



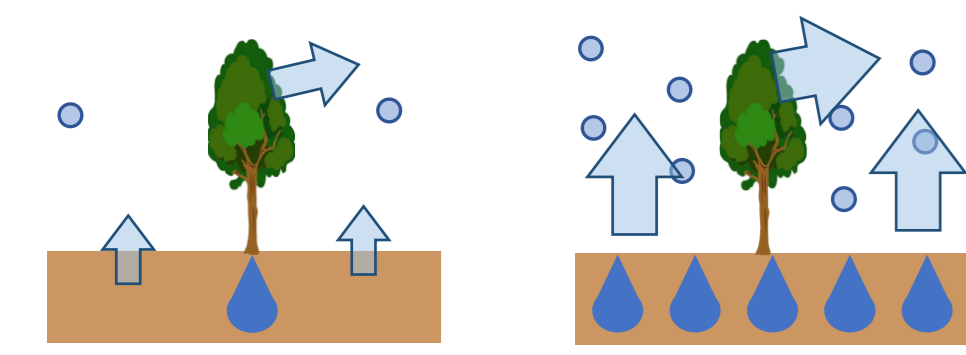
Introduction

Vascular epiphytes represent a substantial portion of global forest biodiversity but are also highly susceptible to the effects of anthropogenic land use and climate change. Understanding the environmental variables controlling the distributions of these plants is fundamental to biodiversity conservation.

At broad spatial scales, water availability is a major determinant of epiphyte growth and richness distribution, but varies with gradients in precipitation, air humidity, and the occurrence of cloudy fog (e.g., Hietz et al. 1995; Krefl et al. 2004; Ding et al. 2016). In addition, local factors such as wind speed affects the amount of water vapor diffusion, and soil water content affects the strength of evapotranspiration, both of which relate to water availability. At local scales, with apparently similar precipitation, water availability can be highly heterogeneous due to hydrogeomorphological conditions in topographically variable watersheds. For example, ridges typically have lower soil water content and higher exposure to wind than valley bottoms. These factors may affect the occurrence and species richness of vascular epiphytes.

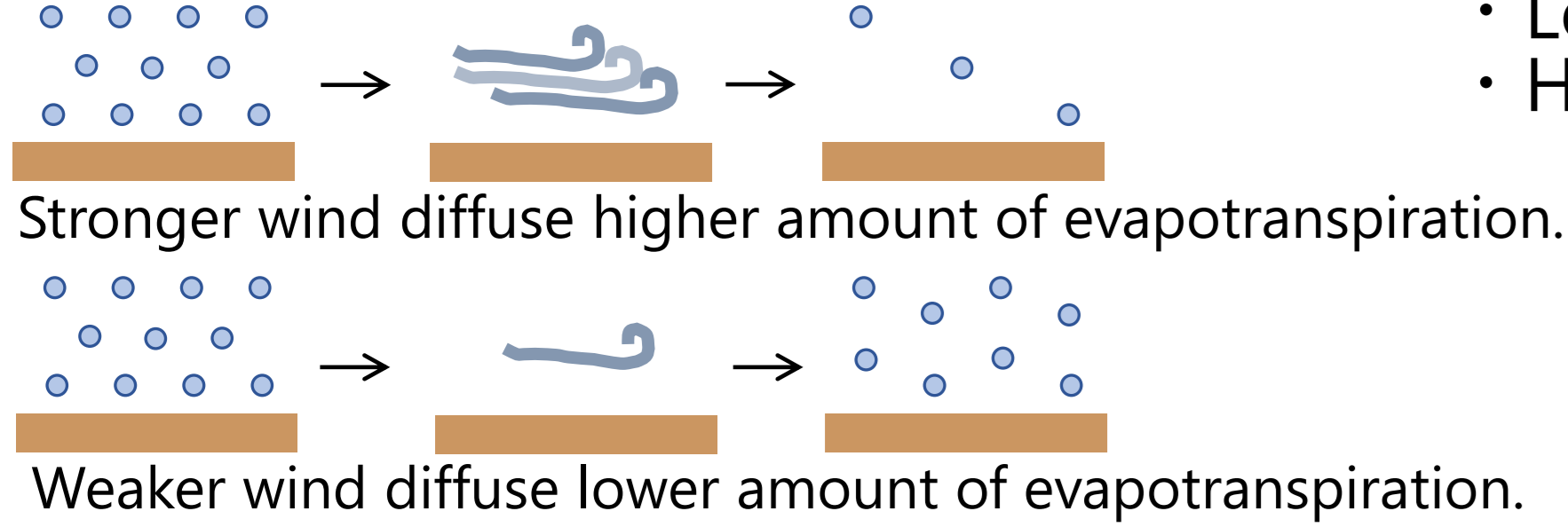
◆ **Soil water content** affects the amount of evapotranspiration.

Lower humidity on ridges with
 • Higher wind exposure
 • Lower soil water content



◆ **Wind speed** affects the amount of water vapor diffusion.

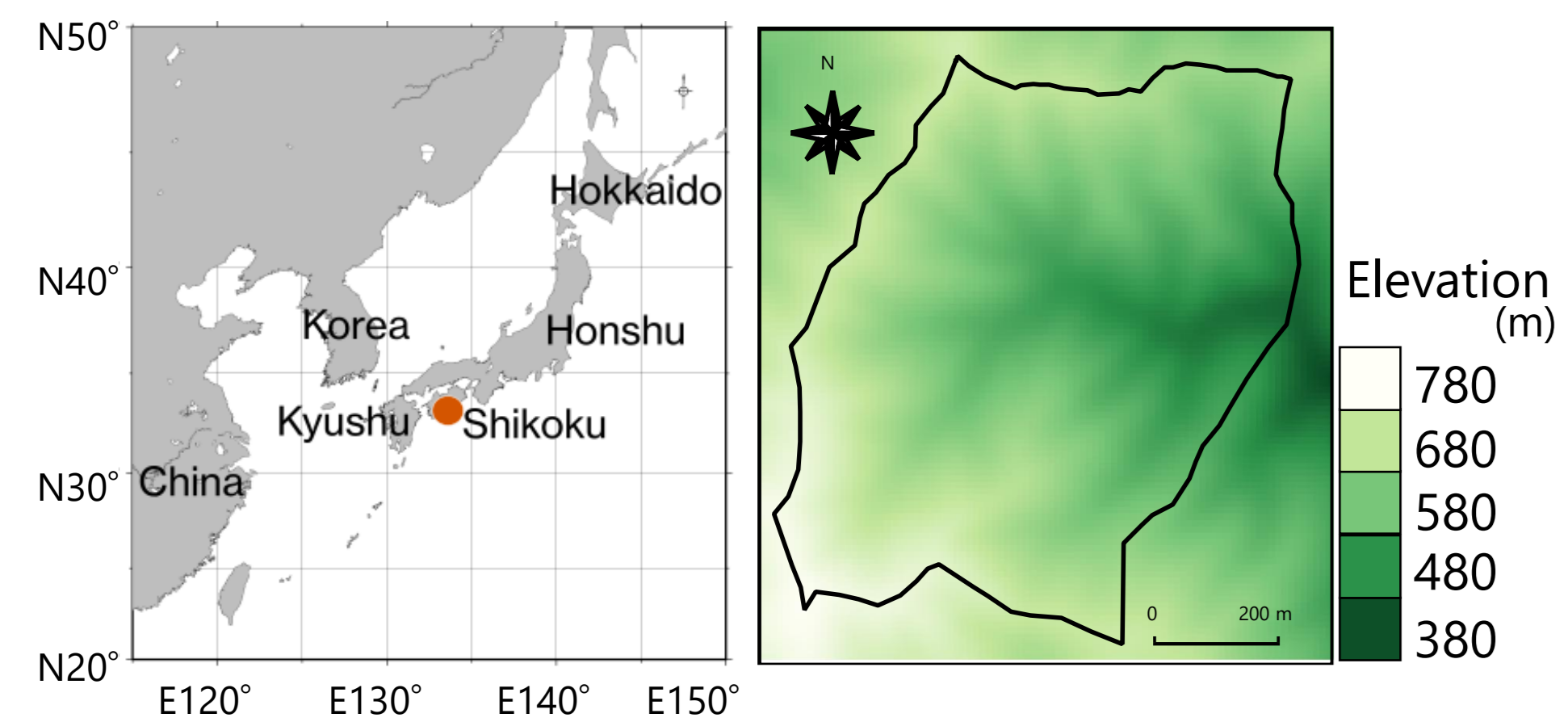
Higher humidity in valley bottoms with
 • Lower wind exposure
 • Higher soil water content



Question

Is the occurrence and distribution of vascular epiphytes affected by variation in water availability at local scales with apparently similar precipitation?

Study area

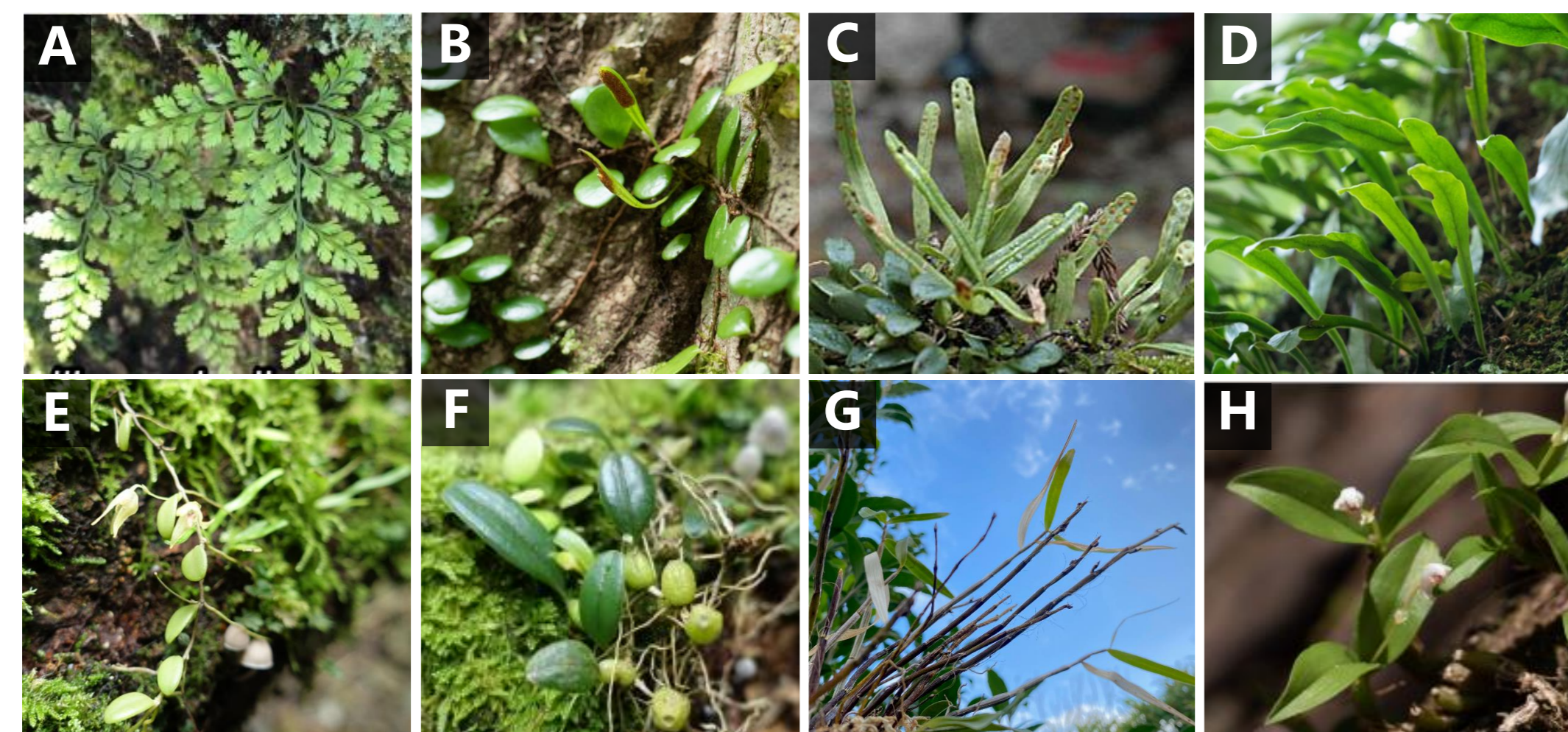


The study area is a 52 ha watershed located in Shikoku, southwestern Japan. The watershed is dominated by mature conifer and evergreen broadleaf mixed forests in a temperate-humid climate. The mean annual precipitation and temperature are 2,700 mm and 13 degree-C, respectively.

Fig. 1 Maps of location and elevational gradient of study area.

Target species

- Ferns**
 A: *Davallia mariesii*
 B: *Lemmaphyllum microphyllum*
 C: *Lepisorus onoei*
 D: *Loxogramme salicifolia*
- Orchids**
 E: *Bulbophyllum drymoglossum*
 F: *Bulbophyllum inconspicuum*
 G: *Dendrobium moniliforme*
 H: *Eria japonica*



The occurrences and species richness along the ridge-valley gradient

Methods: Epiphyte occurrences within the study area were surveyed using a point census of 308 randomly selected trees > 5 cm in diameter at breast height, located adjacent to forest trails. We used generalized linear mixed models, Bayesian estimation, and Markov chain Monte Carlo sampling to assess the occurrence of eight target epiphytes (four ferns and four orchids) as a function of two focal topographic variables: openness and a topographic wetness index (TWI). We also assessed total annual solar radiation (TASR) and host tree species and size as random effects.

The formula of GLMMs

$$z_{ij} \sim \text{Bernoulli}(\psi_{ij})$$

$$\psi_{ij} = a \times \text{Openness}_{ij} + b \times \text{TWI}_{ij} + c \times \text{TASR}_{ij} + d \times \text{Size}_{ij} + e[\text{host}_j] + d_i$$

z_{ij} : Detection or non-detection of epiphytic species i on target tree j . These were assumed to follow a Bernoulli distribution.
 ψ_{ij} : Probabilities of occurrence of epiphytic species i on target tree j .
 a, b, c, and d: Coefficients of Openness, TWI, TASR and DBH of host trees of species i on target tree j .
 e: Random coefficient of host tree j .
 d: Random coefficient of species i .

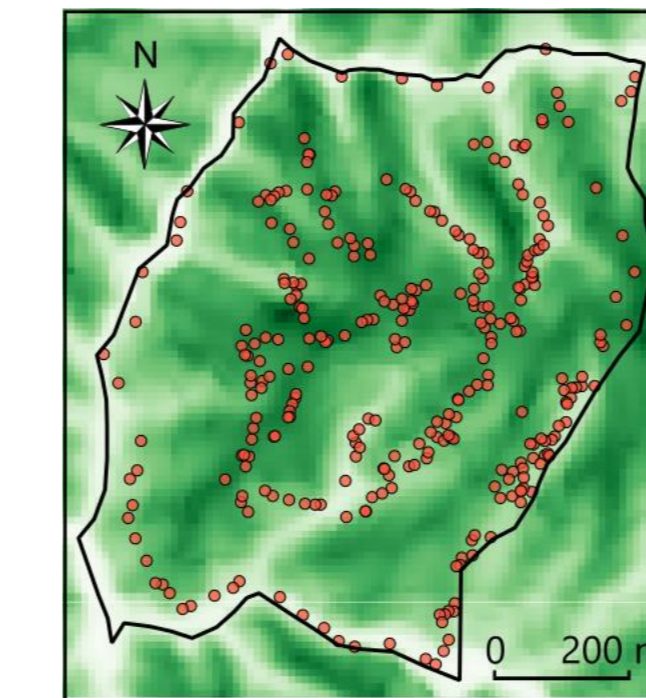


Fig. 3 Locations of the 308 surveyed trees in the study area.

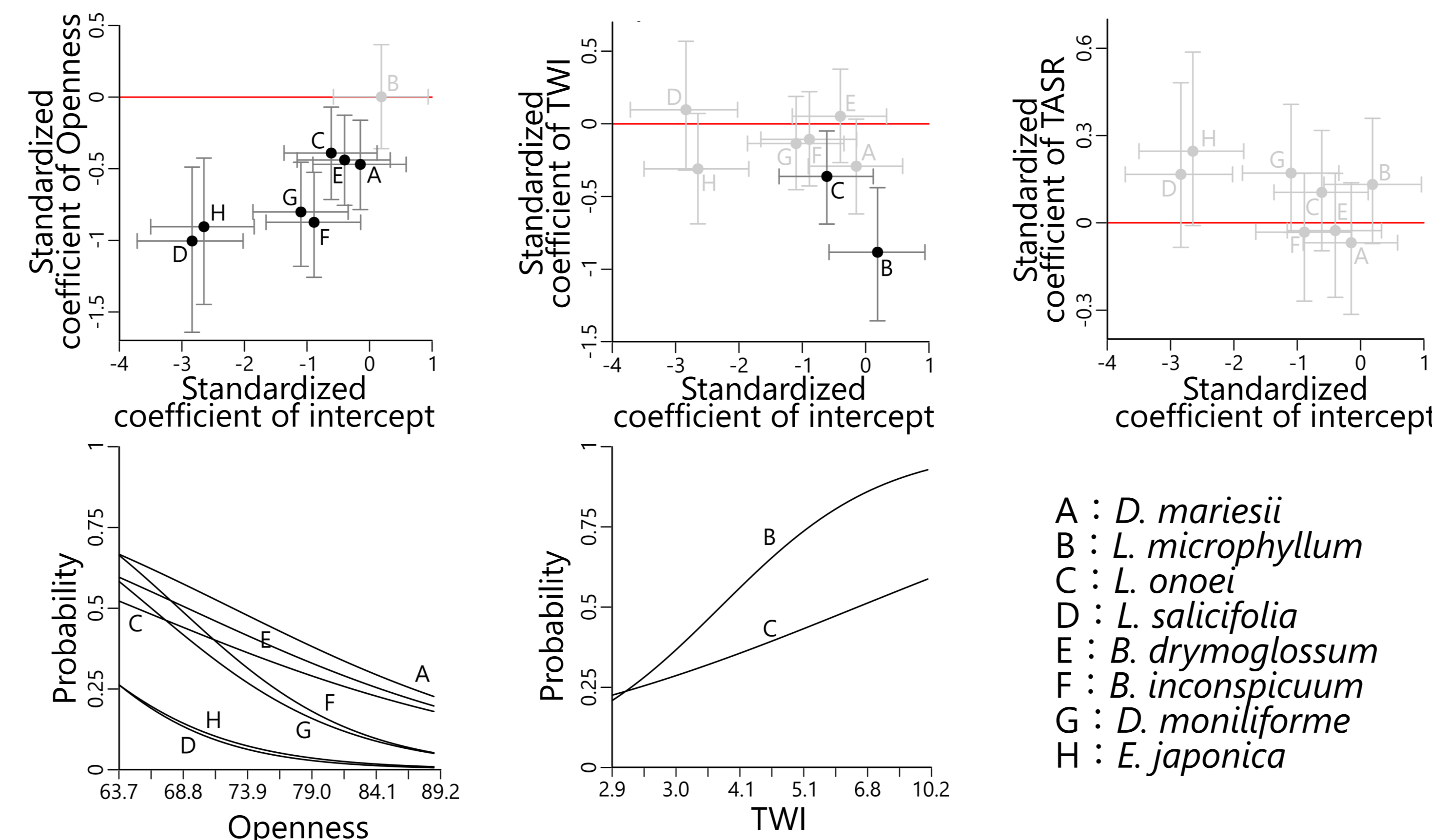


Fig. 4 Two-dimensional posterior distributions of the intercepts and coefficients of openness, TWI, and TASR (upper panels), and response curves of target species as a function of openness and TWI (lower panels).

★ The probability of occurrence of all species excluding *L. microphyllum* declined with increasing openness, and that of *L. microphyllum* and *L. onoei* declined with declining TWI values.

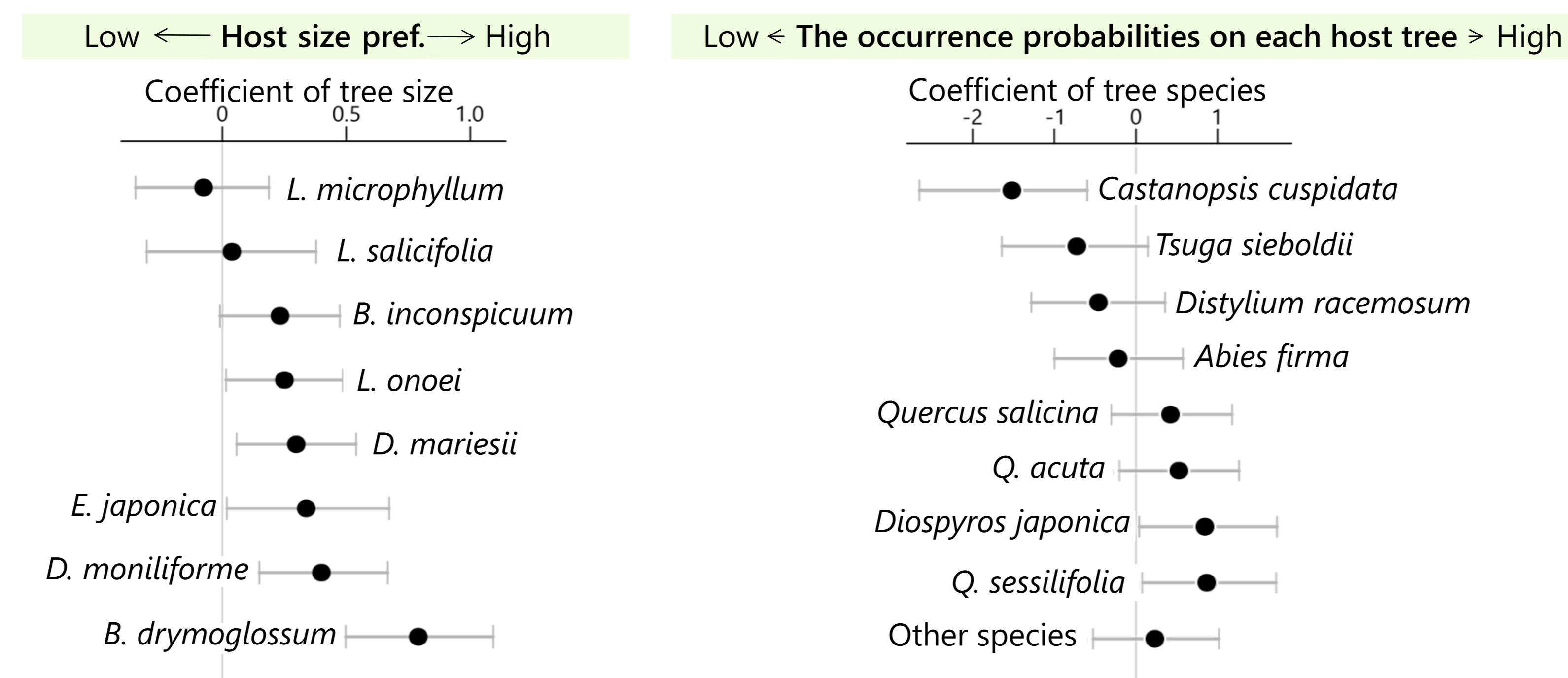
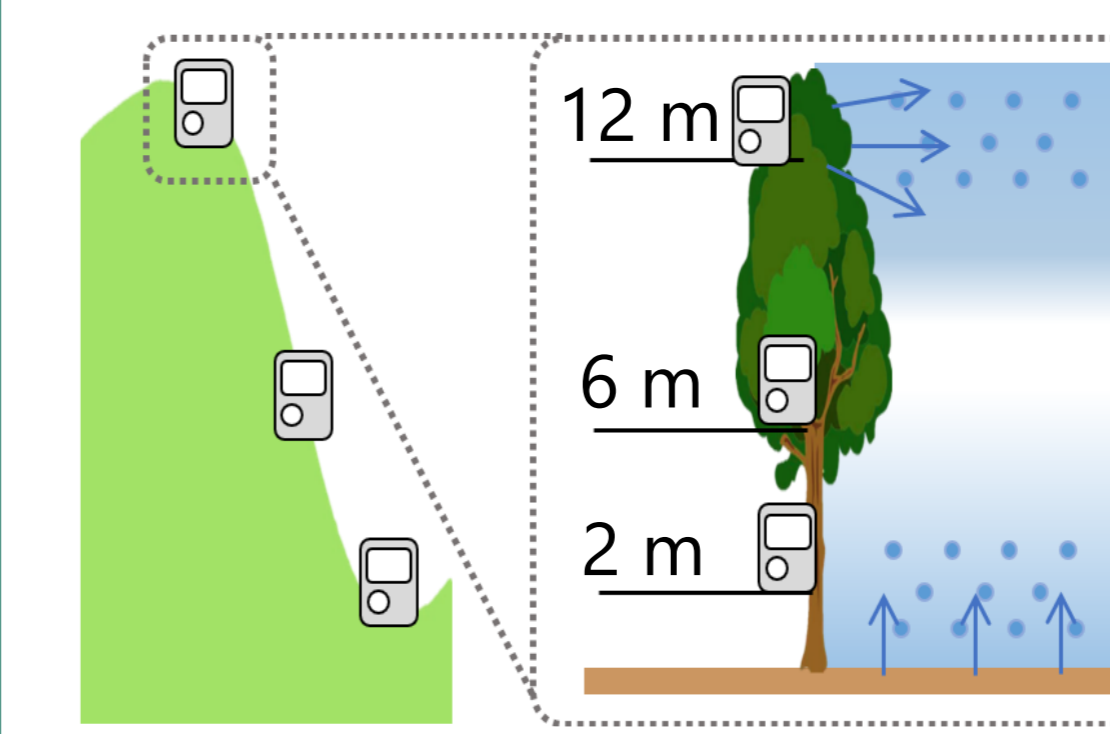


Fig. 5 Posterior distributions of the coefficients of host tree species and size (included as random effects).

Conclusion

Even in local areas with apparently similar precipitation, variation in water availability, driven by local topographic factors, affects the occurrence and distribution of vascular epiphytes.

Air humidity along the ridge-valley gradient



Methods: Air humidity was assessed at 2, 6, and 12 m above the ground at three sites (a ridge, slope, and valley bottom) at 15-min intervals from September 2020 to April 2021.

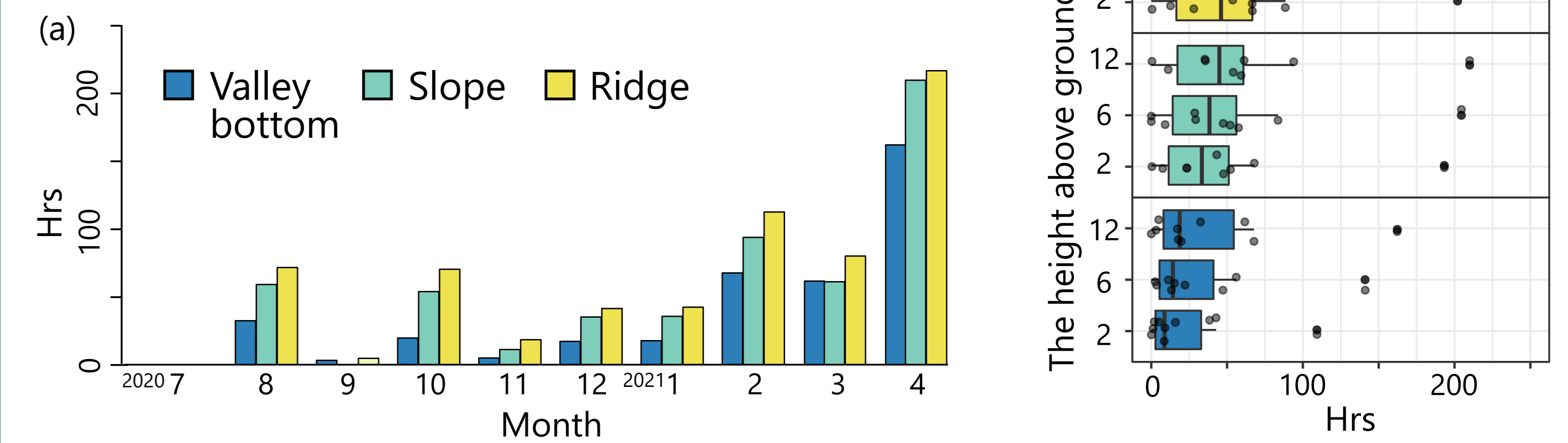


Fig. 2 Air humidity along the (a) ridge-valley and (b) vertical gradients. Hrs; Monthly total hours with <60% air humidity.

- ★ Air humidity was lowest at the ridge site and highest in the valley bottom throughout the measurement period.
- ★ Air humidity was lowest at 12 m and highest at 2 m in any site, and the air humidity at 2 m was highest in the valley bottom.
- ★ At any height above ground, air humidity was lowest at the ridge site with higher value of openness and highest in the valley bottom with lower value of openness.
- ★ Variation in air humidity along the ridge-valley gradient is likely driven by variation in wind speed and soil water content.

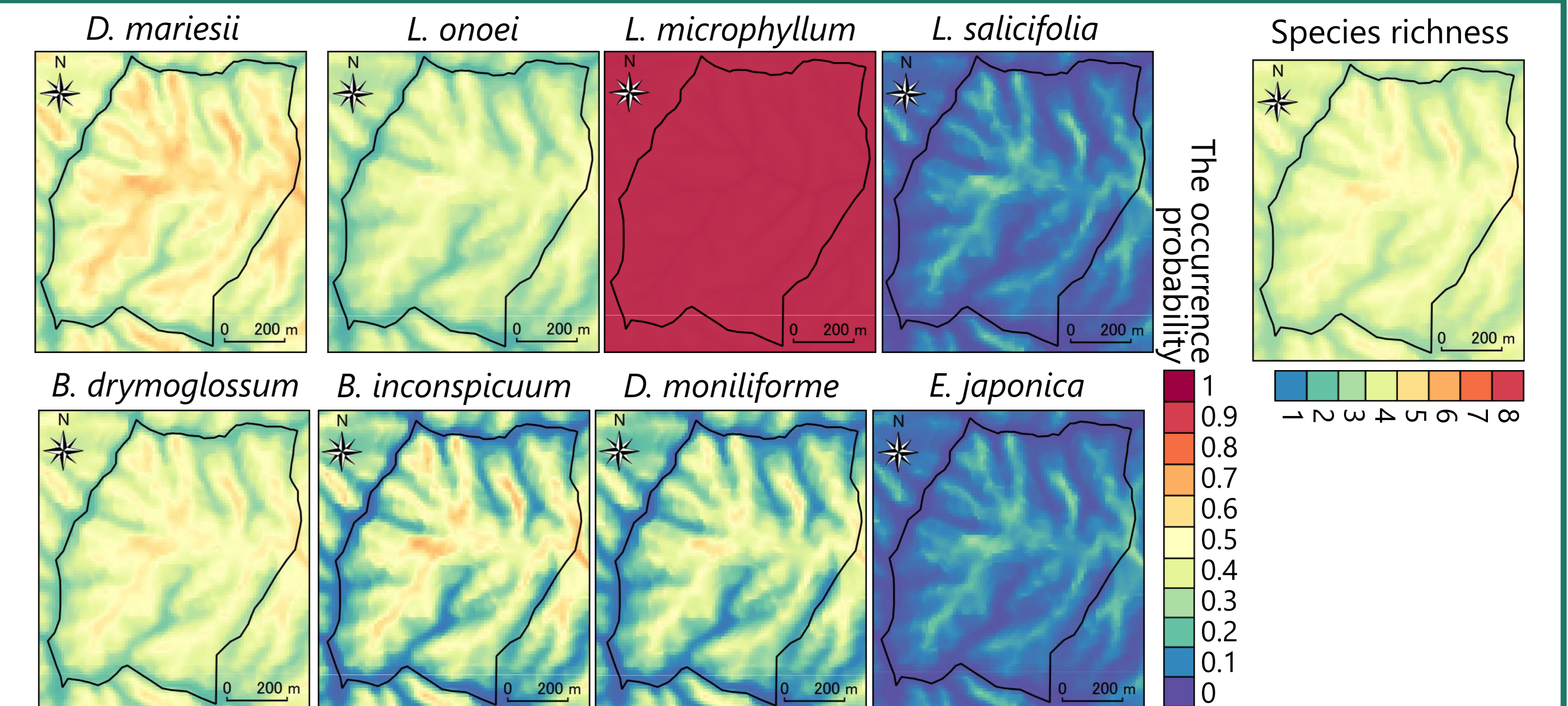


Fig. 6 Distribution maps showing predicted occurrence and species richness for the eight target vascular epiphyte species in the study area.

- ★ *L. microphyllum* was uniformly distribution across the study area, whereas the distributions of the remaining species were biased toward the valley bottom.
- ★ The observed decrease in the occurrence probability and species richness of the target species with increasing elevation likely reflects the concurrent decrease in air humidity.
- ★ Our results indicate that the spatial distributions of vascular epiphyte species are limited by water availability at small spatial scales in areas with apparently similar precipitation.