Original Article

Vulnerability to xylem embolism as a major correlate of the environmental distribution of rain forest species on a tropical island

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ABSTRACT

Increases in drought-induced tree mortality are being observed in tropical rain forests worldwide and are also likely to affect the geographical distribution of tropical vegetation. However, the mechanisms underlying the drought vulnerability and environmental distribution of tropical species have been little studied. We measured vulnerability to xylem embolism (P_{50}) of 13 woody species endemic to New Caledonia and with different xylem conduit morphologies. We examined the relation between P_{50}, along with other leaf and xylem functional traits, and a range of habitat variables. Selected species had P_{50} values ranging between -4.03 and -2.00 MPa with most species falling in a narrow range of resistance to embolism above -2.7 MPa. Embolism vulnerability was significantly correlated with elevation, mean annual temperature and percentage of species occurrences located in rain forest habitats. Xylem conduit type did not explain variation in P_{50}. Commonly used functional traits such as wood density and leaf traits were not related to embolism vulnerability. Xylem embolism vulnerability stands out among other commonly used functional traits as a major driver of species environmental distribution. Drought-induced xylem embolism vulnerability behaves as a physiological trait closely associated with the habitat occupation of rain forest woody species.

Key-words: angiosperms; cavitation; drought resistance; elevation; environmental gradients; functional traits; vesselless angiosperms; wood density.

INTRODUCTION

Climate projections predict changes in rainfall regimes and soil moisture, forecasting more severe and widespread droughts in many areas (Dai 2013). Global changes in rainfall, combined with increased temperature, are likely to cause tree mortality and biogeographic shifts in vegetation in many parts of the world (Adams *et al*. 2009; Allen *et al*. 2010). Moreover, strong shifts in rainfall are expected to affect forest areas of tropical regions (Chadwick *et al*. 2015). Given that an increase in tropical rain forest tree mortality due to water stress has already been observed (Phillips *et al*. 2010) and because most angiosperm species are operating within a narrow hydraulic safety margin (Choat *et al*. 2012), the survival and distribution of tropical rain forest trees clearly seem threatened by drought.

A major goal in plant ecology is to understand the links between functional traits and species distribution (Violle & Jiang 2009). However, while the distribution of plant species along environmental gradients has been well documented, the plant traits and physiological mechanisms driving the distribution of tropical species are poorly known (Engelbrecht *et al*. 2007). The identification of plant traits underlying the distribution of species along environmental gradients can be very important in the selection of highly informative key ecological traits (Westoby & Wright 2006). Detecting informative plant traits and their interactions with environmental variables is especially important for understanding the likely fate of current vegetation types in the context of global climate change (Allen *et al*. 2015; Breshears *et al*. 2005). Therefore, analysing key eco-physiological traits related to drought vulnerability and plant water use is essential in understanding current and projected distribution patterns of plant species in tropical rain forests, the most species rich ecosystems of the world.

According to the tension-cohesion theory, water transport through xylem is driven by surface tension during leaf transpiration and the integrity of the water column is maintained by cohesion between the water molecules and adhesion between the water column and xylem conduit walls (Tyree 1997; Tyree & Zimmermann 2002). Water movement is prone to dysfunction because highly negative xylem pressures may arise during a drought event. Highly negative xylem pressures can disrupt the cohesion between the water molecules, producing gas bubbles by cavitation (Tyree & Sperry 1989). Cavitation may result in large embolisms inside the xylem conduits, blocking water flow. According to the air-seeding hypothesis, such embolisms can propagate from a gas-filled conduit to a functional conduit

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through the lateral interconduit pits (Cochard *et al.* 2009; Delzon *et al.* 2010; Tyree & Zimmermann 2002). Plant drought resistance can be assessed by measuring vulnerability to xylem embolism via P_{50}, the negative pressure at which 50% of hydraulic conductivity is lost, a commonly used parameter in ecophysiological research. It has been shown that vulnerability to embolism (hydraulic failure) predicts drought-induced mortality in gymnosperm and woody angiosperm species in both temperate and tropical forests (Barigah *et al.* 2013; Brodribb & Cochard 2009; Rowland *et al.* 2015; Urli *et al.* 2013).

Given the strong selective force exerted by water stress on vegetation (Brodribb *et al.* 2014), the distribution of plant species along environmental gradients can be expected to be significantly influenced by their vulnerability to xylem embolism (Pockman & Sperry 2000). Global meta-analyses have shown that embolism vulnerability (P_{50}) is related to climate variables such as mean annual precipitation (MAP) and mean annual temperature (MAT) (Choat *et al.* 2012; Maherali *et al.* 2004). These studies have shown that tropical evergreen angiosperm species native to high rainfall areas are among the most vulnerable species. Because of the relation between embolism resistance and habitat occupation, it has been suggested that xylem embolism vulnerability can be useful for distinguishing plant adaptive strategies (Anderegg 2015; Lens *et al.* 2013). However, tropical rain forest angiosperms, occurring in high rainfall habitats with MAP above 2000 mm, are currently poorly studied. Among the rain forests of the world, the ecology of wet rain forests of high-elevation tropical islands is among the least documented in spite of their high percentage of endemic species and the endangered status of their floras (Harter *et al.* 2015; Kier *et al.* 2009; Loope & Giambelluca 1998). In this study, we analyse embolism vulnerability of rain forest species and its relation to environmental distribution in New Caledonia, a megadiverse oceanic archipelago with high endemism.

Because of its outstanding plant species richness and the level of threat to its flora, New Caledonia is recognized as a global biodiversity hotspot (Myers *et al.* 2000). Previous work has shown that biodiversity hotspots are highly vulnerable to climate change, reinforcing their status as global conservation priorities (Bellard *et al.* 2014; Malcolm *et al.* 2006). A characteristic feature of the New Caledonian flora is an overrepresentation of early diverging angiosperm lineages belonging to the ANA grade and the magnoliids (Pillon 2012). Recent research demonstrated that *Amborella trichopoda* (Amborellaceae), the sister species to all other extant angiosperms, along with some 60 other magnoliid and Chloranthaceae species endemic to New Caledonia have high environmental niche overlap in habitats with low evaporative demand characterized by moderate diurnal variations in temperature ($\leq 7\,^\circ C$) and MAP greater than ~2000 mm year^{-1} (Pouteau *et al.* 2015). However, the ecophysiological mechanisms behind this habitat preference, and in particular the potential role of vulnerability to drought-induced xylem embolism, have not been investigated.

Interestingly, these groups of angiosperm species have a broad diversity of xylem conduit anatomies that range from vesselless, tracheid-only wood, to vessel-bearing woods with scalariform or simple perforation plates (Fig. 1). The wood of some of these taxa (either vesselless wood or woods with narrow vessels including vessel elements having long scalariform perforation plates) is thought to resemble conditions primitive with respect to the majority of the angiosperms, which have short, wide vessel elements with simple perforation plates (Carlquist 2012; Hacke *et al.* 2007; Olson 2012). It has been hypothesized that the evolution of vessels may have provided angiosperms with increased hydraulic efficiency compared with wood comprising only tracheids as conductive structures (Carlquist 1975; Sperry 2003). However, a possible physiological trade-off during early vessel evolution may have increased vulnerability to drought-induced xylem embolism (Sperry 2003). Species with vessel elements bearing scalariform perforation plates may be more vulnerable to embolism than vesselless angiosperms (Sperry *et al.* 2007), suggesting that vessels with scalariform perforation plates should be mostly limited to wet habitats because of the risk of hydraulic failure in drier environments.

Beyond xylem conduit structure, wood and leaf traits have also been suggested as being linked with resistance to xylem embolism or drought tolerance. Wood structural investment, as quantified in part by wood density (WD), has been suggested to be a predictor of drought tolerance, given that some studies found WD to be negatively related to P_{50} (Chave *et al.* 2009; Delzon *et al.* 2010; Hacke *et al.* 2001; Markesteijn *et al.* 2011). Leaf dry mass per unit leaf area (LMA) has been
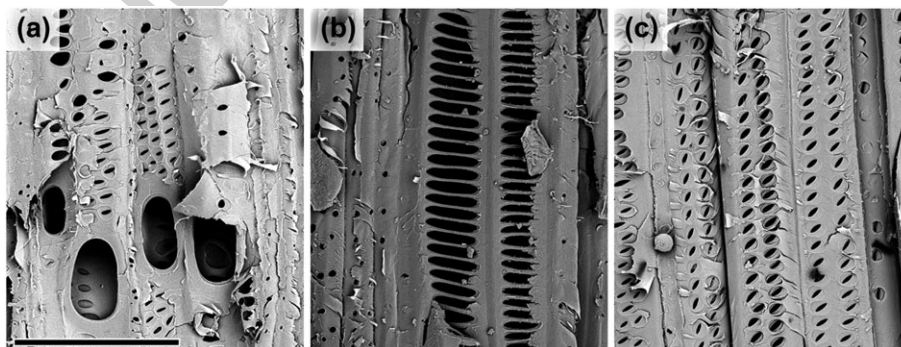
Figure 1. Illustration of different xylem conduit morphologies as seen in radial view with scanning electron microscopy. (a) Vessel elements with simple perforation plates in *Cryptocarya aristata*. (b) Vessel elements with scalariform perforation plates in *Hedycarya cupulata*. (c) Tracheids with many, distinctly bordered pits in *Zygogynum crassifolium*. Scale bar, 80 μm for a and b, 100 μm for c.

suggested as another key trait reflecting leaf and whole plant function (Poorter *et al.* 2009). Increases of leaf tissue thickness in dry and hot localities with compelling solar radiation may prevent leaf water loss and result in higher LMA values (Niinemets 2001). It has been suggested that LMA increases as a response to drought stress across species (Poorter *et al.* 2009). Therefore, higher LMA values in drought-exposed species can be considered as adaptive responses to water stress operating at the leaf level. This is supported by several studies showing that LMA increases with water stress (Cunningham *et al.* 1999; Fonseca *et al.* 2000; Niinemets 2001; Wright *et al.* 2004, 2005). Therefore, a reasonable prediction might be that LMA should be negatively related to embolism vulnerability in rain forest species. Leaf vein density (VD) has also been suggested to be related to species climatic distribution (Blonder & Enquist 2014). Moreover, it has been shown that higher values of VD are observed in species growing in sites of higher evaporative demand (Sack & Scoffoni 2013). As a consequence, a negative relationship between VD and P_{50} can be expected.

In summary, our work aims to (1) test the relationship between xylem vulnerability to embolism and distribution along environmental gradients of rain forest species; (2) test for differences in xylem vulnerability to embolism between vesselless and vessel-bearing species; and (3) assess the association of commonly used functional traits such as wood density, leaf mass per area and leaf vein density with xylem embolism vulnerability in rain forest species. Understanding the relation between the distribution of insular rain forest species and their trait values could help to identify the main organismal attributes that allow ecological differentiation by drought resistance in this rich and sensitive biome.

MATERIALS AND METHODS

Study site, plant material and sampling

New Caledonia is an archipelago located north of the Tropic of Capricorn in the southwest Pacific Ocean (Fig. 2 inset). The
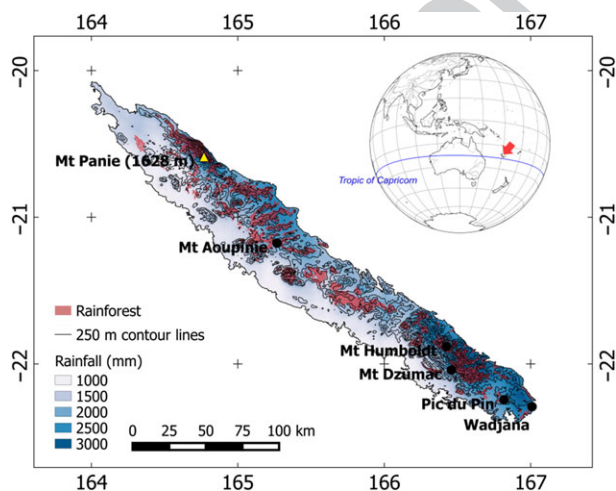
Figure 2. Map of New Caledonia with rain forest, elevation and rainfall distributions along the main island. Sampled rain forest localities are indicated in the map.

main island (*Grande Terre*, 16 000 km^2) has a central mountain range that runs along the entire island. The highest points are Mt. Panié (1628 m) in the north and Mt. Humboldt (1618 m) in the south (Fig. 2). New Caledonia has a tropical climate with a marked dry season from June to November. As a consequence of *Grand Terre*'s topography and the resulting rain shadow effect, MAP ranges from 800 mm year^{-1} along the western coastal plains to 4500 mm year^{-1} on the eastern slopes of the mountain chain (Météo-France 2007) (Fig. 2). Mean annual temperature in lowland areas is between 27 and 30 °C but varies along the elevational gradient with an environmental lapse rate of ~0.6 °C 100 m^{-1} elevation (Maitrepierre 2012). *Grande Terre* is mainly covered by substrates derived from volcano-sedimentary rocks, but the southern third of the island and some isolated massifs on the northwestern coast have substrates derived from ultramafic rocks (Fritsch 2012). A combination of climate, substrate and human-induced disturbance determines the presence of different vegetation types in New Caledonia. Terrestrial vegetation types are commonly classified into summit shrubland, rain forest, low-elevation scrubland (known as *maquis*), savanna and dry sclerophyll forest. Rain forest, the most species-rich vegetation type, with more than 2000 native vascular plant species, now covers ~3800 km^2 on the main island (Birnbaum *et al.* 2015) (Fig. 2). The diversity of habitats in New Caledonia, along with the extensive cover of rain forest, provides an ideal context for testing expectations regarding associations between plant traits and environmental gradients.

We studied xylem embolism vulnerability of 13 woody rain forest species endemic to New Caledonia (Table 1). Species were selected to represent a diversity of xylem conduit anatomies (Fig. 1). Additionally, we based our sampling on the study of Pouteau *et al.* (2015) to represent New Caledonian non-monocot/eudicot angiosperm species with different levels of habitat marginality (i.e. occupation of distinct habitats). Our sampling also included two rain forest eudicots with long scalariform perforation plates (Paracryphiaceae; Table 1), a condition though to be primitive with respect to the simple perforation plates observed in most angiosperms. The diversity of xylem conduit morphologies spanned by our sampling enabled us to test possible differences in embolism vulnerability between co-occurring vessel-bearing and vesselless angiosperms. Samples were collected at five rain forest locations of *Grande Terre*: Mt. Aoupinié, Mt. Dzumac, Mt. Humboldt, Pic du Pin and Wadjana (Fig. 2). Maximum conduit lengths were assessed on five branches per species by injecting air at 2-bars and cutting the apical end of the water-immersed stem section until the air bubbles emerged. This procedure allowed us to select species with suitable conduit lengths, shorter than the rotor plate (27 cm) used for embolism vulnerability measurements, to avoid a potential open conduit artefact with the Cavitron technique (Martin-StPaul *et al.* 2014).

Measurements of embolism vulnerability

We collected 15 sun-exposed branches per species at pre-dawn. Branches were immediately defoliated and wrapped in moist paper, sealed in plastic bags and stored in the dark for

Table 1. Xylem embolism vulnerability parameters and functional traits of 13 New Caledonian rain forest species

Species	Family	Conduit type	P_{12} (MPa)	P_{50} (MPa)	P_{88} (MPa)	Slope (% MPa^{-1})	WD (g cm^{-3})	VD (mm mm^{-2})	LMA (g m^{-2})
Amborella trichopoda	Amborellaceae	tracheid	−2.3 (0.29)	−2.7 (0.19)	−3.0 (0.17)	177.2 (68.9)	0.508 (0.004)	3.7 (0.19)	93.1 (36.9)
Ascarina rubricaulis	Chloranthaceae	vessel (scal)	−1.6 (0.49)	−2.2 (0.26)	−2.9 (0.25)	97.5 (47.1)	0.472 (0.030)	4.7 (0.13)	106.7 (19.9)
Cryptocarya aristata	Lauraceae	vessel (sim)	−0.8 (0.31)	−2.0 (0.22)	−3.2 (0.39)	43.9 (9.1)	0.542 (0.007)	8.6 (0.30)	174.9 (16.2)
Hedycarya cupulata	Monimiaceae	vessel (scal)	−1.5 (0.43)	−3.2 (0.23)	−4.9 (0.54)	31.1 (7.2)	0.540 (0.053)	5.4 (0.23)	76.2 (8.8)
Hedycarya parvifolia	Monimiaceae	vessel (scal)	−2.0 (0.28)	−3.1 (0.09)	−4.1 (0.28)	48.8 (12.4)	0.590 (0.066)	6.3 (0.19)	112.0 (21.9)
Kibaropsis caledonica	Monimiaceae	vessel (scal)	−1.6 (0.38)	−2.4 (0.21)	−3.3 (0.33)	65.8 (21.6)	0.682 (0.029)	5.8 (0.35)	117.2 (11.5)
Nemuaron viellardii	Atherospermataceae	vessel (scal)	−1.4 (0.29)	−2.3 (0.16)	−3.2 (0.31)	61.8 (18.2)	0.626 (0.034)	5.3 (0.20)	173.1 (18.9)
Paracryphia alticola	Paracryphiaceae	vessel (scal)	−0.8 (0.25)	−2.1 (0.35)	−3.4 (0.62)	40.2 (9.4)	0.630 (0.010)	2.3 (0.21)	86.0 (18.9)
Quintinia major	Paracryphiaceae	vessel (scal)	−0.9 (0.35)	−2.5 (0.34)	−4.0 (0.53)	33.3 (6.1)	0.652 (0.060)	7.5 (0.24)	214.5 (25.2)
Zygogynum acsmithii	Winteraceae	tracheid	−2.4 (0.06)	−2.7 (0.10)	−3.0 (0.15)	173.0 (31.2)	0.583 (0.001)	4.8 (0.30)	142.9 (21.5)
Zygogynum crassifolium	Winteraceae	tracheid	−3.6 (0.31)	−4.0 (0.26)	−4.5 (0.23)	125.8 (37.9)	0.674 (0.043)	5.8 (0.18)	309.3 (33.7)
Zygogynum stipitatum	Winteraceae	tracheid	−2.2 (0.27)	−2.4 (0.26)	−2.7 (0.27)	214.0 (58.1)	0.455 (0.045)	4.8 (0.05)	85.7 (8.2)
Zygogynum thieghemii	Winteraceae	tracheid	−1.9 (0.20)	−2.2 (0.28)	−2.5 (0.36)	168.2 (43.5)	0.605 (0.026)	5.0 (0.22)	216.3 (14.4)

Mean values (and standard deviation) of xylem embolism parameters and functional traits measured in this study. Note: 'scal' means that xylem vessels consist of elements with scalariform perforation plates; 'sim' refers to vessel elements with simple perforation plates. LMA, leaf mass per area; WD, wood density; VD, leaf vein density.

transport. Prior to taking measurements, branches were debarked and cut to a standard length of 27 cm. Xylem embolism resistance was measured using a Cavitron, a centrifugation-based apparatus that lowers the negative pressure in xylem segments while simultaneously measuring hydraulic conductance (Cochard 2002; Cochard *et al.* 2005). We followed Delzon *et al.* (2010) for the test procedure. The percentage loss of conductance (PLC) of the stems was measured in 0.5 MPa pressure steps using the software Cavisoft v4.0, which calculates PLC with the following equation:

$$PLC = 100 \times \left(1 - \frac{K}{K_{max}}\right),$$

where K is the stem conductance at a given pressure and K_{max} ($m^2 MPa^{-1} s^{-1}$) is the maximum conductance of the stem, calculated under xylem pressures close to zero. The increase in PLC with decreasing pressure, allowed us to produce vulnerability curves (VC) for each species (Fig. 3). VCs were fit with a sigmoid function (Pammenter & Van Der Willigen 1998) using the next equation:

$$PLC = \frac{100}{\left[1 + \exp\left(\frac{S}{25} \times (P\text{-}P_{50})\right)\right]},$$

where S (% MPa^{-1}) is the slope of the vulnerability curve at the inflexion point and P_{50} (MPa) is the xylem pressure inducing 50% loss of conductance. The slope of the vulnerability curve (S) is a good indicator of the speed at which embolisms affect the stem (Delzon *et al.* 2010). Additionally, we used our VCs to calculate P_{12} and P_{88}, which are respectively the 12% and 88% loss of conductance. P_{12} and P_{88} are physiologically significant indexes because they are thought to respectively reflect the initial air-entry tension producing embolisms and the irreversible death-inducing xylem tension (Urli *et al.* 2013). Mean values of embolism vulnerability parameters correspond to the average values of four to 11 samples per species.
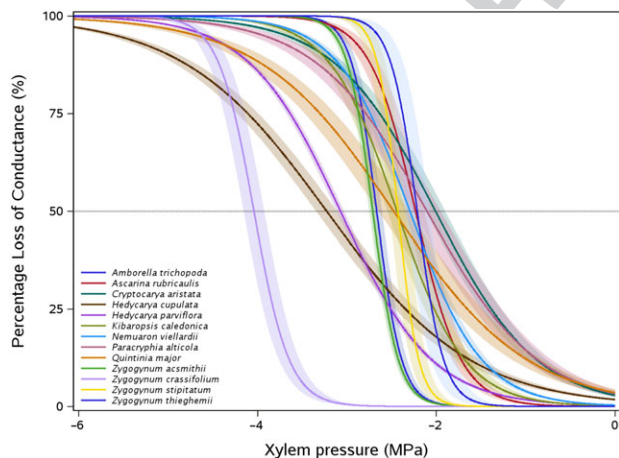

Figure 3. Mean vulnerability curves for each of the 13 studied species showing percentage loss of hydraulic conductance in xylem (%) as a function of xylem pressure (MPa). Shaded bands represent standard errors, and 50% loss in conductance is indicated by a horizontal dotted line.

Measurements of stem and leaf functional traits

Wood density ($g\,cm^{-3}$) was calculated using 4-cm-long wood segments, from five branches sampled for embolism resistance measurements. Wood volume was calculated using the water displacement method. We oven-dried wood samples at 70 °C for a minimum of 72 h until constant mass. WD was calculated as dry mass over fresh volume. We measured LMA ($g\,m^{-2}$) on 15 leaves, petioles included, borne by the branches used for embolism vulnerability measurements. Leaves were scanned using a portable scanner (CanoScan LiDE 25, Canon, Japan). Leaf area was calculated from the scanned images using ImageJ 1.47v. (NIH Image, Bethesda, MD, USA). Leaves were then oven-dried at 70 °C for 72 h and weighed. LMA was calculated as the leaf dry mass over leaf area. Leaf VD (in $mm\,mm^{-2}$), also known as leaf vein length per unit leaf area, was measured on five additional leaves. Sections of leaf tissue (~2 cm^2) were cut from the middle third of the lamina. Leaf sections were cleared in 5% NaOH and rinsed with distilled water. Clearing time varied from 20 to 72 h depending on the species. After clearing, leaf veins were stained using 0.1% aqueous toluidine blue for 5–10 min and mounted in a glycerol solution. We imaged the mounted sections at 5× using a light microscope (Leica DM5000B; Leica Microsystems, Wetzlar, Germany). Vein lengths on digital images were measured using ImageJ 1.47v.

Species environmental distribution

Species distribution was obtained from occurrence records in two datasets: (1) the New Caledonian Plant Inventory and Permanent Plot Network made up of 201 plots measuring 20 × 20 m (Ibanez *et al.* 2014) and 8 additional plots measuring 100 × 100 m distributed across rain forests of *Grande Terre* and (2) specimens in the Herbarium of Noumea. The mean number of occurrences per species was 71. The species with the fewest number of collections was *Zygogynum acsmithii* (Winteraceae) with 14 occurrences, and the most collected species was *Hedycarya cupulata* (Monimiaceae) with 171 occurrences. When several occurrences were located within a distance of 500 m, we kept a single occurrence positioned at the centroid to avoid overweighting locations that have been oversampled. For each location, five environmental metrics were computed: (1) MAP to test whether the association between P_{50} and rainfall observed at a global scale (Choat *et al.* 2012; Maherali *et al.* 2004) also applies at the island-wide scale; (2) MAT to test whether the association between P_{50} and temperature observed at a global scale (Choat *et al.* 2012; Maherali *et al.* 2004) applies at the island-wide scale; (3) mean temperature of the driest quarter (MTDQ) to quantify species tolerance to drought and heat stress that peaks during the driest period characterized by a high evaporative demand; (4) elevation as a proxy of the fine-scale distribution of climate on high-elevation islands; and (5) the frequency of occupation of rain forest habitats as a proxy of micro-climatic conditions, such as local water availability, light exposure and disturbance regimes tolerated by the selected species. MAP data were extracted from a 1 km resolution grid produced by Météo-France

through the AURELHY model by interpolating rainfall records from 1991 to 2000 (Météo-France 2007). MAT and MTDQ data were extracted from the WorldClim database (Hijmans *et al.* 2005). Elevation was derived from a 10 m resolution digital elevation model provided by the *Direction des Infrastructures*, *de la Topographie et des Transports Terrestres* of the Government of New Caledonia. Each location was associated with the appropriate pixel on which it was centred. Finally, percentage of occurrence in rain forest was estimated using a vegetation map in the form of a shapefile published in the Atlas of New Caledonia (Jaffré *et al.* 2012). Mean and extreme values of each environmental metric gathered for the 13 studied species are provided in Table S1.

Data analyses

Before the analyses, we confirmed the normal distribution of values for all variables measured (Shapiro-Wilk test; $\alpha = 0.05$). To recognize groups of species with similar embolism vulnerabilities, we used one-way analyses of variance with post hoc Tukey's honest significant difference using 95% confidence intervals to compare P_{50} values, along with other embolism vulnerability indexes across species. Independent *t*-tests were used to compare embolism vulnerability parameters between vessel-bearing and vesselless species. Linear regressions were used to determine the relationship of P_{50} with environmental data. Regression lines are shown only when relationships were significant. Pearson's correlation analyses were used to evaluate the relationship between xylem embolism vulnerability, leaf and stem functional traits and environmental correlates of species distribution. Correlations were considered significant at $P < 0.05$. Finally, to place the New Caledonian rain forest species in a global perspective, we combined our data with the worldwide dataset of Choat *et al.* (2012). To confirm a link between MAP and P_{50} at a global scale, we fit a linear relationship on $\log_{10}$-transformed data. To facilitate the $\log_{10}$ transformation of P_{50} values, we used the method of Maherali *et al.* (2004) converting P_{50} values from negative to positive prior to data transformation. All analyses were performed using R v.3.2.3 (R Core Team 2015).

RESULTS

Xylem embolism vulnerability of New Caledonian rain forest angiosperms

Vulnerability curves varied considerably among species (Fig. 3). P_{50} varied twofold across species (Fig. 4), with significant interspecific variation ($F = 28.34$; $P < 0.001$) (Fig. 4). Similar significant variation in P_{12} ($F = 30.63$; $P < 0.001$), P_{88} ($F = 23.54$; $P < 0.001$) and vulnerability curve slopes ($F = 14.82$; $P < 0.001$) was observed across species. The mean P_{50} of rain forest angiosperms was -2.60 MPa, with most species falling into a narrow range of P_{50} values between -2.0 and -2.7 MPa (Fig. 4). The highest P_{50} was -2.0 MPa for *Cryptocarya aristata*. Both *Hedycarya* species had a similar vulnerability level with P_{50} just below -3.0 MPa. *Zygogynum crassifolium* had the lowest P_{50}, at -4.03 MPa, standing out
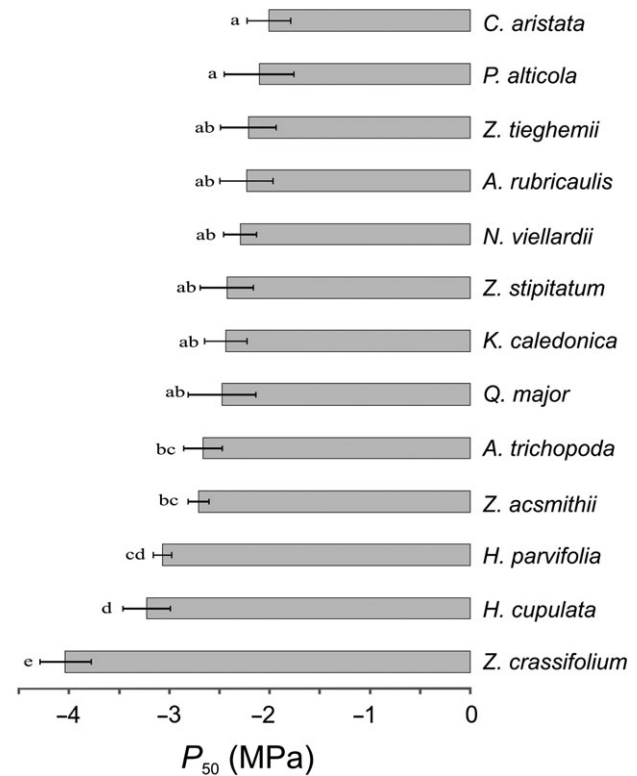

Figure 4. P_{50}, xylem pressure inducing 50% loss in conductance, of 13 New Caledonian rain forest species. Different letters indicate significant differences between species at $P < 0.05$. Standard errors are represented by bars.

from the rest of the species (Figs 3 & 4). Slopes of the vulnerability curves, which reflect the rate at which embolisms occur, varied sevenfold across species (Fig. 3; Table 1), with the lowest slope of 31% MPa^{-1} recorded for *H. cupulata* (Fig. 3) and the steepest slope of 214% MPa^{-1} measured in *Zygogynum stipitatum* (Fig. 3). The three embolism vulnerability indexes measured (P_{12}, P_{50} and P_{88}), which indicate xylem tensions at which different percentages of hydraulic conductivity are lost, all correlated well with each other. P_{50} was significantly correlated with P_{12} ($r = 0.76$; $P = 0.002$) and P_{88} ($r = 0.72$; $P = 0.004$), suggesting that embolism vulnerability acts similarly at different drought intensities across species. P_{50} was not correlated with the cavitation curve slope ($r = -0.05$; $P = 0.85$). However, the cavitation curve slope was related to P_{12} ($r = -0.63$; $P = 0.02$) and P_{88} ($r = 0.58$; $P = 0.04$), suggesting that the speed of embolism occurrence is related to these parameters of embolism resistance across the sampled species.

P_{50} of vessel-bearing species (-2.48 MPa) was not significantly different from P_{50} of vesselless species (-2.81 MPa) ($t = -0.92$; $P = 0.391$) (Fig. 5). P_{88} was also similar between both groups of xylem conduit elements morphologies ($t = 1.16$; $P = 0.28$). Differences were only observed for P_{12} ($t = 3.43$; $P = 0.013$), with vessel-bearing species having higher P_{12} values (-1.34 MPa) than vesselless species (-2.49 MPa) (Fig. 5). A significant difference was detected when comparing the slopes of the vulnerability curves between both xylem conduit morphologies ($t = 7.42$; $P \leq 0.001$): on average, vessel-bearing
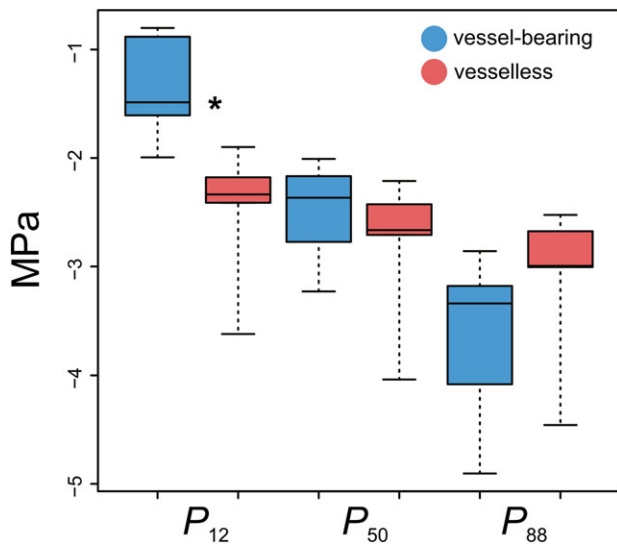
Figure 5. Box plot of embolism vulnerability indexes for vessel-bearing species and vesselless species. Boxes show the median, 25th and 75th percentiles, and bars indicate maximum/minimum values. Significant differences of embolism vulnerability indexes at $P \leq 0.05$ between conduit morphologies are indicated with an asterisk.

species had much lower slopes (53% MPa^{-1}) than vesselless species (172% MPa^{-1}).

Relation of species environmental distribution with xylem embolism vulnerability and other functional traits

P_{50} was positively correlated with the proportion of species occurrences located in rain forest areas (Fig. 6a), indicating that species that are less present in rain forest areas have greater xylem embolism resistance. For instance, *Paracryphia alticola*, which had the most rain forest-restricted distribution, with 91% of its occurrence records in rain forest areas (Table S1), had a high P_{50} of -2.10 MPa, ranking among the least resistant species (Fig. 4). On the other hand, *Z. crassifolium*, for which only 24% of occurrences were in rain forest areas (Table S1), was the most resistant to xylem embolisms with a P_{50} of -4.03 MPa (Fig. 4). P_{50} was also related to species mean elevational distribution (Fig. 6b), indicating that species from lower elevations are less vulnerable to xylem embolism. P_{50} was negatively associated with MAT (Fig. 6c). P_{12} was also largely related to species distribution variables and MAT (Table 2). Both P_{12} and P_{50} were correlated with the MTDQ (Table 2). For other stem and leaf traits, significant relationships were detected only between LMA and rain forest occupancy (Table 2). Embolism vulnerability indexes were the only biological variable that correlated with more than one environmental variable (Table 2). Vulnerability to embolism was not associated with MAP within our group of species (Fig. 6d; Table 2). The probability of an association between P_{50} and MAP was marginally significant ($P = 0.0509$) when considering a 5% significance level. However, the relationship between P_{50} and MAP was highly significant when including our data in the

global P_{50}-MAP dataset of Choat *et al.* (2012), suggesting that New Caledonian rain forest species fit this global-scale relationship (Fig. 7).

Relationships between vulnerability to embolism and leaf and xylem functional traits

P_{50} was not associated with any of the wood and leaf functional traits. WD scaled negatively with P_{50}, but the relationship was not significant ($r = -0.24$; $P = 0.435$). Similarly, LMA was not correlated with P_{50} ($r = -0.37$; $P = 0.214$). VD was not related to P_{50} ($r = -0.06$; $P = 0.840$). P_{12} and P_{88} were also not associated with any of the traits measured (not shown).

DISCUSSION
Association between xylem embolism vulnerability and habitat occupation of tropical rain forest angiosperms

We show that vulnerability to xylem embolism correlates with the percentage of occupancy of rain forest habitats by angiosperm species, with P_{50} explaining 47% of the occurrence of angiosperm species in rain forest areas (Fig. 6a). This result suggests that embolism vulnerability influences habitat occupation even within a moderate climatic gradient. For instance, species such as *A. trichopoda*, which occurs with a frequency of 82% in rain forest areas, may be restricted to moist habitats because of the risk of suffering hydraulic failure in drier locations. Likewise, *Z. crassifolium*, the most embolism resistant species in our study (Fig. 3), had the lowest occurrence in rain forest areas (24%). Consequently, relative to the other studied species, *Z. crassifolium* occurred in locations with the lowest rainfall regimes recorded in this study (Table S1; Fig. 6d). It thus appears that higher resistance to xylem embolism allows species to occupy drier habitats such as scrublands. Because mean trait values of plant species correspond to their position along environmental gradients (Violle & Jiang 2009), the occurrence of species with higher embolism resistance in drier habitats likely reflects the importance of resistance to xylem embolism as an adaptive response to water deficit (Maherali *et al.* 2004). For instance, *Callitris tuberculata*, the species with the highest embolism resistance ever measured ($P_{50} = -18.8$ MPa), inhabits extremely dry areas of Western Australia in zones with MAP lower than 180 mm at its most extreme margin (Larter *et al.* 2015). At the other end of the embolism vulnerability spectrum are species from moist habitats such as the tropical rain forest, which experience xylem embolisms under xylem pressures close to -1 MPa (Choat *et al.* 2012).

Our work provides evidence of a relationship between species elevational distribution and embolism vulnerability, with highland species being more vulnerable to xylem embolism (Fig. 6b). For instance, *P. alticola*, the second most vulnerable species measured here (Fig. 3), had the highest elevational range (mean = 1011 m; Table S1). This relation between species elevational distribution and embolism vulnerability, along with the negative relation between embolism resistance and MAT
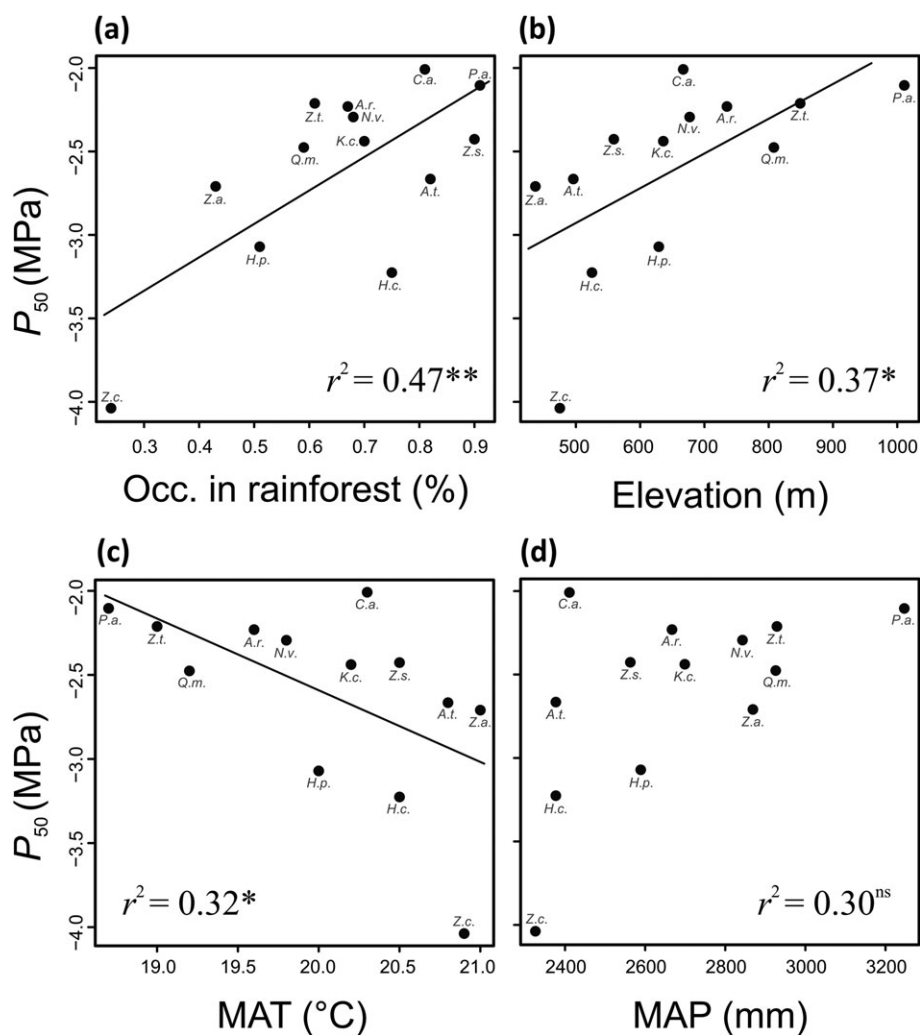
Figure 6. Relationships between proportion of occurrences in rain forest (a), elevation (b), mean annual temperature (c) and mean annual precipitation (d) and vulnerability to embolism (P_{50}) of New Caledonian rain forest species. Points represent mean values per species. Species initials are provided. ns = non-significant at $P = 0.0509$; * $P \leq 0.05$; ** $P \leq 0.01$.

Table 2. Correlations of environmental variables with embolism vulnerability parameters and functional traits

		MAP (mm)	MAT (°C)	MTDQ (°C)	Elevation (m)	Rain forest occupancy (%)
P_{12} (MPa)	*r*	0.48	**−0.65**	**−0.71**	**0.69**	**0.64**
	P	0.094	**0.016**	**0.006**	**0.008**	**0.017**
P_{50} (MPa)	*r*	0.55	**−0.56**	**−0.65**	**0.61**	**0.68**
	P	0.051	**0.044**	**0.015**	**0.025**	**0.009**
P_{88} (MPa)	*r*	0.33	−0.18	−0.25	0.21	0.37
	P	0.263	0.559	0.401	0.484	0.213
Slope (% MPa^{-1})	*r*	−0.15	0.40	0.36	−0.41	−0.07
	P	0.630	0.180	0.232	0.164	0.816
WD (g cm^{-3})	*r*	0.36	−0.24	0.07	0.24	−0.48
	P	0.22	0.422	0.816	0.431	0.092
VD (mm mm^{-2})	*r*	−0.38	0.24	0.28	−0.16	−0.27
	P	0.200	0.420	0.348	0.588	0.376
LMA (g m^{-2})	*r*	−0.06	0.003	0.30	−0.02	**−0.71**
	P	0.839	0.990	0.321	0.934	**0.006**

Pearson's correlation coefficients (*r*) and *P*-values (*P*) of bivariate cross-correlations. Bold values indicate significant correlations at $P \leq 0.05$. LMA, leaf mass per area; MAP, mean annual precipitation; MAT, mean annual temperature; MTDQ, mean temperature of the driest quarter; WD, wood density; VD, leaf vein density.
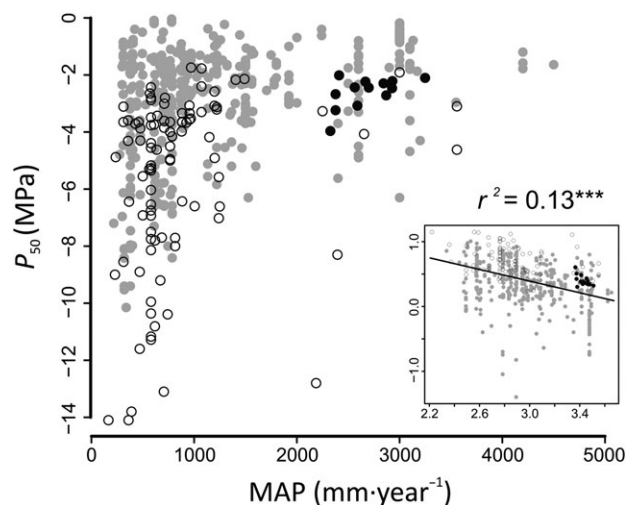
Figure 7. Vulnerability to embolism as a function of mean annual precipitation (MAP) at a global scale. The 13 New Caledonian insular rain forest species analysed in this study fit the global pattern of P_{50}-MAP. Different symbols represent gymnosperm species (open circles), angiosperm species (grey circles) and New Caledonian rain forest angiosperm species (black circles). Inset: Negative relationship between MAP and embolism resistance using $\log_{10}$-transformed data. P_{50} values were converted from negative to positive to facilitate $\log_{10}$ transformation. The coefficient of determination corresponds to the relationship after $\log_{10}$-transformation. Additional data obtained from Choat *et al.* (2012). *** $P \leq 0.001$.

(Fig. 6c), has essential conservation implications for the flora of the New Caledonian rain forests. Temperature increases have already been recorded in New Caledonia over the last three decades at a rate of 0.25 °C per decade. Using the same rate, local climate models suggest that MAT could increase by ~2.5 °C over the next century (Cavarero *et al.* 2012). Upward shifts of organisms' elevational distributions are expected as climate changes (Parmesan & Yohe 2003; Walther *et al.* 2002). Extensive upslope shifts toward cooler areas have been documented by several studies of temperate and tropical plant species, indicating that this displacement is already ongoing in different biomes (Colwell *et al.* 2008; Feeley *et al.* 2011; Feeley *et al.* 2013; Lenoir *et al.* 2008; Morueta-Holme *et al.* 2015; Urli *et al.* 2014). Given that temperature-induced upward shifts in species distribution are ultimately restricted by dispersal and resource availability (Walther *et al.* 2002), montane rain forest angiosperms can be assumed to have a limited ability to respond to increasing temperatures because of a reduced range to disperse into suitable microrefugia. The vulnerable populations of New Caledonian rain forest angiosperms restricted to high elevational ranges could therefore face extinction if temperature and evaporative demand keep increasing at the same pace.

Previous analyses have shown that average annual rainfall is related with species embolism vulnerability across biomes (Brodribb & Hill 1999; Choat *et al.* 2012; Maherali *et al.* 2004). Among the environmental variables analysed in our study within a single biome, MAP was the only one marginally unrelated to embolism vulnerability (Fig. 6d). This disagreement in the relationship linking P_{50} and MAP likely stems from the difference in scale between former global approaches and

our island-wide study. At such a fine scale, the MAP raster we used probably had a resolution too coarse (1 km) to render the actual amount of water available for plants, which depends on microclimatic effects that were better captured by fine-scale layers such as the digital elevation model and the rain forest map. In addition, averaged variables such as MAP appear to be of lower predictive power than extreme climate variables like MTDQ, which are recognized as good predictors of species distribution as they are related to plant mortality (Zimmermann *et al.* 2009). Finally, we can question the ability of the MAP raster interpolated from 121 points (i.e. one meteorological station per 150 km^2), most of which are located at low elevation, to account for the complex distribution of MAP resulting from a double gradient of elevation and windwardness.

In contrast to MAP, the distribution of MAT is much easier to estimate because it mainly arises from a single elevational gradient through the environmental lapse rate (Maitrepierre 2012). In spite of the lack of a relation between MAP and embolism vulnerability at the island-wide scale, a strong relationship was detected between both variables when including our data in a global context (Fig. 7). Our study thus increases the representation of angiosperm species from moist habitats, which were less represented in that study as compared with plant species from drier habitats (Fig. 7). We show that species endemic to the rain forest of New Caledonia fit the pattern described by this global sample, occupying the upper end of the embolism vulnerability range (Fig. 7). This finding confirms that across continental and insular ecosystems, high embolism vulnerability is observed in species growing in high rainfall conditions.

Poor differentiation of embolism resistance between vessel-bearing and vesselless species: insights into vessel evolution

It has been suggested that species bearing vessel elements with scalariform perforation plates are more vulnerable than vesselless angiosperms (Sperry *et al.* 2007). However, we did not observe significant differences in embolism vulnerability between vesselless and vessel-bearing species (Fig. 5). Only slight differences were observed at the onset of embolism formation (P_{12}), with vessel-bearing species being less resistant (Fig. 5). This suggests a lack of differentiation in embolism vulnerability across species with different xylem conduit anatomies, with slight differences at low xylem tensions. The low values of embolism resistance in species with vessels elements with long scalariform perforation plates, and similarity in embolism resistance between tracheids and vessels, support the hypothesis that angiosperm vessels could not have evolved in xeric habitats because of limitations caused by embolism risk (Carlquist 2012; Sperry *et al.* 2007). Despite initially embolizing at less negative pressures, vessel-bearing species had much lower embolism vulnerability curve slopes compared with vesselless species, suggesting that after the start of cavitation, embolism propagation proceeds slower in vessel-bearing species. Current research highlights the great importance of xylem

ultrastructure, with characters such as pit membrane structure playing a key role in embolism resistance (Jansen & Schenk 2015; Lens *et al*. 2011; Lens *et al*. 2013; Li *et al*. 2016; Schenk *et al*. 2015). The lack of differentiation in embolism resistance between vesselless and vessel-bearing angiosperms suggests that evolutionary changes in xylem conduit types are not associated with ultrastructural anatomical changes. Further research on ultrastructural characteristics of interconduit pits would be needed to discern which xylem properties allow variation in embolism vulnerability in tropical rain forest angiosperms with various xylem conduit types.

Weak association between xylem embolism vulnerability and common functional traits in a tropical rain forest

Selection likely favours thicker vessel walls in resisting deformation under increasingly negative pressures (Hacke *et al*. 2001). In line with this expectation, previous work has shown a negative relation between P_{50} and wood density in angiosperm species (Hao *et al*. 2008; Jacobsen *et al*. 2005; Markesteijn *et al*. 2011; Pratt *et al*. 2007). Surprisingly, despite being negatively related, we did not find a significant association between wood density and embolism vulnerability in our sample of New Caledonian rain forest species. By analyzing the same number of species that we studied here, Markesteijn *et al*. (2011) showed a strong negative relation between WD and P_{50} in species of tropical dry forest, a drought-prone biome. Moreover, Hao *et al*. (2008) showed a negative relation between WD and P_{50} in 10 species from very contrasting environments (savanna and forest). Hacke *et al*. (2001) showed that the relationship between P_{50} and wood density across a wide range of species is curvilinear. In their analysis, the slope of the curve is lower in species with wood densities between 0.4 and 0.7 g cm^{-3}, corresponding to the WD values of the species measured in this study (Table 1). The curve then becomes much steeper with increasing embolism resistance, corresponding to wood density values above ~0.7 g cm^{-3}. This suggests a lack of selective pressure for greater structural investment in increasing conductive safety in the wood of tropical rain forest species. Wood structure can therefore be modulated for diverse competing functions in environments where water stress is not substantial.

A relation between xylem embolism vulnerability and LMA could be expected because it has been shown that LMA increases over environmental gradients as a response to drought stress (Wright *et al*. 2005). However, our study shows that LMA and P_{50} are decoupled along the limited range of LMA that New Caledonian rain forest species span. This result agrees with similar findings in neotropical dry forests (Markesteijn *et al*. 2011; Méndez-Alonzo *et al*. 2012). Moreover, it has been shown that leaf life span, which is strongly related to LMA (Wright *et al*. 2004), is not related to P_{50} in plants of an Asian tropical dry forest (Fu *et al*. 2012). The lack of a relationship between LMA and embolism vulnerability observed in both rain forest and dry forest species (Markesteijn *et al*. 2011; Méndez-Alonzo *et al*. 2012) suggests that there is a certain degree of variation in LMA for a given embolism vulnerability. The absence of a relationship between a key hydraulic trait such as xylem embolism resistance and commonly measured functional traits such as WD and LMA forewarn further research on the risk of using these traits as indicators of drought tolerance when only a limited range of variation in such functional traits is measured.

The second foliar trait considered in our study, leaf VD, has been shown to be strongly positively related to functions such as leaf hydraulic conductivity and photosynthetic capacity (Brodribb *et al*. 2007; Brodribb *et al*. 2010; Feild & Brodribb 2013; Sack & Scoffoni 2013). According to the so-called hydraulic safety-efficiency trade-off hypothesis, safety in hydraulic conductivity should be selected against conductive efficiency (Tyree & Zimmermann 2002). In this regard, a positive relation between VD and P_{50} can be expected, with conductive-efficient species also being more vulnerable. However, this correlation was the weakest of those involving the traits measured in our study. Previous studies have shown that leaf P_{50} and leaf hydraulic efficiency, a trait that is strongly related to VD, is not correlated in woody species across different biomes (Blackman *et al*. 2010; Nardini & Luglio 2014). Our results provide new evidence of the absence of such trade-off within a sample of New Caledonian rain forest species, which show low hydraulic efficiency, as reflected by their low values of VD and also low embolism resistance. It has been recently shown that numerous species share this profile, having both poor hydraulic efficiency and safety (Gleason *et al*. 2016). Future research would be needed to identify the environments favouring the presence of species with this apparently non-optimal hydraulic profile.

Among the traits measured in our study, xylem embolism vulnerability is the most correlated to environmental variables (Table 2). This relation may indicate that xylem embolism vulnerability provides a measure that relates more closely to the ecological differentiation of tropical angiosperms. Plant hydraulic physiology is strongly linked with photosynthetic assimilation and derived carbon uptake (Brodribb 2009). It has been suggested that hydraulic failure is the main underlying mechanism of rain forest tree mortality (Rowland *et al*. 2015). Drought-induced rain forest dieback may therefore alter the primary production and functional composition of one of the richest ecosystems of the world, consequently diminishing significant amounts of biomass and carbon storage (Malhi *et al*. 2009; Phillips *et al*. 2009; Phillips *et al*. 2010). Xylem embolism resistance may thus play a major role in the maintenance of primary productivity and plant function. Our findings emphasize the importance of xylem embolism vulnerability as a main driver of rain forest species distribution. The incorporation of such a key ecophysiological trait into process-based distribution models would be relevant to estimate the response mechanisms of rain forest plant species to global climate change.

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Table S1. Environment and habitat variables measured for the 13 rain forest species studied.

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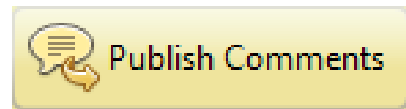
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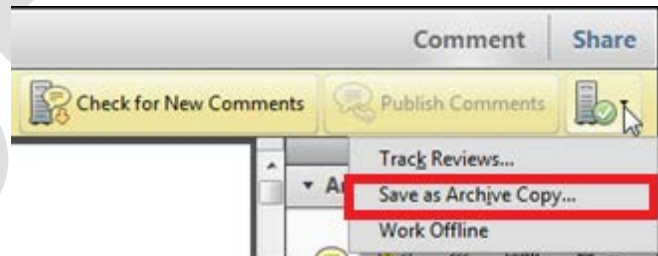
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