range of Taiwan and only the area east of this line was analysed in this study.

insufficient sampling. To mitigate a sampling effect, we used MaXent (version 3.3.3k) species distribution models (SDMs) to fill in the distribution gaps (Phillips *et al*. 2006). MaXent puts no weight on the absence of a species in a grid cell and is therefore particularly suited. For predictor variables, we used 30 environmental variables, including nine topographic variables, 16 climatic (12 precipitation-related and four temperature-related) variables and five land-cover/vegetation indices (Appendix 1). The resolution of the variables was identical to that of the typhoon disturbance measure (1-km^2 grid).

From the initial 331 species in the epiphyte database we excluded rare species (79) and species that could not be validated in the SDMs (93), leaving 156 species (78 ferns, 25 orchids, 15 dicots and 38 hemis) for which we predicted the potential presence in each of the 1-km^2 grid cells. Due to the complex effect of the central mountain range on cyclone circulation, we only considered cells east of the central range, 10 725 cells in total. After modelling, the average number of projected species records (391 659 in total) in each cell was 36.5, ranging from 2 to 81 species per cell (Figure 2). For more detailed information on the epiphyte SDMs, see Hsu *et al*. (2014).

Typhoon disturbance

We analysed the pathways and strengths over time of all typhoons recorded by the Taiwanese Central Weather Bureau (CWB) that approached the east coast of Taiwan from 1958 to 2006, 167 in total. The CWB officially releases a typhoon warning when tropical cyclones reach sustained winds of at least 62 km h^{-1}; note that this wind speed is considerably less than a Category 1 hurricane (119–153 km h^{-1}) on the Saffir–Simpson Hurricane Wind Scale (Schott *et al.* 2012). In Taiwan, typhoons are

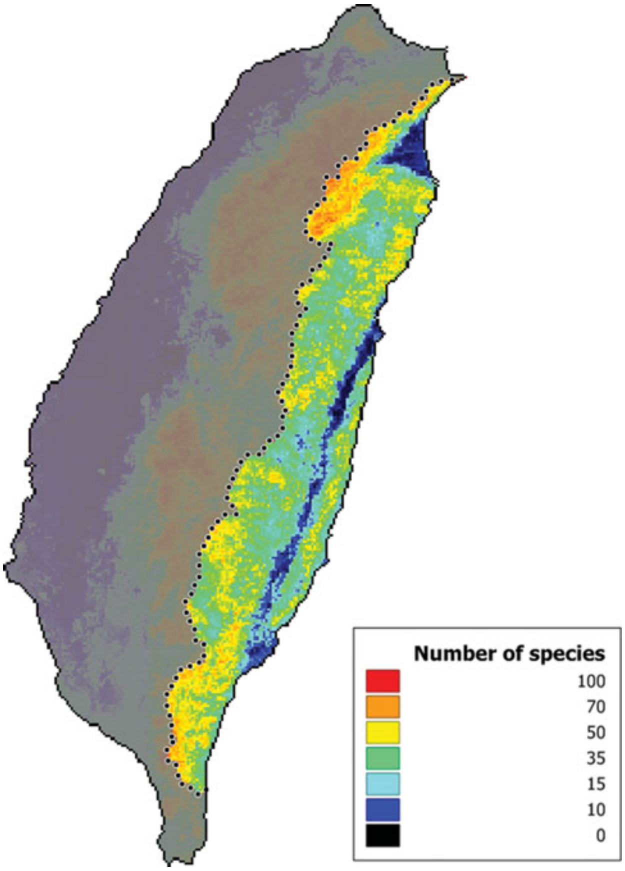

Figure 2. Modelled epiphyte species richness in 1-km^2 grid cells in Taiwan. The dotted line indicates the highest point in the central mountain range of Taiwan and in this study only the area east of this line was analysed for the effect of typhoons.

categorized as mild (62–117 km h^{-1}), moderate (118–183 km h^{-1}) or severe (>183 km h^{-1}). First, the track of each typhoon was traced as circles around the eye with radii of Beaufort scale 7 and 10, corresponding to sustained winds of at least 50 km h^{-1} and 89 km h^{-1}, respectively (Lin *et al.* 2006). Next, the accumulated number of hits in each cell of the species distribution 1-km^2 grid was calculated for each wind-speed cohort, yielding two separate cyclone disturbance variables (B7 and B10) as a proxy for cyclone disturbance. While there was overlap between the two levels of disturbance (when a cell is hit by a B10 cyclone it also counts as a B7 hit), B7 envelopes were generally more extensive, and the eye of a recorded typhoon did not always land on the island.

Analyses

The effect of tropical cyclone disturbance, namely the frequency of B7 and B10, on general and subcategory epiphyte species richness in the grid cells was tested with Pearson correlation analysis. We used a direct gradient ordination analysis, canonical correspondence analysis (CCA), to assess the influence of cyclone disturbance on epiphyte distribution (ter Braak 1986). For species data, we used the projected occurrences of 156 epiphyte species in the 1-km^2 grid cells. The environmental variables (30) were the same predictors as used in the SDMs. These variables were first subjected to a principal component analysis (PCA) to avoid multicollinearity. The first two PCA components, correlated with temperature and rainfall, together explained 52% of the variation in the data. Both PCA components were retained in the CCA, as opposed to a third component that had little additional explanatory value (9%). For more information on the PCA, see Hsu *et al.* (2014). Next, we performed a partial CCA on the species distribution with the two cyclone disturbance measures, B7 and B10 frequencies, as environmental predictor variables and the two PCA components as covariables. The significance of the first extracted CCA axis that is constrained to be correlated with typhoon frequency was tested using a Monte Carlo test (999 permutations). The above analyses were performed in R, version 3.4.4, with vegan, a community ecology package available for free at https://cran.r-project.org/web/packages/vegan.

RESULTS

From 1958–2006, a total of 179 typhoon warnings were issued by the Central Weather Bureau, and we analysed 167 typhoons that approached Taiwan towards the east coast. The 1-km^2 grid cell typhoon disturbance map shows areas with dissimilar frequencies of B7 and B10 cyclones (Figure 3). Most severe typhoons in Taiwan apparently land on the east coast at about one-third of its northern point.

The correlation analysis between the B7 and B10 frequencies in the 1-km^2 grid cells (10 725 cells) and the projected epiphyte richness therein (Table 1) shows that typhoon disturbances generally have a significant negative impact on total epiphyte richness and its various components, with the exception of lesser B7 cyclones, which are positively correlated with hemiepiphyte richness (Figure 4).

The partial CCA shows that typhoons also exert an influence on the distribution of epiphytes. After subtracting the variation in the species data that was related to temperature and rainfall (PCA component-1 and -2), both axes related to typhoon frequency explained together 1.6% of the variance (Figure 4). Even though this is a relatively small amount of explained variation, the Monte Carlo permutation test showed that the first typhoon-related axis is nevertheless significantly ($P < 0.01$) different from randomly generated axes.

Table 1. A matrix of Pearson's r correlation coefficients between typhoon frequencies and modelled epiphyte species richness in 1-km^2 grid cells in Taiwan (n= 10 725). Typhoons were divided into two categories: wind speed Beaufort scale 7 (B7) and 10 (B10). Epiphyte species richness (EP, 156 spp.) was divided into several categories: ferns and lycophytes (ferns, 78 spp.), dicotyledons (dicots, 15 spp.), orchids (orchids, 25 spp.) and hemiepiphytes (hemis, 38 spp.). Correlation coefficients are all significant (P < 0.001), except the correlation between hemis and ferns (indicated by an asterisk).

	B7	EP	Ferns	Orchids	Hemis	Dicots
B10	– 0.71	– 0.08	– 0.06	– 0.05	– 0.07	– 0.03
	B7	– 0.07	– 0.15	– 0.05	0.15	– 0.03
		EP	0.91	0.62	0.38	0.69
			Ferns	0.68	– 0.01*	0.49
				Orchids	– 0.19	0.15
					Hemis	0.45
						Dicots

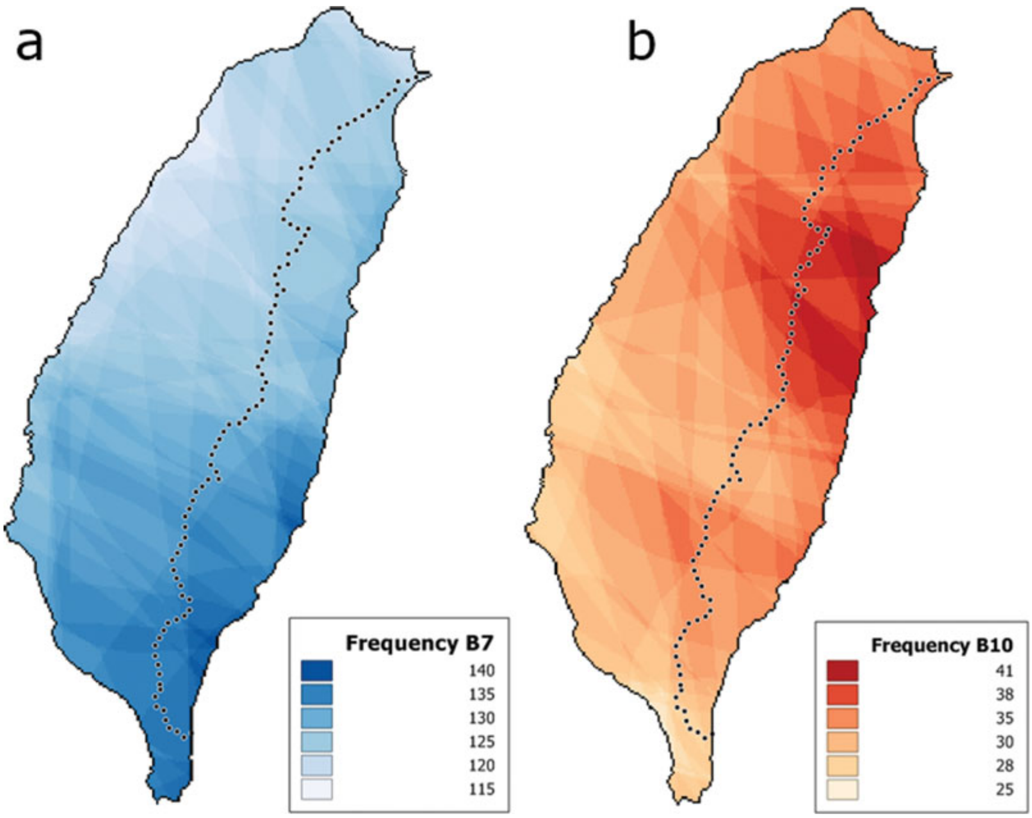

Figure 3. Typhoon frequencies in Taiwan from 1958–2006 in 1-km^2 grid cells, 167 typhoons in total (data from Taiwanese Central Weather Bureau). Tracks and eyes of typhoons were plotted as circles with radii of wind speed Beaufort scale 7 (B7) and 10 (B10) and the accumulated number of hits in each cell was calculated for both wind-speed cohorts, yielding two cyclone frequency maps (a: B7 and b: B10) as a proxy for cyclone disturbance. The dotted line on each map indicates the highest point in the central mountain range of Taiwan and only the area east of this line was analysed in this study.

DISCUSSION

Studies on the effect of typhoons in the North-West Pacific are scarce, in particular on arboreal communities such as epiphyte vegetation. As has been observed in the Atlantic area (Oberbauer *et al.* 1996), anecdotal evidence indicates that epiphyte dislodgement by a typhoon may be extensive (R. Hsu pers. obs.). In Taiwan, fallen bird's-nest ferns and tree branches with epiphytes on the forest floor are very common after a typhoon event, as well as tree falls with heavy loads of epiphytes. The moderate typhoon Soudelor in 2015 caused more than 300 tree falls in the Taipei Botanical Garden (R. Hsu pers. obs.). Our previous study (Hsu *et al.* 2014) suggested the regional patterns of epiphyte distribution could be related to prevailing winds (north-east monsoons and

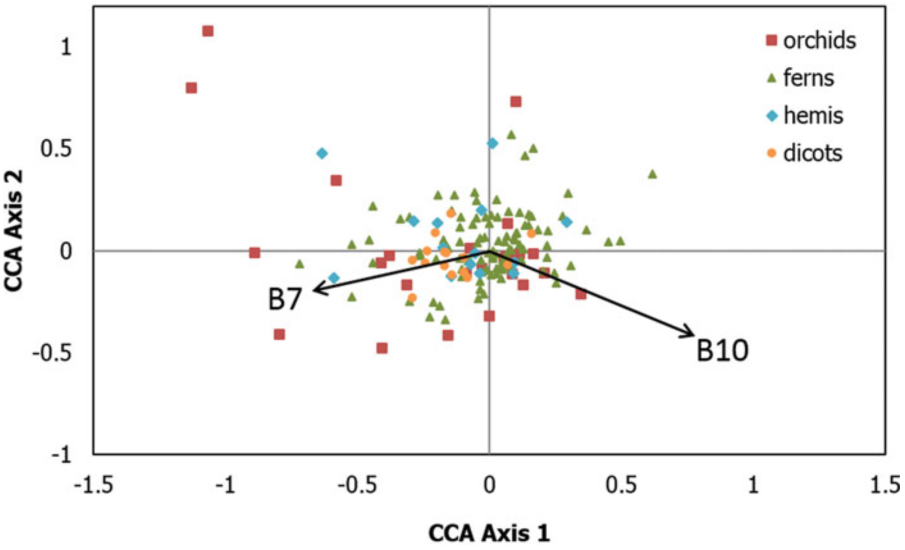

Figure 4. Ordination diagram of a partial canonical correspondence analysis of epiphyte species in 10 725 1-km^2 grid cells in east Taiwan with the frequencies of two cyclone strengths, Beaufort scale 7 and 10 (arrows), as explanatory variables. Covariables are related to temperature and water availability. Epiphyte species are arranged by subcategory: orchids (red squares), ferns (green triangles), hemiepiphytes (blue diamonds) and dicotyledons (orange circles). The first axis is significant (Monte Carlo, $P < 0.01$), explaining 1.6% of the variance.

south-west air flows) that create an additional source of seeds and rainfall. The present study suggests that, over the long-term, typhoons also have an effect on overall epiphyte richness (negative) and the distribution of epiphyte assemblages in the landscape.

Our analysis included 167 recorded typhoons that landed on the east coast of Taiwan between 1958 and 2006. Mild B7 cyclones generally prevailed in the south of the island, while heavy B10 cyclones were more predominant in the north. The differing frequency distribution pattern between the two types of cyclones made a separate analysis of both types of event feasible. Analysing the typhoon frequency over a *c*. 50-y period in 1-km^2 grid cells, we found that B7 and B10 cyclones both had a significantly negative effect on the number of species recorded within those cells. Nonetheless, we observed that B7 cyclones exerted a positive influence on hemiepiphyte richness; this may well be a non-causal relationship, since hemiepiphytes are mostly found in the tropical lowlands at the southern peninsula of Taiwan (Hsu *et al*. 2014), which coincides with the higher frequency of B7 cyclones in the south. Batke & Kelly (2015) suggested that hurricane disturbance on mechanically dependent plants is greatly influenced by their attached position and life form. Hence, we cannot rule out that particular hemiepiphytes, such as strangler figs and aroids, which seem relatively resistant to direct winds, may derive a benefit from the accompanying cyclone precipitation during these relatively warm months. Consequently, rain and wind should be regarded as independent factors, as previously advocated in hurricane research (Lugo 2008).

Ordination analyses also indicated that typhoons have a significant influence on the distribution of epiphytes. However, since typhoons are often associated with periods of great rainfall and rainfall was also one of the predictors in the SDMs, there are clearly some caveats. Indeed, correlation analyses showed that both B7 and B10 wind scales were significantly correlated with the rainfall-related PCA component-2 (Pearson's $r = -0.44$ and 0.32, respectively; $P < 0.001$). To minimize circularity, we performed a partial CCA, in which we entered rainfall (PCA component-2) and temperature (PCA component-1) as covariables. This partial ordination analysis showed that typhoons have a significant influence on epiphyte communities, independently of temperature and rainfall-related variables. Nevertheless, the amount of explained variation by the first extracted axis was low (1.6%). However, it should be noted that the actual amount of variation explained by the first axis, correlated with typhoons, is much higher since the variation correlated with temperature and water availability, PCA-1 and PCA-2, was removed from the data (as covariables) and these PCA components that together explained 52% of the variation in the data were highly correlated with typhoons.

In conclusion, our analyses suggest that historical typhoons have a long-term effect on the distribution of epiphytes in Taiwan and locally shape both species richness and community composition. As a follow-up to this indirect study, we recommend *in situ* monitoring of epiphyte vegetation, particularly in the north-east of the island, where B10 typhoons are most frequent.

Acknowledgements

We thank Hsu-Hsin Shen for keying in typhoon data. We are grateful to Dr Yue-Joe Hsia, Teng-Chiu Lin and Hone-Jay Chu for their advice on interpreting historical typhoons in Taiwan and we thank Dr Ming-Yu Fan and Ya-fen Chan for guidance on the statistical analyses. We thank an anonymous reviewer for the valuable comments.

LITERATURE CITED

BASNET, K., LIKENS, G. E., SCATENA, F. N. & LUGO, A. E. 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. *Journal of Tropical Ecology* 8:47–55.

BATKE, S. P. & KELLY, D. L. 2015. Changes in the distribution of mechanically dependent plants along a gradient of past hurricane impact. *AoB Plants* 7:plv096.

BENZING, D. H. 1998. Vulnerabilities of tropical forests to climate change: the significance of resident epiphytes. *Climatic Change* 39:519–540.

CASCANTE-MARÍN, A., OOSTERMEIJER, G., WOLF, J. & FUCHS, E. J. 2014. Genetic diversity and spatial genetic structure of an epiphytic bromeliad in Costa Rican montane secondary forest patches. *Biotropica* 46:425–432.

CHANG, Y.-H. 2001. *A study on the effect of wind on forest structure at Fushan Experimental Forest*. Department of Geography. National Changhua University of Education, Changhua. 108 pp. (In Chinese.)

CHAZDON, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6:51–71.

CHU, H.-J. 2014. Spatiotemporal analysis of vegetation index after typhoons in the mountainous watershed. *International Journal of Applied Earth Observation and Geoinformation* 28:20–27.

CHU, H.-J., LIAU, C.-J., LIN, C.-H. & SU, B.-S. 2012. Integration of fuzzy cluster analysis and kernel density estimation for tracking typhoon trajectories in the Taiwan region. *Expert Systems with Applications* 39:9451–9457.

CHUANG, Y.-C. 2005. *The crown disturbance of a typhoon in Nanjenshan Forest Ecosystem*. Department of Forestry, National Pingtung University of Science & Technology, Pingtung. 102 pp. (In Chinese.)

CREESE, C., LEE, A. & SACK, L. 2011. Drivers of morphological diversity and distribution in the Hawaiian fern flora: trait associations with size, growth form, and environment. *American Journal of Botany* 98:956–966.

DAWSON, J. 1963. New Caledonia and New Zealand – a botanical comparison. *Tuatara* 11:178–193.

GENTRY, A. H. & DODSON, C. H. 1987. Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden* 74:205–233.

GOODE, L. K. & ALLEN, M. F. 2008. The impacts of Hurricane Wilma on the epiphytes of El Edén Ecological Reserve, Quintana Roo, Mexico. *Journal of the Torrey Botanical Society* 135:377–387.

HILTON, R. G., GALY, A., HOVIUS, N., CHEN, M.-C., HORNG, M.-J. & CHEN, H. 2008. Tropical-cyclone-driven erosion of the terrestrial biosphere from mountains. *Nature Geoscience* 1:759–762.

HSU, R. C.-C. & WOLF, J. H. D. 2009. Diversity and phytogeography of vascular epiphytes in a tropical-subtropical transition island, Taiwan. *Flora* 204:612–627.

HSU, R. C. C., WOLF, J. H. D. & TAMIS, W. L. M. 2014. Regional and elevational patterns in vascular epiphyte richness on an East Asian Island. *Biotropica* 46:549–555.

KANG, R. L., LIN, T. C., JAN, J. F. & HWONG, J. L. 2005. Changes in the normalized difference vegetation index (NDVI) at the Fushan Experimental Forest in relation to typhoon Bilis of 2000. *Taiwan Journal of Forest Science* 20:73–87.

KELLY, D. L., O'DONAVAN, G., FEEHAN, J., MURPHY, S., DRANGEID, S. O. & MARCANO-BERTI, L. 2004. The epiphyte communities of a montane rain forest in the Andes of Venezuela: patterns in the distribution of the flora. *Journal of Tropical Ecology* 20:643–666.

KRESS, W. J. 1986. The systematic distribution of vascular epiphytes: an update. *Selbyana* 9:2–22.

LEE, M.-F., LIN, T.-C., VADEBONCOEUR, M. A. & HWONG, J.-L. 2008. Remote sensing assessment of forest damage in relation to the 1996 strong typhoon Herb at Lienhuachi Experimental Forest, Taiwan. *Forest Ecology and Management* 255:3297–3306.

LIN, T.-C., HAMBURG, S. P., HSIA, Y.-J., LIN, T.-T., KING, H.-B., WANG, L.-J. & LIN, K.-C. 2003. Influence of typhoon disturbances on the understory light regime and stand dynamics of a subtropical rain forest in northeastern Taiwan. *Journal of Forest Research* 8:139–145.

LIN, T.-C., HAMBURG, S. P., LIN, K.-C., WANG, L.-J., CHANG, C.-T., HSIA, Y.-J., VADEBONCOEUR, M. A., MCMULLEN, C. M. M. & LIU, C.-P. 2011. Typhoon disturbance and forest dynamics: lessons from a northwest Pacific subtropical forest. *Ecosystems* 14:127–143.

LIN, Y.-H., TSAI, J.-M., LAI, J.-T. & LIN, Y.-C. 2006. The development and applications of the historical typhoon analysis system (HTAS) – the disturbance regime of typhoons in Hengchun Peninsula. *National Taiwan Museum Quarterly* 59:50–60. (In Chinese.)

LUGO, A. E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecology* 33:368–398.

MABRY, C. M., HAMBURG, S. P., LIN, T.-C., HORNG, F.-W., KING, H.-B. & HSIA, Y.-J. 1998. Typhoon disturbance and stand-level damage patterns at a subtropical forest in Taiwan. *Biotropica* 30:238–250.

MIGENIS, L. E. & ACKERMAN, J. D. 1993. Orchid-phorophyte relationships in a forest watershed in Puerto Rico. *Journal of Tropical Ecology* 9:231–240.

MÚJICA, E., RAVENTÓS, J., GONZÁLEZ, E. & BONET, A. 2013. Long-term hurricane effects on populations of two epiphytic orchid species from Guanahacabibes Peninsula, Cuba. *Lankesteriana* 13: 47–55.

OBERBAUER, S. F., VON KLEIST, K., WHELAN, K. R. T. & KOPTUR, S. 1996. Effects of Hurricane Andrew on epiphyte communities within cypress domes of Everglades National Park. *Ecology* 77:964–967.

PHILLIPS, S. J., ANDERSON, R. P. & SCHAPIRE, R. E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.

REYES-BETANCORT, J. A., SANTOS GUERRA, A., GUMA, I. R., HUMPHRIES, C. J. & CARINE, M. A. 2008. Diversity, rarity and the evolution and conservation of the Canary Islands endemic flora. *Anales del Jardin Botanico de Madrid* 65:25–45.

SCHOTT, T., LANDSEA, C., HAFELE, G., LORENS, J., TAYLOR, A., THURM, H., WARD, B., WILLIS, M. & ZALESKI, W. 2012. The Saffir-Simpson hurricane wind scale. *NOAA/National Weather Service [Internet]*:1–4.

TER BRAAK, C. J. F. 1986. Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179.

TSAI, F., HWANG, J.-H., CHEN, L.-C. & LIN, T.-H. 2010. Post-disaster assessment of landslides in southern Taiwan after 2009 Typhoon Morakot using remote sensing and spatial analysis. *Natural Hazards and Earth System Sciences* 10:2179–2190.

WU, C.-C. & KUO, Y.-H. 1999. Typhoons affecting Taiwan: current understanding and future challenges. *Bulletin of the American Meteorological Society* 80:67–80.

ZOTZ, G. 2013. The systematic distribution of vascular epiphytes – a critical update. *Botanical Journal of the Linnean Society* 171:453–481.

Appendix 1. Environmental predictors that were used for modelling the distribution of epiphyte species in 1-km^2 grid cells in Taiwan. Predictors included four temperature-related (1–4), 12 precipitation-related (5–16), nine topographic variables (17–25), and five land-cover/vegetation indices (16–30). * Indicates predictors that were only used in the model building of rare species (i.e. with < 80 occurrences). For more details, see Hsu *et al.* (2014).

Predictor		Description	Unit
1	Tmean*	Annual mean temperature	°C
2	TcoldM	Mean temperature of coldest month	
3	TdryQ	Mean temperature of driest quarter	
4	Tsd*	The standard deviation of the monthly mean temperatures	No dimension
5	Pannual*	Annual precipitation	mme
6	PdryM	Precipitation of driest month	
7	PdryQ	Precipitation of driest quarter	
8	PcoldQ	Precipitation of coldest quarter	
9-14	P.1, P.4, P.5, P.6 P.7*, P.10*	Monthly rainfall: January, April, May, June, July, October	
15	Pdef	Water deficiency: monthly precipitation minus doubled monthly mean temperature	No dimension
16	Pcv*	The coefficient of variation of the monthly mean precipitation	No dimension
17-18	Eastness* Northness*	Aspect transformed by sin(aspect rad) and cos(aspect rad)	Ordinal: 0–8
19	Soilcode	Soil category	Cardinal: 0–9
20	SoilPH	Soil alkalinity	Ordinal: 0–9
21	Estd	The standard deviation of elevation within 1-km^2	No dimension
22	Elevation	Altitude above sea level	M
23	Dto3000*	The distance to the nearest location above 3000 m (asl)	
24	DtoSea	The distance to the nearest coast	
25	DtoRiver	The distance to the nearest river	
26	Landcover*	Land-cover classification	Cardinal: 0–27
27-30	EVI.1–4	Monthly enhanced vegetation index, EVI.1: April–May, EVI.2: June–September, EVI.3: NE monsoon initiation, October–November, EVI.4: slow growth season, December–March.	No dimension