1 Title

2 **The role of plant functional traits in shrub distribution around alpine frost hollows**

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11 **Abstract**

12 Introduction/Aims: Functional traits aid understanding species distribution and community
13 composition along environmental gradients. However, studies that detail trait measurements
14 along fine scale environmental gradients are lacking for many vulnerable ecosystems. In this
15 paper, we quantify how plant traits may explain the composition of shrubs in one such
16 vulnerable system—frost hollows in the Bogong High Plains of Southeastern Australia.

17 Methods: We measured species composition and a suite of traits (shrub height, stem specific
18 density, leaf area and specific leaf area (SLA), xylem vessel area and density, and leaf bud
19 traits) for shrub species in 10 m × 10 m quadrats that span the transition from hilltops down
20 into frost hollows. We used ordinal regression to model vegetation composition by relating
21 the changes in shrub species occurrence along frost hollow gradients to each trait, and across
22 multiple traits. We also assessed intraspecific trait variation along gradients.

23 Results: Several traits explained the position of species along a gradient of cold-air
24 accumulation (slopes leading into frost hollows). The most important traits were maximum
25 shrub height, leaf area and xylem traits, which were clearly related to species location on the
26 slopes in single trait models. More complex relationships were revealed with multi-trait
27 models, which indicated that shorter species, those with smaller leaves and larger buds for
28 their leaf size, and those with lower vessel density were more likely to be found toward the
29 bottom of the slope. Within species, taller individuals and those with denser stems were also
30 more common upslope.

31 Conclusion: Our results suggest a shift in ecological strategies in frost hollows: the
32 advantages of being taller and having large leaves may be diminished in these stressful
33 environments. Shrubs that are shorter and have smaller leaves may also be better at avoiding

34 the risk of frost damage. Our study shows how the fine-scale turnover of shrub species
35 composition around frost hollows relates to plant functional traits, and captures the allocation
36 trade-offs between coping with environmental stress and being competitive within these plant
37 communities.

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39 Keywords: alpine vegetation, cold-air drainage, environmental gradients, habitat filtering,
40 intraspecific trait variation, plant height, leaf area, vegetation gradient, woody species

41

42 **Introduction**

43 Trait-based approaches are becoming more popular as a means of addressing community
44 assembly theory (Mouillot et al. 2013) and particularly habitat filtering (Weiher et al. 2011).
45 This synthesis is increasingly addressed with statistical modelling, e.g., using functional traits
46 to characterise species distribution and relations to spatial variation in the environment (e.g.,
47 de Frenne et al. 2011; Pollock et al 2012; Jamil et al 2013; Laughlin et al, 2014).

48 Most studies of trait-environment relations have focused on variation in functional traits
49 across broad-scale spatial and environmental gradients, e.g., plant height along latitudinal
50 gradients (Moles et al. 2009). In such broad gradient studies, usually across regional or global
51 scales ($\sim 10\text{-}10^4$ km), the high species turnover is typically related to trait variation across
52 species and studies have mainly focused on trait variation between species (McGill et al.
53 2006; Shipley et al. 2006). The importance of functional traits in relation to species turnover
54 across fine-scale environmental gradients ($\sim 10\text{-}10^2$ m) is less well known, but gaining
55 attention (e.g., Mason et al. 2012; Price et al. 2014; Pescador et al. 2015). In this study, we
56 investigate how plant functional traits relate to species occurrence across a fine-scale
57 environmental gradient in an alpine landscape in South-East Australia.

58 Alpine landscapes have short growing seasons and are typically exposed to highly variable
59 environmental conditions such as temperature (Laughlin and Kalma 1990; Körner 2003).
60 This leads to rapid turnover in alpine vegetation across short distances (Billings 1974; Choler
61 2005; Körner 2007), such as that characteristic of frost hollows. Frost hollows form when
62 dense cold air drains downslope into valley bottoms, causing lower daily minimum
63 temperatures at the bottom of slopes (Gudiksen et al. 1992; Gustavsson et al. 1998; Dy and
64 Payette 2007; Vosper and Brown 2008). Frost hollows are common at high elevation in
65 South-East Australia (Moore & Williams 1976; Williams 1987; Huber et al. 2011).

66 Vegetation turnover relates to these changes in air temperatures (Williams and Ashton 1987),
67 and, typically, there is a loss of woody shrub species downslope into frost hollows (Williams
68 1987). Trees are restricted to hilltops, because juvenile trees are more susceptible to cold
69 stress and photoinhibition (Ball et al. 1991), resulting in an inverted treeline. Closed
70 heathlands dominate the side slopes, and open grasslands with sparse shrubs are typically
71 found at the bottom of the slopes where it is colder and more exposed (Williams 1987). Aside
72 from this qualitative description of vegetation turnover into frost hollows, these unique
73 ecosystems remain relatively understudied.

74 While studies have looked at the drivers of treelines (Körner and Paulson 2004; Körner
75 2012), less emphasis has been placed on frost hollows, inverted treelines and how species and
76 functional traits are influenced by cold-air drainage and accumulation. With projected
77 increases in global temperatures, the risk of severe freezing events in alpine vegetation
78 environment is also expected to rise (Inouye 2000; Woldendorp et al. 2008). Alpine
79 landscapes typically contain many endemic and range-restricted species and are therefore
80 **vulnerable** to the effects of rising temperatures (Theruillat and Guisan 2001).

81 In this study, we investigated how functional traits of shrubs influence their distributions
82 along a gradient of cold air accumulation in alpine frost hollows within the Bogong High
83 Plains in North-East Victoria, Australia. We measured plant traits that are likely to influence
84 performance under the risk of frost and soil moisture (Table 1), including commonly
85 measured traits (vegetative height, specific stem density, leaf area and specific leaf area), and
86 less commonly measured traits (i.e. xylem traits and size of leaf buds). We first looked at
87 how, at a community level, these traits vary across different parts of the slopes of frost
88 hollows. We then used an ordinal regression model to establish that species have affinity with
89 particular positions along the slope, and examined how the probability of occurrence at

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different parts of the slope might be related to different functional traits. Given what is known about these traits, we expected to find shorter species with smaller, denser leaves more common toward slope bottoms. Species with higher stem specific density, and with few large xylem vessels may be more common in frost hollows as well. We also examined these relationships at an intraspecific (within-species) level; trait variation within species was also measured for a number of traits, namely height, leaf area, SLA and specific stem density and its response along the gradients analysed.

Methods

Study area and sampling design

Data on species occurrences and functional traits were collected from Bogong High Plains in North-Eastern Victoria, Australia between November 2011 and May 2012 (the austral summer). The Bogong High Plains are located on alpine and subalpine plateaus at elevations between 1500 and 1900 m in the Great Dividing Range. Air temperatures vary widely, ranging from -20°C in the winter to above 30°C in the summer months (Williams 1987).

We selected 23 frost hollows, which spanned a range of elevations and steepness, and had a gradation of vegetation types. One or two transects were laid out at each frost hollow, depending on accessibility. Transects varied in length and steepness, running from open woodland to open heathland. Thirty-six transects in total were established along north- and south-facing slopes of these frost hollows.

We set up three 10 m by 10 m plots along each transect, where we collected shrub species occurrence and trait data. Plots at the top of the slopes were placed in open woodlands. Bottom plots were located in open heathland on flatter areas at the bottom of the slope. The middle plots were placed approximately midway between the plots at the top and bottom of

113 the slope. Because the sites differed in lengths and steepness of slopes, the distances between
114 plots also varied in length and altitudinal gradients.

115 Some frost hollows in the area may occur within wetlands and bogs (Wahren et al. 1999).
116 Soil properties like soil moisture and chemistry may therefore change along the slopes
117 towards the frost hollows. In this study, we selected sites that were well-drained to avoid
118 confounding the effects of soil moisture and temperature. Soil depth and moisture were
119 similar between frost hollows and side slopes (data not shown). We also measured
120 temperatures at different positions for three of the slopes demonstrating that the bottom of the
121 slope reaches lower temperatures and spends more time at sub-zero temperatures (see
122 Appendix S1).

123 *Study species and plant functional traits*

124 All shrub species that occurred within the 108 plots were recorded (3 plots on each of 36
125 transects). Trees and herbaceous species were excluded from this study as they could have
126 different ecological strategies (Körner 2012). We recorded the relative foliage projective area
127 of each species within each plot as a percentage of the total area of the plot. Functional traits
128 that relate to a plant's susceptibility to frost damage were selected, and measured from a
129 subset of individuals for each species (see Table 1 for a list of functional traits).

130 We measured vegetative height from three individuals of each species within each plot, and
131 maximum height of each species was obtained from across all the measured individuals. The
132 number of replicates per species ranged from three to 268 individuals, and depended on
133 species occurrences across all plots; some species were only present in one plot.

134 Leaf area and specific leaf area (SLA) of each species were measured from a subset of
135 individuals: because occurrences varied greatly between species, the number of individuals

136 from which leaf trait measurements were taken varied for each species, ranging from three to
137 78 individuals per species. Average one-sided leaf area was measured using ImageJ software
138 (Schneider et al. 2012). Because most species had small leaves, we measured average leaf
139 area and dry mass in batches of multiple leaves. Leaves were oven-dried at 70°C for 72 hours
140 and their dry mass obtained (Pérez-Harguindeguy et al. 2013). SLA was calculated as the
141 ratio of the one-sided area of each group of leaves to its dry mass (Pérez-Harguindeguy et al.
142 2013).

143 We measured stem specific densities of each species from a subset of individuals across all
144 sites; sample size for each species ranged from one to 24 individuals. Stem cuttings 50 mm
145 long were removed 200 mm from the tip of the stems. The fresh volume of each stem cutting
146 was determined using the volume displacement method (Hacke et al. 2000; Pérez-
147 Harguindeguy et al. 2013), and stem specific density was calculated from the ratio of stem
148 dry mass to fresh volume. We recorded xylem anatomical traits from two individuals of each
149 species. Transverse stem cross sections, each 0.1 mm thick and extending from pith to bark,
150 were made using a microtome. Sections were photographed under a compound microscope,
151 and xylem traits measured using ImageJ (Schneider et al. 2012). We calculated the lumen
152 fraction from the ratio of xylem lumen area to the total area of the section, the average cross-
153 sectional area of each xylem vessel, and measured the vessel density of each stem section, i.e.
154 the number of xylem vessels per unit area, by dividing the number of vessels observed in
155 each section by the total area of the section (Zanne et al. 2010).

156 We measured leaf bud traits from two to five individuals of each species. Terminal leaf buds
157 from were dissected longitudinally to expose the apical meristems. We photographed them
158 under a dissecting microscope, and analysed their properties using ImageJ (Schneider et al.
159 2012). We measured the cross-sectional area of each leaf bud, as a representation of the

160 overall bud size. We also calculated the proportion of cross-sectional area attributed to air
161 space, as a measure of leaf bud compactness.

162 *Data analysis*

163 Species median trait values (across all measured individuals) were used over means because
164 they were less sensitive to outliers, except for height where we used maximum recorded
165 values for each species. We conducted correlation tests and principal component analyses
166 across our species trait values to observe how traits were related (Appendix S3). To observe
167 how average trait values at a plot level were distributed at different positions along slopes
168 into frost hollows, we calculated the community-weighted trait median/maximum (CWM)
169 values of each plot, by multiplying the species relative abundance by its trait
170 median/maximum value (Garnier et al. 2007). We also examined how relative abundances of
171 each species, as well as total abundance of shrubs, changed downslope across all our transects
172 (Appendix S2).

173 We then examined the distribution of shrubs around frost hollows using occurrence of each
174 shrub species at each of the plots. We used an ordinal regression model of how plant traits
175 explain species' positions along a slope. Given that the response variable is categorical and
176 ordered, i.e., species occurred in the bottom, middle or top plots, an ordinal linear regression
177 was better suited than a generalised linear regression. An ordinal scale takes into account that
178 the categories are successional and does not specify equal differences between the categories
179 (Agresti 2010; Guisan and Harrell 2000). We used a cumulative logit-link proportional odds
180 model (Walker and Duncan 1967). It is based on cumulative probabilities and models the
181 probability of a species occurring at a position along the slope, based on its trait values
182 (Equation 1).

$$183 \text{ logit } [\Pr(Y \leq y_{ij})] = (\beta_0 + \beta_i X_i + \gamma + \varepsilon_{ij}) \quad (\text{Equation 1})$$

184 $\Pr(Y \leq y_{ij})$ is the cumulative logit probability of species i with trait value X_i occurring at a
185 plot j that is in position along the slope, $Y = 1, 2, 3$ for the bottom, middle or top plot
186 respectively. β_i refers to the coefficient of each trait, with β_0 representing the constant and ε_{ij}
187 the residual error term. Here we have used a varying-intercepts mixed-effects model, where
188 the random effect term (γ) is the departure of each species from the mean across all
189 individuals.

190 Separate models were first run for each trait, followed by a series of models with various
191 combinations of traits. We took care to include combinations of traits that described different
192 aspects of a plant. Trait variables for each species were log-transformed to normalise
193 distributions, then centred on zero and scaled by subtracting their means and dividing by
194 twice the standard deviation (Gelman 2008). Analyses were carried out using the ‘ordinal’
195 package (Christensen 2013) in R statistical software (R Development Core Team 2015). The
196 model coefficients show the relationship between the traits and the probability of occurrence
197 along the slope. We also examined relationships between each of the measured traits across
198 all species, and calculated an average model across models within 2 AICc units of the best
199 model (Appendix S4). Model averaging was conducted using the ‘MuMIn’ package (Bartoń
200 2016).

201 We also tested for the contribution of variation within each species for plant height, leaf area,
202 SLA and stem specific density. We ran similar ordinal regression models, but instead of just
203 using trait median values for each species, we included species plot-recorded trait median
204 values (trait median values among individuals within each plot). Where plot trait values were
205 not recorded, species trait median values were used in place.

206 **Results**

207 Traits were correlated across the 19 shrub species with 3 principal components explaining
208 over 70% of variation in traits (See Appendix S3). PC1 represented variation from plants
209 with large leaves and buds, with light stems to small leaved shrubs with small buds and dense
210 stems. PC2 represented vasculature with many, small vessels (and high lumen fraction) or
211 fewer, larger vessels, and PC3 represented a range from tall shrubs with compact buds (and
212 low SLA) to short shrubs with airy buds (and high SLA). At the community level, we found
213 community-weighted maximum height and median leaf area decreased downslope into frost
214 hollows (Figure 1): communities with taller species and species with larger leaves were more
215 commonly found toward the top of the slope.

216 The 19 shrub species varied in abundance and occurrence along slopes. Some (e.g. *Kunzea*
217 *muelleri* and *Asterolasia trymalioides*) had higher occurrence in frost hollows, while others
218 were less likely to be in frost hollows as displayed by the species random effect in ordinal
219 regression models (Figure 2). Patterns in abundances were similar to those estimated from the
220 occurrence data used by the ordinal regressions (see Appendix S2). The results of the single
221 trait ordinal regression models suggested that across the 19 shrubs, species that were shorter
222 had smaller leaves and larger xylem vessels were more likely to be found at the bottom of the
223 slope (Figure 3). The strongest effect was for leaf area (trait coefficient = 0.95 ± 0.33
224 SEM)— compared to the largest-leaved species (~97.5 percentile) in our dataset, the
225 smallest-leaved species (~2.5 percentile) had about seven times greater odds of being found
226 towards the bottom of slopes. The effect for plant maximum height was also positive ($0.40 \pm$
227 0.20 , Figure 3). This smaller (but more certain) effect means that compared to the tallest
228 species, the shorter species were about 2.5 times more likely to be found towards valley
229 bottoms. Vessel density decreased downslope, and mean vessel area increased (Figure 3),

230 suggesting that shrubs with larger and fewer xylem vessels were more common toward frost
231 hollows. The effect for vessel area was stronger and more certain; species with the largest
232 vessels had about 2.7 times greater odds of being found lower on the slope than species with
233 the smallest vessels (Figure 3). All other effects were smaller and the 95% confidence
234 intervals overlapped zero. Trait coefficients for SLA and specific stem density were
235 negatively associated with position along the slope; species with denser wood or a higher
236 SLA were more likely to occur toward the bottom of the slope. Bud traits showed fairly weak
237 responses; shrubs with smaller buds were more common towards the bottom of the slope, but
238 this relationship was very uncertain. There was no relationship between the percentage of air
239 space within leaf buds and species position along the slope.

240 Among models with multiple traits, the best model according to AICc included leaf area,
241 maximum height, xylem vessel density and bud size (Figure 3, Appendix S5); leaf area,
242 maximum height and vessel density decreased downslope into frost hollows while bud size
243 increased. Leaf area had the strongest relationship, followed by height and vessel density, and
244 leaf bud size. Interestingly, leaf bud size had a negative relationship with species occurrence
245 along a slope when in multi-trait models, unlike in a single-trait model with only bud size.
246 This implies that given their leaf size, species with bigger buds were more common
247 downslope. Leaf area, maximum height and xylem vessel density were present in all the
248 models that make up the average model, and each had a relative importance of 1. Bud size
249 was also present, with negative coefficients, in many of these models, and had a relative
250 importance of 0.9. The remaining traits had lower relative importance.

251 Incorporating intraspecific trait variation by using the measurements made in particular plots
252 resulted in stronger and more certain effects for height and stem specific density, smaller but
253 more certain effects for leaf area, and greater certainty that SLA was not influential (Figure

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254 3). This suggests that not only were taller species more likely to be found towards the top of
255 the slope, taller individuals within species more common toward the top of the slope.
256 Likewise, within species, individual shrubs with higher stem density may be more common
257 towards frost hollows.

258 **Discussion**

259 Maximum shrub height and leaf area showed strong relationships with species distribution
260 along slopes leading into frost hollows. Shrub species associated with frost hollows were
261 shorter with smaller leaves, relatively larger buds, and lower xylem vessel densities. Models
262 which included intraspecific variation confirmed that the effect of position on height and
263 stem density holds for individuals within a species as well. Taken together, these results
264 suggest a shift in ecological strategies in response to cold-air accumulation. Avoiding frost
265 damage by being short with small leaves might outweigh the competitive advantages of being
266 taller and having larger leaves in this ecosystem.

267 Plants respond to extremely low temperatures in two main ways. First, lower temperatures in
268 frost hollows constrain plant growth: tissue formation at the meristem is inhibited at
269 temperatures close to zero Celsius (Körner and Paulsen 2004). There is also an increased
270 likelihood of frost events in frost hollows, and plants are more susceptible to frost damage
271 (Moore and Williams 1976), photoinhibition and the disruption of photosynthetic activity at
272 low temperatures (Ball et al. 1991; Blennow et al. 1998; Venn et al. 2011).

273 Even though taller species have a competitive advantage for light (Westoby et al. 2002;
274 Moles et al. 2009), this trait is selected against in frost hollows, where ambient temperatures
275 reach sub-zero levels more frequently. Similarly, the competitive advantages of larger leaves
276 are lower in frost hollows where there is greater exposure to severe temperatures (Nicotra et
277 al. 2011; Reich 2014). Plants with smaller leaves might also be associated with higher leafing

278 intensity (Milla 2009; Milla and Reich 2011, Dombroskie and Aarssen 2012), which relates
279 to higher secondary growth and a larger bud bank for recovery after damage to tissues e.g.,
280 frost damage (Yan et al. 2012).

281 Although plants with larger xylem vessels are more susceptible to freezing-induced xylem
282 cavitation (Davis et al. 1999; Hacke et al. 2000; Zanne et al. 2010), this might not be a strong
283 driver of shrub species distribution around frost hollows. Differences in specific stem density
284 along the slope may be driven by other physical or structural properties of wood like growth
285 rate (Chave et al. 2009) and leaf size (Ackerly 2004; Cavender-Bares et al. 2004; Wright et
286 al. 2007), rather than hydraulic conductivity (Preston et al. 2006; Baraloto et al. 2010;
287 Ziemińska et al. 2015).

288 Many of our multiple regression models suggest bud size contributed to explaining species
289 occurrence along the slopes, together with the other traits. Given that the apical meristem is
290 the point of primary growth in a plant, it is important we understand how leaf bud
291 morphology relates to environmental stress. Measurements of bud traits have only recently
292 moved to quantifying bud size (e.g., Alla et al. 2013); previous studies largely focus on the
293 number and position of buds (e.g. Klimešová and Klimeš 2007; Vesik and Westoby 2004;
294 Alla et al. 2011), or on phenological traits such as the timing of bud opening (e.g. Damascos
295 et al. 2005; Bennie et al. 2010; Basler and Körner 2012). While we have introduced a few
296 methods of measuring and quantifying bud morphology, these methods need to be developed
297 to better explore how buds relate to protecting meristems against extreme environments.

298 Previous work has shown the importance of considering intraspecific trait variation when
299 looking at shifts in functional traits at small spatial scales (Albert et al. 2010; Jung et al.
300 2010; Bolnick et al. 2011). Extended analyses (e.g., variance partitioning, discussed in Violle
301 et al. 2012) could refine our understanding of the contribution of intraspecific trait variation

302 to relationships with environmental gradients. In this study, the intraspecific results largely
303 agree with the results using species mean values, which is stronger evidence that the trait
304 relationships are biologically driven as they apply both within and between species.
305 Nevertheless, trait variation between species is still larger than within species, and species
306 turnover and trait variation between species give a better description of the relationship with
307 the environment.

308 *Conclusion*

309 It is well-known that cold-air drainage and temperature inversion drive broad-scale patterns
310 in vegetation and community assemblages in frost hollows in the Australian Alps and
311 elsewhere. Here, we show that this fine-scale compositional turnover of shrubs can be
312 explained by functional traits. The ordinal regression model presents a simple but clear way
313 of describing how the changes of woody species distribution relate to plant functional traits
314 (leaf size, height, stem vasculature and bud size). This study also highlights the need for a
315 better means of quantifying the properties of leaf buds, which are an important, yet
316 understudied aspect of plant growth and their responses to the environment. Future work
317 could incorporate environmental variables to further improve our understanding of how
318 functional traits are correlated with a gradient of cold-air accumulation.

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513 Figure 1. Community-weighted median/maximum (CWM) traits between positions along the
514 slope (Bottom, Middle or Top of slope). Lines in grey are regression lines between CWM and
515 position. Units are described in Table 1.

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517 Figure 2. Shrub species propensity to be found at higher or lower positions on the slope as

518 displayed by the shift in species intercepts from a model without traits. Positive values

519 indicate a species is more likely than average to be found toward the top of the slope, while

520 negative values imply that a species is more likely than average to be found towards the

521 bottom of the slope. Error bars show the variance of the conditional probability of each

522 species at its respective point.

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526 Figure 3. Regression coefficients of ordinal regression models used to explain species
527 position along a slope with models using trait median /maximum values (blue), models based
528 on individual trait values (red) for selected traits (maximum height, leaf area, SLA and
529 specific stem density), and multi-trait models (grey). Species was included as a random effect
530 in each model. Positive values mean the trait is likely to increase toward the top of the slope.
531 Error bars are 95% confidence intervals.

532

533 Table 1: List of plant functional traits measured, their descriptions and expected responses to position along slopes around frost hollows.

Trait	Description	Expected response	References
Maximum potential height (cm)	Vertical distance from the ground to the top of the foliage layer	Taller species tend to occur in less stressful environments, expect shorter species in frost hollows	Westoby et al. 2002; Moles et al. 2009; Pérez-Harguindeguy et al. 2013
Specific leaf area (SLA) (cm ² g ⁻¹)	Ratio of one-sided leaf area to oven-dry mass	Expect species with lower SLA in frost hollows: leaf size decreases with decreasing temperature	Westoby et al. 2002; Nicotra et al. 2011; Pérez-Harguindeguy et al. 2013; Reich 2014
Average leaf area (mm ²)	Average one-sided leaf surface area	Expect species with smaller leaves to be more common in frost hollows	Pérez-Harguindeguy et al. 2013
Stem-specific density (gcm ⁻³)	Ratio of stem dry mass to fresh volume	Expect species with denser stems to be more common in frost hollows	Hacke et al. 2000; Hacke and Sperry 2001; Pérez-Harguindeguy et al. 2013; Kasia Ziemińska et al. 2015
Xylem lumen fraction	Proportion of stem cross-sectional area occupied by xylem lumen	No change expected	Zanne et al. 2010
Vessel density (mm ⁻¹)	Number of xylem vessels per unit area of stem transverse cross-section	Expect species with higher vessel densities to be more common in frost hollows, as a means of reducing risk of cavitation	Zanne et al. 2010
Mean vessel area (mm ²)	Average cross-sectional area of a xylem vessel	Expect smaller mean vessel area for species more common in frost hollows to overcome freezing-induced cavitation risk	Davis et al. 1999; Hacke et al. 2000; Zanne et al. 2010
Leaf bud size (mm ²)	Longitudinal cross-sectional area of the leaf bud	Unknown	-
Proportion of air space within leaf bud	Area of air space in the leaf bud cross-section, as a fraction of the total longitudinal cross-sectional area	Unknown	-

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