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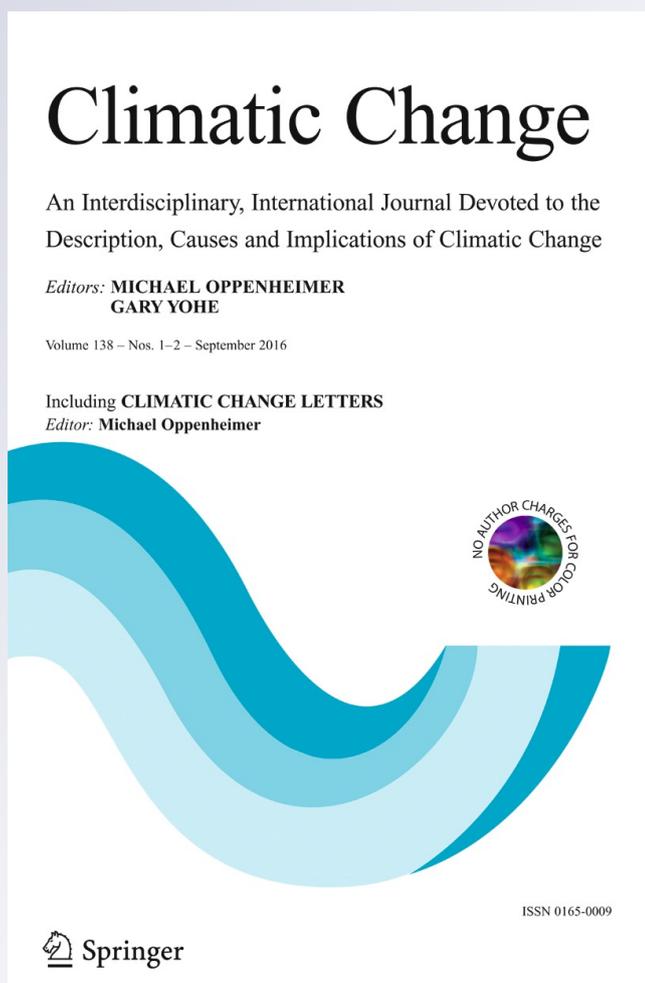
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Fern species richness and abundance are indicators of climate change on high-elevation islands: evidence from an elevational gradient on Tahiti (French Polynesia)

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Abstract Inherent characteristics of island species make them particularly susceptible to anthropogenic changes and need to be assessed to implement appropriate conservation strategies. The impacts of climate change are increasingly being investigated along elevational gradients since they provide natural laboratories to study how species respond to climatic variation. Ferns are particularly sensitive to air humidity and temperature and are therefore potentially useful as bio-indicators. This study addresses the question of whether the distributions of fern species richness and abundance have climatic correlates along an elevational gradient on the tropical volcanic island of Tahiti (French Polynesia). Analyses were conducted on two datasets: island-wide richness was estimated using published data on species elevational ranges, and local richness and abundance were addressed through a transect survey. Correlations with water availability, temperature, area availability, and a randomly-generated species richness pattern were investigated. Results showed that both diversity and abundance varied in association with climate. Rainfall was collinear with diversity in the lower half of the elevational gradient ($R^2 = 0.97$), while temperature was the most important climatic correlate

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for diversity in the upper half ($R^2 = 0.98$). The number of terrestrial fern individuals and epiphytic fern cover were both correlated with temperature ($R^2 = 0.86$ and 0.81 , respectively). Our results imply that impacts of climate change on ferns on Tahiti might include change in diversity and abundance, and increased extinction risk due to low overlap between current and projected species distributions. Ferns represent important indicator organisms that can be used to study species distributional responses to climate change in island ecosystems.

Keywords Climate envelope · Global warming · Mountain ecology · Pacific islands

1 Introduction

Although islands account for only 5 % of the Earth's emergent land area, they harbor a disproportionately high fraction of global biodiversity: e.g., one quarter of the worldwide vascular flora is endemic to islands (Kier et al. 2009). However, inherent characteristics of island species (e.g., small population sizes, low functional redundancy, small habitats, isolated evolution) leave them highly vulnerable to rapid anthropogenic changes (Fordham and Brook 2010). Besides major threats including habitat loss and invasion by alien species (Caujapé-Castells et al. 2010), islands are expected to experience an increase of mean annual temperature ranging from 1.3 °C to 2.8 °C on average by the end of the century (Harter et al. 2015). The potential impacts of rising sea-level in atolls and low-lying islands are well known, but it is much less appreciated that increasing temperature also threatens island montane ecosystems (Loope 1995; Krushelnicky et al. 2013).

The potential impacts of climate change are increasingly being investigated using elevational gradients because they provide a useful system to understand how species and communities respond to climatic variation (Lloret and González-Mancebo 2011; Hsu et al. 2014a). Despite intensive effort to understand patterns and causes of species distributions along elevational gradients during the last few centuries, no emerging consensus has been reached on a definitive pattern and underlying mechanisms (Grytnes and McCain 2007). A meta-analysis including 204 elevational gradients of species richness (SR) has indicated a pattern of monotonic decrease in SR with elevation in 25 % of gradients, and a hump-shaped pattern (i.e., maximal SR at mid-elevations) in nearly 50 % (Rahbek 2005). When accounting for the area effect, according to which the regional pool of species decreases with elevation as a result of the decline of elevational band area (McCain 2007), the proportion showing a hump-shaped distribution reaches 80 % (Rahbek 2005). A number of hypotheses have been proposed to explain hump-shaped SR patterns (Grytnes and McCain 2007). In the absence of a single clear explanation, it is likely that the factors influencing distribution patterns of SR depend on the organism(s) studied and local conditions (Rahbek 2005; McCain 2007).

Ferns (Monilophytes) and so-called 'fern allies' (Horsetails, Whisk Ferns, and Lycophytes), for convenience grouped under the non-monophyletic term 'ferns' hereafter, have the potential to be excellent bio-indicators of climate change because they are particularly sensitive to water availability and temperature (Benzing 1998; Zotz and Bader 2009). It has been established that the elevational distribution of fern SR is closely related to climatic factors at local (Hemp 2001; Bhattarai et al. 2004; Krömer et al. 2005; Kluge et al. 2006) and global scales (Kessler et al. 2011). Fern SR has been demonstrated to be lower in dry lowlands and on cool summits than in mid-elevation areas, and different climatic factors (air humidity and temperature, respectively) have been posited to control fern SR on both sides of the SR peak (Krömer et al. 2005; Kessler et al. 2011). In contrast, stochastic

processes such as the mid-domain effect (MDE), according to which species ranges distributed randomly within a bounded space are expected to overlap more in the center than at either end (Grytnes and McCain 2007), might modify the pattern of fern SR, but to a lesser extent than climate (Bhattarai et al. 2004; Kluge et al. 2006; Kessler et al. 2011).

Although previous fern studies have focused on how SR varies with elevation (Hemp 2001; Bhattarai et al. 2004; Krömer et al. 2005; Kluge et al. 2006; Kessler et al. 2014), patterns and drivers of fern SR along an elevational gradient have rarely been addressed on oceanic islands. In a study on the Virgin Islands (Lesser Antilles), fern SR was reported to reach maximum values at high elevations, but no quantitative data were provided (Proctor 1989). On La Réunion Island (Mascarene archipelago), the effect of area on fern SR was documented, but no further explanatory factors were investigated (Karger et al. 2011). In Taiwan (East China Sea), climate change impacts on epiphytic ferns and orchids have been explored, but using a method that ignores the potentially important area effect and neutral processes (Hsu et al. 2014b). More recently, the predictive power of area and isolation as well as of climatic factors for explaining local and regional SR was investigated in the Southeast Asian archipelago, but the elevational distribution of SR was not addressed (Karger et al. 2014).

Tropical oceanic islands differ in several respects from continental mountains that may affect the distribution of SR with elevation. Tropical montane cloud forests harbor a high amount of fern SR (Bhattarai et al. 2004), and their elevation varies between the mainland and islands, depending on many meteorological (air moisture content, wind velocity and direction) and topographical (mountain size, distance to the sea) effects (Loope 1995; Loope and Giambelluca 1998). The typical elevation for tropical montane cloud forests on large, mainland mountains is between 2000 m and 3500 m, while on high-elevation islands, it is found at much lower elevations (e.g., ~1000 m in Hawaii; Loope and Giambelluca 1998). Other distinctiveness of high-elevation islands includes (i) the over-representation of ferns in island floras compared to continents due to higher long-distance dispersal ability relative to most spermatophytes (Smith 1972; Florence 1993); and (ii) steep climate gradients along an abrupt topography that create a wide variety of habitats within a small area. Thus, one can question whether results obtained from continents apply to high-elevation islands.

Understanding the effects of climate change on plant communities at island-wide and local scales is urgently needed for mitigation of future anthropogenic impacts on oceanic islands (Harter et al. 2015). In the present study, we aim to identify climate correlates for island-wide and local fern SR and abundance on high-elevation islands to establish a preliminary assessment of the potential effects of climate change on island montane ecosystems. We used the tropical high volcanic island of Tahiti (French Polynesia) in the South-East Pacific Ocean as a model system. If fern diversity arises from stochastic processes (e.g., the MDE), future climate change is unlikely to cause major distributional shifts of ferns. In contrast, if distribution of fern diversity stems from deterministic processes related to temperature or/and water availability, changes in richness must be expected unless appropriate conservation strategies are rapidly adopted.

2 Materials and methods

2.1 Tahiti and its fern flora

Tahiti (17.5–18.0°S; 149–150°W) is the largest (1042 km²) and most densely populated (183,000 inhabitants in 2012; <http://www.ispf.pf>) island of French Polynesia. This high

volcanic island belonging to the Society archipelago was formed by the emergence of two volcanoes 0.3–1.7 My ago: larger Tahiti Nui in the north-west, and smaller Tahiti Iti in the south-east (Online Resource 1). With three summits above 2000 m including Mt. Orohena (2241 m), Mt. Pito Hiti (2110 m) and Mt. Aorai (2066 m), Tahiti Nui is by far the highest hotspot volcano of French Polynesia and of the South Pacific. The climate is tropical with mean annual temperature of 26.5 °C and annual rainfall of about 1700 mm in the coastal plain of the leeward coast of Tahiti Nui (Faa'a airport meteorological station), reaching 4000 mm on the windward coast and Tahiti Iti, and up to 8000 mm in the center of Tahiti Nui (Laurent et al. 2004).

A total of 180 native fern species is currently recorded in Tahiti (Florence 2016). They belong to 71 genera and 23 families, and include 37 species endemic to French Polynesia (21 % of the total), 25 endemic to the Society archipelago (14 %), and 11 endemic to the island of Tahiti (6 %; Online Resource 2). Ferns are overrepresented in Tahiti, as they account for 36 % of the total native vascular flora of the island (out of 495 species total) (Florence 1993), while this proportion reaches 27 % in the Pitcairn islands (South-East Pacific Ocean), 25 % in Fiji (South-West Pacific Ocean), 15–17 % in Hawaii (Meyer 2013; Vernon and Ranker 2013), 10 % in New Zealand, 8 % in New Caledonia (South-West Pacific Ocean), and 1 % in California, continental USA (Smith 1972).

2.2 Literature-based data on island-wide fern species richness

Minimum and maximum elevations were extracted for each fern species from the fern flora of French Polynesia (Florence 2016), and it was assumed that each species occurs continuously throughout this range. Elevations in Florence (2016) are based on specimens deposited in the herbaria of Paris [P], Kew [K], Bishop Museum of Honolulu [BISH] and Tahiti [PAP] that were measured in the field with altimeters whose accuracy was assumed sufficient with regard to the vertical resolution used in the analyses (100 m). When the elevational range of a taxon was not specified in Florence (2016) for the island of Tahiti, the elevational range given for the Society Islands was used. When a taxon was observed outside the elevational range described by Florence (2016), unpublished personal observations were preferred to maximize the reliability of range sizes (Online Resource 2). The total elevational gradient on Tahiti (0 to 2200 m) was then divided into 100 m bands, and SR calculated for each band based on the elevational ranges of each species. Naturalized alien species (seven species recorded in Tahiti) were not considered in our sampling. Rare endemic taxa known from a single occurrence (singletons), i.e. without an elevational range, (including *Grammitis meyeri* J. Florence (Polypodiaceae), *Pteris nadeaudii* E. Drake (Pteridaceae) and *Selaginella setchelli* O.C. Schmidt ex O.C. Schmidt (Selaginellaceae)) were also excluded from the analyses.

2.3 Plot-based data on local fern species richness and abundance

Local SR and abundance of ferns were investigated in 16 permanent plots measuring 14 m × 14 m (196 m²) set up in forested gulches along the trail leading to the summit of Mt. Aorai (2066 m), located on the leeward side of Tahiti (Online Resource 1). Plots were located from 612 m to 2048 m elevation, with two replicated plots at each of the eight sampled elevations. Pairs of plots at similar elevation were set up at a distance ranging from 20 m to 50 m so that the captured fern communities were significantly overlapping (Bray-Curtis dissimilarity index = 0.26 ± 0.09). The total area inventoried at each elevation (392 m²) is a

standard area thought to be sufficient for sampling fern community diversity (Kessler et al. 2011). Whereas the literature survey allows identifying elevational trends in SR across the entire island, this sampling design, covering one third of the 100 m elevation bands that constitute the total elevational gradient, was used to analyze changes in SR and abundance at the local scale.

Three metrics were measured for each plot: (i) fern species richness; (ii) the proportion of area covered by ferns (first estimated in 49 2 m × 2 m subplots then rescaled to the entire plot area by averaging subplot values); and (iii) the number of ramets (used as a proxy for the number of individuals). Gametophytes (ferns at the haploid stage of the life cycle) and unfertile sporophytes that could not be identified with certainty because of their small size were not considered. The three metrics were analyzed by growth habit: terrestrial ferns (growing on the ground) and epiphytic ferns *sensu lato* (growing above ground level), including epiphytic ferns *sensu stricto* (growing on other vegetation) and epilithic ferns (growing on rocks). Island-wide fern SR was not analyzed by growth habit because most species (60 %) were found under multiple growth habits, with high variation depending on elevation (Online Resource 2).

2.4 Hypothetical drivers of fern species richness and abundance

Three hypothetical factors thought to influence fern SR and abundance were evaluated: (i) climate (water availability and temperature), (ii) the area effect, and (iii) the MDE.

2.4.1 Climate

Climatic conditions have been posited as explaining elevational SR patterns either directly (Grytnes and McCain 2007; Kessler et al. 2011) or indirectly through energy availability and ecosystem productivity (Kessler et al. 2014). A 120 m-resolution rainfall map derived from an interpolation of records from 43 meteorological stations (Laurent et al. 2004) was used to calculate the average rainfall for each 100 m elevational band.

As only 15 meteorological stations are equipped with thermometers across Tahiti, no fine-scale temperature map is currently available (Laurent et al. 2004). As a result, elevation was used as proxy for island-wide temperature. Elevation was derived from a 5 m-resolution digital elevation model (Service de l'Urbanisme, Government of French Polynesia) and used to calculate average temperature, assuming a decrease of 0.6 °C per 100 m increase in elevation. This environmental lapse rate has been measured in Tahiti through radiosondes (telemetry instrument packages carried into the atmosphere by a weather balloon that transmits atmospheric parameters by radio to a ground receiver; Pouteau et al. 2010).

Micro-climatic conditions (relative humidity and temperature) in plots were recorded using data loggers (MidgeTech RHTemp 1000 IS) set to record once per hour in five of the eight sampled elevations (between 996 m and 2048 m; Online Resource 3). Devices started and finished recording at different times from 12 October 2013 to 6 February 2015 with no overlap between all devices. Plots with the longest recording period (from 12 October 2013 to 30 January 2015) were located at 996 m and 1221 m. The lowest of them (996 m) was used to compute the difference between the climate recorded in this reference plot and the climate recorded in other plots during periods of synchronous data. The between-plot mean relative humidity differential (designated ΔRH) and between-plot mean temperature differential (ΔT) were then calculated. To examine whether local SR and abundance of ferns are correlated with

water availability and temperature, we tested for a linear relationship between the three plot metrics (SR, cover, and number of individuals) and meteorological records (ΔRH and ΔT).

2.4.2 The area effect

The conical shape of mountains means that less habitat is available for species as elevation increases, and this can influence SR of each elevational band because of the basic SR/habitat area relationship described by Arrhenius (1921):

$$SR = cA^z$$

where c is a constant that equals the number of species that the elevational band would support if it was confined to a square unit, A is the area of the elevational band and z is a constant describing the slope in a log-log species-area plot. Since island-wide SR is expected to decrease with elevation due to the decrease in size of the elevational band areas, the correlation between empirical island-wide SR and the log-transformed planar area calculated for each 100 m elevational band was tested with a linear model.

Although the use of equal-area plots in transect studies is thought to control for the influence of area on local SR, local communities are composed of species drawn from a regional pool shaped by historical factors, biotic interactions and environmental preferences other than those related to elevation (Ricklefs 1987). Thus, the effect of area on island-wide SR is also thought to influence local SR through the so-called ‘indirect area effect’ (Romdal and Grytnes 2007). This association was also explored using a linear regression.

2.4.3 The mid-domain effect

The MDE theory assumes that hard boundaries (i.e., the top and bottom of an elevational gradient) constrain the size and placement of species ranges such that randomly distributed species ranges cluster near the center of the domain, producing unimodal SR patterns even in the absence of any environmental effect (Grytnes and McCain 2007). Previous fern studies have reported a shift of the island-wide SR peak towards low elevations, which is not expected under the MDE theory, and might mean that other factors act in conjunction with geometry (Karger et al. 2011; Hsu et al. 2014b). McCain (2007) suggests that the species-area relationship may cause an underestimation of the strength of the MDE at the regional scale because MDE simulations are area-independent, unlike empirical SR. Therefore, for the island-wide approach, we generated a null SR pattern that accounts for both the MDE as well as for the area available in each 100 m elevation band (the area effect).

Island-wide and local SR were compared to the average of 10,000 Monte Carlo simulations of a null model. Null communities were initially simulated under an MDE model using the software RangeModel 5.0 with empirical species range sizes and random range mid-points (Colwell 2008). Arrhenius’ equation was then used to incorporate the area effect as follows. The z value was empirically determined by calculating the slope of the double-log species-area relationship in which each point corresponds to a 100 m elevational band (McCain 2007). This method provided a significant species-area relationship on a log-log scale ($R^2 = 0.81$, P -value < 0.001) and yielded a z value of 0.20. Finally, the MDE null communities were used for c (the area-independent SR) to yield null communities that accounted for both MDE and the area effect (McCain 2007).

2.5 Identifying environmental correlates for fern species richness and abundance

Fern SR and abundance were analyzed in relation to water availability, temperature, area and MDE plus area using pairwise linear regressions. Since it has been demonstrated that climatic correlates of fern diversity can differ on both sides of the SR peak (Krömer et al. 2005; Kessler et al. 2011), island-wide analyses were first performed along the whole gradient, then above and below the observed SR peak separately. On Tahiti, maximum SR is expected in cloud forests at mid elevations because these habitats have reduced solar radiation and vapor pressure deficit, and general suppression of evapotranspiration such that epiphytes can co-occur with terrestrial ferns. Above this point, summits and ridges experience low nocturnal temperatures, relatively drier conditions, persistent winds and more sunlight, and these extreme climatic conditions may not be suitable for many fern species. A major drawback of such a gradient division approach is that it ignores potential interactions between multiple factors that might potentially overlap at the middle of the SR peak. The divided analysis was only conducted for the island-wide dataset, as the number of plots (eight) was insufficient to split the elevational gradient for local diversity.

2.6 Climate change scenarios

Predictions of future climate were used to estimate potential shifts in fern distributions. To our knowledge, there are to date no published data about the latest emissions scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) for Tahiti or French Polynesia. Therefore, we downloaded downscaled global maps at 30 arcsecond resolution for present and future climate on the portal provided by the Research Program on Climate Change, Agriculture and Food Security (CCAFS; <http://ccaafs-climate.org/>). Selected scenarios were RCP2.6 (aggressive mitigation scenario) and RCP8.5 (worst case scenario) generated by the global circulation model CSIRO-Mk3.6. Delta values were calculated from present records and future scenarios. All pixels covering the island of Tahiti were averaged to obtain one single average delta value for the whole island because the scale of CCAFS data is incompatible with the topographical complexity of the island, and precludes analyzing projected changes for different elevations.

Evolutionary responses of fern species to climate change will depend on whether their environmental niches will shift or remain unchanged over time (i.e., degree of niche conservatism) (Wiens et al. 2009). Possible evolutionary responses of species to climate change range from total conservatism of species' climatic niches (species will have to migrate to track habitat to survive) to complete adaptation to new climate (no change from the current species distribution required). The most realistic scenario is, however, likely to be in-between: a species-specific response controlled by biotic interactions and multiple abiotic factors other than mean temperature (e.g., water balance, climate seasonality and extremes, canopy cover), and affected by a time lag in migration (Renwick and Rocca 2015). Here, we used the most pessimistic risk scenario (total conservation of species' climatic niches) to project change in species elevational distributions under RCP2.6 and RCP8.5 assuming a lapse rate of 0.6 °C per 100 m (Pouteau et al. 2010).

3 Results

3.1 Island-wide species richness

The island-wide elevational SR pattern was collinear with climatic factors, including annual rainfall at low elevations and temperature at high elevations (Fig. 1). Island-wide SR showed a hump shape, starting with 80 species at sea-level, reaching a maximum of 120 species between 600 m and 1000 m (Online Resource 4), and falling to 12 species at the highest point, on the summit of Mt. Orohena (2241 m). Although island-wide SR decreased in the upper half of the elevational gradient, the proportion of endemic species (including archipelago-endemics and island-endemics) doubled in comparison to the lower half (Online Resource 5). Over the whole elevational gradient, climatic factors were the worst predictors of island-wide SR (rainfall: $R^2 = 0.01$; P -value = 0.65; temperature: $R^2 = 0.61$; P -value < 0.001). The best correlate was the random pattern of SR produced under the combination of the MDE and the area effect ($R^2 = 0.83$; P -value < 0.001; Fig. 1). Nevertheless, when considering each side of the SR peak (800 m) separately, a much stronger relationship between climate and island-wide SR was observed (Fig. 1). The most powerful correlate for island-wide SR was rainfall in the lower half of the gradient ($R^2 = 0.97$; P -value < 0.001) and temperature in the upper half ($R^2 = 0.99$; P -value < 0.001).

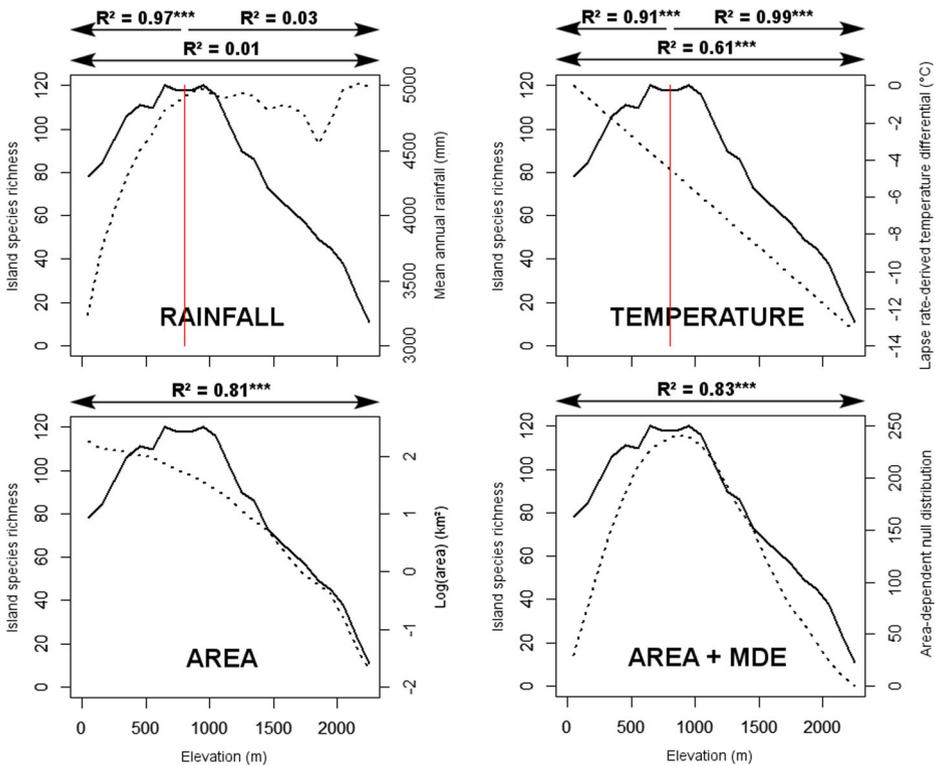


Fig. 1 Coefficient of determination (R^2) between island-wide species richness (left Y-axis) and hypothetical environmental correlates (right Y-axis). The double-headed arrow indicates regression including the whole elevational gradient, the left-pointing arrow for the lower side of the peak only, and the right-pointing arrow for the upper side of the peak only. * indicates $0.050 > P\text{-value} \geq 0.010$, ** $0.010 > P\text{-value} \geq 0.001$, and *** $P\text{-value} < 0.001$

3.2 Local species richness

A total of 92 species (51 % of the known fern species of Tahiti) belonging to 47 genera (66 %) and 23 families (100 %) were observed during the plot survey on Mt. Aorai (2066 m). Local SR also exhibited a broadly hump-shaped pattern along the elevational gradient with a peak of 40 species recorded at mid-elevation (1006 m; Fig. 2a). The exact elevation of the SR peak differed between the local dataset and the island-wide dataset (1000–1100 m vs. 600–1000 m, respectively) so that patterns of local SR and island-wide SR significantly differed ($R^2 = 0.01$; P -value = 0.87), but became similar when the area effect on island-wide SR was accounted for ($R^2 = 0.61$; P -value < 0.05).

Linear regression indicated substantial but non-significant influence of relative humidity ($R^2 = 0.74$; P -value = 0.06), and no influence of temperature ($R^2 = 0.02$; P -value = 0.83), the indirect area effect ($R^2 = 0.01$; P -value = 0.87) or the MDE ($R^2 = 0.11$; P -value = 0.41) on the elevational pattern of local SR. Distribution of local SR across different growth habits remained relatively stable along elevation with 10–20 % of strictly epiphytic species, 35–50 % of species occurring in both strata, and 35–50 % of strictly terrestrial species throughout (Fig. 2a). However, the proportion of terrestrial species locally reached 60 % at mid-elevations (1006 m), which could help explain the hump-shaped distribution of local SR. Local SR was associated with air temperature for terrestrial species ($R^2 = 0.88$; P -value < 0.05), but no association between climate and local SR for other growth habits was discernible ($R^2 < 0.64$; P -value > 0.11).

3.3 Local abundance

The surface area covered by terrestrial ferns did not significantly change with elevation, and fluctuated from 50 % to 90 % of plot area throughout the transect ($R^2 = 0.31$; P -value = 0.17; Fig. 2b). As a result of this apparent independence from elevation, neither air relative humidity ($R^2 = 0.01$; P -value = 0.89) nor temperature ($R^2 = 0.44$; P -value = 0.22) explained the distribution of terrestrial fern cover. In contrast, epiphytic fern cover significantly varied with elevation, from 2 % at 612 m elevation to 60–90 % above 1300 m ($R^2 = 0.71$; P -value < 0.05; Fig. 2b). This increase in epiphytic fern cover with elevation appeared closely related to the reduction of temperature ($R^2 = 0.81$; P -value < 0.05) but not with the increase of humidity ($R^2 = 0.33$; P -value = 0.32).

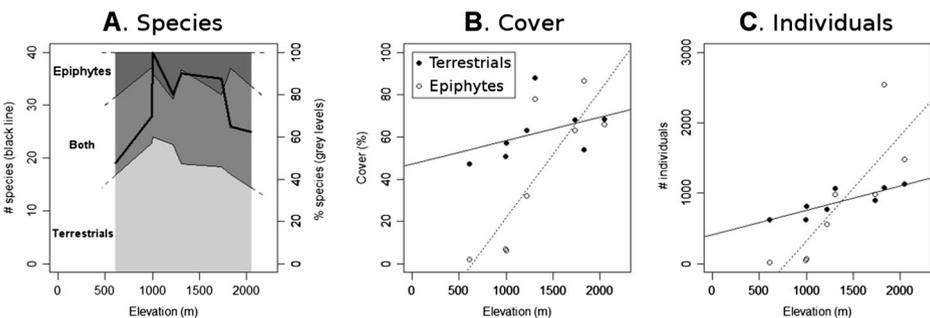


Fig. 2 a Fern local species richness along an elevational gradient on Mont Aorai, Tahiti. The *thick black line* (left Y-axis) shows the total number of fern species found in plots and grey levels (right Y-axis) indicate the relative proportion of terrestrial species (light grey), epiphyte species (dark grey) and species found under the form of both growth habits (intermediate grey level). b, c Fern abundance expressed as a proportion of surface area covered by ferns (b) and number of individuals (c). The *continuous line* is a linear regression for black points (terrestrial ferns) and the *dotted line* for white points (epiphyte ferns)

The number of individuals increased with elevation for both terrestrial and epiphytic growth habits ($R^2 > 0.70$; P -value < 0.05 ; Fig. 2c). The number of terrestrial fern individuals almost doubled from 612 m to 2048 m; this was correlated with a decrease in temperature ($R^2 = 0.86$; P -value < 0.05) but not with an increase in humidity ($R^2 = 0.66$; P -value = 0.09). The increase in the number of epiphytic individuals was steeper than for terrestrial ferns: from 20 individuals at 612 m to a maximum of 2500 individuals at 1836 m (Fig. 2c). However, this was not significantly correlated with either humidity ($R^2 = 0.47$; P -value = 0.20) or temperature ($R^2 = 0.54$; P -value = 0.15).

3.4 Projected range shifts

On the island of Tahiti, annual rainfall is projected to decrease by 17 % (RCP2.6) to 30 % (RCP8.5), and annual mean temperature to increase by 1.0 °C (RCP2.6) to 3.0 °C (RCP8.5) by 2080. Under these climate warming conditions, species' elevational ranges are assumed to experience an upward shift of 167 m according to RCP2.6 (+1.0 °C) and 500 m according to RCP8.5 (+3.0 °C) by 2080.

4 Discussion

4.1 Patterns and potential causes of fern species richness and abundance in Tahiti

Possible associations between climate and fern communities were investigated through analysis of published data on species' elevational ranges and a transect survey combined with climate data. Our results clearly show that island-wide and local SR, as well as abundance of ferns, all vary along climatic gradients on Tahiti with, however, subtleties depending on the part of the elevational gradient analyzed and growth habit. Island-wide SR showed a hump-shaped pattern culminating slightly below the exact midpoint (600–1000 m). This shift of the island-wide SR peak towards low elevations has also been observed and interpreted as a result of the area effect in the fern flora of the high volcano of La Réunion Island (Karger et al. 2011), and the epiphytic flora of Taiwan (Hsu et al. 2014b). While the island-wide SR pattern appeared to be somewhat influenced by the area effect alone and to a greater extent in conjunction with the MDE, these effects did not explain this pattern better than climatic factors. Overall, our results corroborate many continental studies showing that ferns avoid low water availability at low elevations and low temperatures at high elevations (Krömer et al. 2005; Kluge et al. 2006; Kessler et al. 2011). However, a steeper decrease towards high elevations was observed on Tahiti compared to most continental areas (Kessler et al. 2011). This difference might result from the area effect and reflect the rugged topography of these young volcanoes including knife-edge ridges, steep slopes and deep valleys. Another possible explanation is that the spores that reached the island were less likely to be adapted to the extreme climatic conditions of the summits than to lower elevations, resulting in an under-representation of subalpine species.

Local SR of ferns in Tahiti was found to reach maximum values at mid-elevations (1000–1100 m). This type of pattern was identified as the most frequent in a meta-analysis of 20 fern inventories worldwide including in the volcano of La Réunion Island (Karger et al. 2011; Kessler et al. 2011). As reported for many other mountains, decreasing local SR with elevation observed for the upper half of the gradient (where most plots were located) might be attributable to decreasing temperature (Krömer et al. 2005; Kessler et al. 2011). However, while the MDE and the indirect area effect were found to significantly influence local SR in

previous global meta-analyses (Romdal and Grytnes 2007; Kessler et al. 2011), these effects showed no correlation with local SR in our dataset. A possible explanation is that the strength of the MDE is reduced at small spatial scales compared to larger ones as proposed by Dunn et al. (2007). With regard to the indirect area effect, the potential for long distance dispersal by spores might make ferns less influenced by area than organisms with lower dispersal ability (Romdal and Grytnes 2007). However, local SR was found to be significantly correlated with the area-corrected island-wide SR, which was also observed by Karger et al. (2011) along five elevational transects including La Réunion Island. This result suggests that the difference between local and island-wide SR patterns can be accounted for by the area effect, and that the underlying causes of SR patterns might be the same at both scales. In this context, it is likely that the small number of plots with data loggers (five) precluded detecting significant correlation between local SR and microclimate.

Elevation was also closely associated with a monotonic increase in the abundance of ferns in Tahiti. The decline of air temperature, rather than relative humidity, was identified as the main correlate for the increase in both terrestrial and epiphytic fern abundance (number of individuals and cover, respectively). This finding contrasts with the classical view that epiphytic ferns are particularly sensitive to climate change because they rely on contact with rain or cloud droplets for moisture input, hence responding rapidly to slight changes in air humidity (Benzing 1998; Zotz and Bader 2009). At least four hypotheses can be advanced to explain this difference: (i) the number of plots equipped with data loggers and the periods of pairwise synchronous data (ranging from 68 to 455 days) may be too small to detect a significant effect of relative humidity on fern abundance; (ii) air temperature acts indirectly by controlling key ecological processes such as evapotranspiration, carbon fixation and decomposition, plant productivity and mortality in mountain ecosystems (Kessler et al. 2014); (iii) since ferns have been reported to react to water stress, which combines both relative humidity (high and relatively constant in plots: between 95 % and 100 %) and temperature (much more fluctuating), the observed correlation between temperature and fern abundance reflects a causal effect of water stress rather than temperature per se (Karger et al. 2012); and (iv) fern abundance is driven by periodic drying events influencing plant survival that the between-plot mean relative humidity differential (ΔRH) was unable to capture.

Such a monotonic increase of fern abundance also contrasts with a study on Mt. Kilimanjaro (5895 m), which found that ferns reach maximum abundance in tropical montane cloud forests located at mid-elevation (Hemp 2001). This discrepancy is likely to arise from the much greater height of Mt. Kilimanjaro, which allows for a much wider range of montane vegetation types: there, the cloud forest extends up to 3500 m, and is then successively replaced by subalpine shrubland, alpine herbaceous vegetation, and finally glacier. In contrast, in Tahiti, the cloud forest extends up to the highest summits and ridges where it is replaced by subalpine shrublands from 1600 to 1800 m (Florence 1993; Meyer 2010). Since island-wide and local SR as well as abundance of fern species are at least in part driven by climate, the question then arises as to what distributional changes might be expected due to these environmental requirements under different climate change scenarios.

4.2 Insights into future changes in fern species richness and abundance

Under climate change, at low elevations, the projected decrease in rainfall may result in a loss of fern species while, at high elevations, a gain of species due to warmer conditions might be expected. Thus, overall, global warming in association with drier conditions might result in an

upward shift of fern species ranges. Ferns have been shown to shift their distribution according to their environmental requirements and patterns of intraspecific adaptation (Hsu et al. 2014a; Hsu et al. 2014b). Such differences in distributional responses to climate change are likely to shape novel communities along with positive or negative novel species interactions (Williams and Jackson 2007).

The area effect could exacerbate extirpation/extinction risk associated with an upward shift of fern species ranges because the decline of area with elevation is likely to provide smaller future suitable areas than those currently occupied, and the new areas may not be able to support the same number of species (Arrhenius 1921). It has been shown through niche modeling that over 1000 Hawaiian plant species are expected to experience a decrease of 39 % of their geographical area between current and projected 2100 climate envelopes (Fortini et al. 2013). Using a similar approach, models indicated that the majority of 211 Taiwanese epiphytic ferns and orchids will lose 45–58 % of their current range by 2100 and shift on average to elevations 400 m higher than present (Hsu et al. 2012). However, in Tahiti, if montane fern species are under-represented, there may be vacant niches that species expected to migrate upwards could occupy, thus reducing extinction risk. A lesser known risk associated with the particular topography of high-elevation islands is that an upward shift of species ranges would also lead to increased geographic isolation between meta-populations, since mountains are dissected by deep ravines at higher elevations (Online Resource 6; Hsu et al. 2012). The level of endemism (which was observed here to increase with elevation) is also expected to shift towards the summits, thus posing an immediate threat to this unique flora. Finally, because abundance of ferns (number of terrestrial individuals and area covered by epiphytes) increases with elevation in proportion to the temperature decline, global warming might cause a reduction of fern abundance, especially at higher elevations.

4.3 Extinction risk associated with shifts in species elevational range

'No-overlap' species are those with no overlap between current and future climate envelopes, i.e., species with a current elevational range lower than its projected range. In Tahiti, there are estimated to be up to 12 no-overlap species (7 % of native species) by 2080 according to RCP2.6 and up to 37 no-overlap fern species (21 %) according to RCP8.5 (Online Resource 2). Island endemics with narrow ranges have been identified as more vulnerable to climate change impacts, since they are more exposed to demographic and environmental stochasticity (Caujapé-Castells et al. 2010). Therefore, narrow-ranged endemic species such as *Grammitis meyeri*, *Pteris nadeaudii* and *Selaginella setchelli* are likely to be highly vulnerable to such projected temperature increases. In Taiwan, among 211 vascular epiphytic species evaluated, 10 epiphytes (5 %) including six epiphytic ferns (3 %) are considered no-overlap species according to the A2 scenario for 2100 (Hsu et al. 2012). In Hawaii, it has been showed that 15 % of plant species have non-overlapping current and 2100 climate envelopes (Fortini et al. 2013). The absence of overlap between current and future distributions is likely to have more dramatic effects on seed plants than ferns, since ferns usually produce smaller and more abundant propagules that can disperse over greater distances (Tryon 1970).

Species with no future climate envelope on the island represent an extreme case of vulnerability in which no projected suitable areas exist for the species to persist in the future. Species without a future temperature envelope in Tahiti are those restricted to elevations above 2074 m under scenario RCP2.6 and above 1741 m under scenario RCP8.5. The endemic species *Grammitis fredericis-jacobi*, whose lower recorded limit is currently 1800 m, will lose

all temperature-compatible areas by 2080 according to scenario RCP8.5. In a more complex approach linking temperature and water availability together, 5 % of Hawaiian plant species are estimated to lose all suitable habitat by 2100 (Fortini et al. 2013).

5 Conclusion

Our study shows that expected climate change may be potentially deleterious for the native and endemic ferns of Tahiti. The scarcity of detailed studies on the impacts of climate change on ferns and their habitats on high-elevation islands makes our preliminary assessment particularly relevant to a group where the rarity of some taxa makes them particularly vulnerable to future changing ecological conditions. Ferns are important components of the native flora of remote oceanic islands, and it is therefore necessary that these plants be better studied and protected. Fern populations should be carefully monitored and could be used to gauge climate change and species responses in the future. Such monitoring is especially important in all tropical high volcanic islands, where inherent characteristics of island species and ecosystems cause particular vulnerability to anthropogenic changes.

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