

1 **Evolutionary conservatism explains increasing relatedness of plant**
2 **communities along a flooding gradient**

3

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20

21

22 **Brief heading:** Trait conservatism increases relatedness

23 **Summary**

- 24 1. Abiotic filters have been found either to increase or reduce evolutionary relatedness in
25 plant communities, making it difficult to generalize responses of this major feature of
26 biodiversity to future environmental change. Here we hypothesised that the responses of
27 phylogenetic structure to environmental change ultimately depend on how species have
28 evolved traits for tolerating the resulting abiotic changes.
- 29 2. Working within ephemeral wetlands, we tested whether species were increasingly related
30 as flooding duration intensified. We also identified the mechanisms underlying
31 increased relatedness by measuring root aerenchyma volume (RAV), a trait which
32 promotes waterlogging tolerance.
- 33 3. We found that species-specific responses to flooding explained most of the variation in
34 occurrence for 63 vascular plant species across 5,170 plots. For a subset of 22 species,
35 we attributed these responses to variation in RAV. Large RAV specifically increased
36 occurrence when flooding lasted for longer time periods because large RAV reduced
37 above-ground biomass loss. As large RAV was evolutionarily conserved within obligate
38 wetland species, communities were more phylogenetically related as flooding increased.
- 39 4. Our study now shows how reconstructing the evolutionary history of traits that influence
40 species' responses to environmental change can help predict future patterns in
41 phylogenetic structure.

42 **Key-words**

43 disturbance, environmental filtering, functional traits, niche conservatism, phylogenetic
44 clustering, root porosity

45 **Introduction**

46 Evolutionary relatedness among co-occurring species is used to understand community
47 assembly (Webb, 2000; Kraft *et al.*, 2007) and prioritize conservation actions (Isaac *et al.*,
48 2007; Tucker *et al.*, 2012), but generalizing its response to future environmental change is
49 challenging. Many studies have reported increasing relatedness (i.e. convergence in
50 phylogenetic structure) as environments become more stressful or disturbed (Horner-Devine
51 & Bohannan, 2006; Cavender-Bares & Reich, 2012; Anderson *et al.*, 2011; Savage &
52 Cavender-Bares, 2012; Spasojevic & Suding, 2012; Brunbjerg *et al.*, 2012; Purschke *et al.*,
53 2013), with others finding either the reverse pattern or none at all (Bryant *et al.*, 2008; Kluge
54 & Kessler, 2011; Butterfield *et al.*, 2013; Ghosh-Harihar, 2014). The general explanation for
55 this variation – that relatedness depends on whether traits for responding to the dominant
56 abiotic factors at a site are evolutionarily conserved – is generally assumed (Vamosi *et al.*,
57 2009), and rarely considered as more than a statistical pattern (Cavender-Bares *et al.*, 2004,
58 2006; Kraft *et al.*, 2007; Anderson *et al.*, 2011).

59 New process-based models now enable us to test directly how traits have evolved
60 (Beaulieu *et al.*, 2012), in order to develop clearer predictions for how phylogenetic structure
61 and community assembly change along environmental gradients, but we are unaware of any
62 studies that have done so. If the traits that allow species to overcome the selective forces of a
63 given environment have not repeatedly evolved across lineages, such as because of
64 phylogenetic restrictions over potential adaptations, then future environmental change will
65 promote taxa that are clustered within the lineage of the regional species pool where tolerance
66 to the new conditions evolved (Verdú & Pausas, 2007; Helmus *et al.*, 2010). Such
67 evolutionary conservatism may be the inevitable outcome of descent by modification from
68 common ancestors (Crisp & Cook, 2012). Communities will consequently contain species
69 that are more similar in their evolutionary history than expected by chance. By contrast,
70 phylogenetic relatedness may be minimal if species have repeatedly converged upon similar
71 traits with which to respond to abiotic changes. Communities will instead be comprised of
72 species that are less closely related than expected by chance because response traits will be
73 dispersed across lineages (Cavender-Bares *et al.*, 2004). Convergent evolution may arise
74 frequently for traits optimizing metabolic processes, such as photosynthesis (Grime, 2006),
75 but less often for those determining responses to stress and disturbance, which can be
76 optimized in more ways through morphology and development, as well as physiology
77 (Donoghue & Ree, 2000).

78 Traits providing tolerance of a given set of abiotic conditions will certainly enable
79 species to overcome the selective forces of a given environment, known as environmental
80 filtering (Keddy, 1992), but the subsequent responses of phylogenetic structure will also
81 depend on processes such as competitive exclusion and demographic stochasticity (Cavender-
82 Bares *et al.*, 2009; Mayfield & Levine, 2010). For example, close relatives can compete
83 more intensely and exclude each other if their niches are evolutionarily conserved (Burns &
84 Strauss, 2012), leading communities to contain species that are less related than expected by
85 chance (Kraft *et al.*, 2007). By contrast, close relatives may also have similar competitive
86 abilities (Fritschie *et al.*, 2014). If the competitive abilities of close relatives are more similar
87 than their niches, it can lead to closely related species excluding distant relatives (Mayfield &
88 Levine, 2010), resulting in more closely related communities (Kunstler *et al.*, 2012).
89 Opposite outcomes for phylogenetic structure can also arise in each of the two
90 aforementioned examples where traits are convergent (Anderson *et al.*, 2011). Quantifying
91 the variation in community assembly explained by abiotic gradients relative to all other
92 potential sources, such as species identity, can therefore help infer the importance of
93 environmental change in driving future patterns of phylogenetic structure.

94 Here our aim was to provide evidence that the response of phylogenetic structure to
95 environmental change depends upon how traits for enabling species to tolerate abiotic
96 conditions have evolved across lineages. Our study focuses on ephemeral wetlands because
97 these ecosystems are ideal for testing the general role of environmental change. Ephemeral
98 wetlands have strong abiotic gradients over very short distances (i.e. metres, Tanentzap *et al.*,
99 2013), and relatively few traits differentiating species responses (Silvertown *et al.*, 1999;
100 Mommer *et al.*, 2006). We specifically focused on the evolution of a physiological trait, root
101 aerenchyma volume (RAV), which is experimentally known to confer flooding tolerance by
102 facilitating oxygen diffusion under waterlogging and promoting rooting depth (Justin &
103 Armstrong, 1987; Colmer, 2003). We expected that RAV influences the fine-scale
104 distribution of species within our community, and if so, patterns of phylogenetic structure
105 would depend on how this trait had evolved. By combining vegetation surveys with
106 measurements of RAV and a molecular phylogeny, we tested four sequential predictions:
107 **(P1)** More variation in site occupancy along a flooding gradient is explained by species-
108 specific responses to flooding (i.e. interaction between species identity and flooding)
109 than by flooding on its own or local spatial processes. Independent species sorting
110 along environmental gradients has been long studied (Gleason, 1926; Shipley & Keddy,
111 1987), but here we consider its importance relative to community-level processes.

112 (P2) As a larger space for gas exchange can improve tolerance of hypoxia during
113 waterlogging (Justin & Armstrong, 1987; Colmer, 2003), species that occur in sites that
114 are flooded for longer periods will have greater maximum potential RAV.
115 (P3) Greater RAV is found among more closely related species than expected by chance
116 because flooding is a strong selective force. Physiological constraints could have
117 specifically selected against extreme values that are non-adaptive in all cases or
118 obligate wetland species radiated adaptively around an optimum RAV, and we tried to
119 differentiate among such potential scenarios with different macroevolutionary models.
120 (P4) Conservatism in RAV leads to more closely related communities as plots remain
121 flooding for longer.

122

123 **Materials and Methods**

124 *Study area*

125 We studied six ephemeral wetlands (kettleholes) across three sites separated by between ca. 7
126 – 60 km in the Mackenzie Basin, South Island, New Zealand (44°11'S; 170°11'E, area: 0.68-
127 14.9 ha). Sites developed on glacial moraines from the Late Otiran (ca. 45.0-14.5 kya), and
128 have been relatively stable since formation (McGlone, 2009). The kettleholes are fed solely
129 by precipitation and are typically flooded during the Austral winter and dry in summer,
130 though water can accumulate irregularly at any time. In each kettlehole, water levels were
131 measured every minute from December 2006 – December 2010 using Odyssey capacitance
132 water level recorders (Dataflow Systems Ltd., Christchurch, NZ) positioned in the area of
133 lowest elevation (see Supporting Information Fig. S1 and Methods S1). Plant communities
134 are characterized by short prostrate plants (<3 cm tall), including herbaceous dicots and
135 monocots, with taller shrubs sparsely positioned upslope (Table S1 in Supporting
136 Information).

137

138 *Vegetation and flooding survey*

139 We established eight transects ranging in length from 25.4-99.7 m in each kettlehole between
140 November 2008 and January 2009. Transects extended upslope from the central depression
141 of each kettlehole at a random bearing within 45° intervals and at least 5 m beyond the limit
142 of where standing water could accumulate. We randomly positioned 5 cm × 5 cm plots on
143 average every 50 cm along each transect (range of inter-plot distances = 1 – 171 cm), and
144 recorded the presence of all vascular species intersecting each plot ($n = 5170$ plots).

145 Although superficially small, the plots are of an appropriate scale since most plants are only a

146 few mm in diameter, and up to 9 species can be captured within a single plot (Tanentzap *et*
147 *al.*, 2013). We restrict our analyses only to the 63 of 118 total species occurring in >0.2% of
148 plots, as we could not adequately model the occurrences of species that were effectively
149 absent from our landscape.

150 We estimated the flooding regime experienced within each plot by first mapping the
151 bathymetry of each kettlehole using a laser theodolite and calculating the elevation of each
152 plot relative to the lowest point in each kettlehole. Values ranged from 0-2.86 m, with higher
153 elevations never flooded (Fig. S1). Relative elevations were then compared with daily mean
154 water levels to calculate flooding duration for each plot as the number of days that each plot
155 was submerged from Dec 2006-2011. Duration provides more information about the local
156 flooding regime than simply the number of times each plot was flooded, but, nonetheless, is
157 still highly correlated with other measures of flooding (Table S2).

158

159 *Phylogenetic inference*

160 We constructed a molecular-based phylogeny for our 63 study species using four markers
161 covering both nuclear (*ITS1-5.8S-ITS2*) and plastid (*rbcL*, *matK*, *trnL-trnF*) DNA regions in
162 order to incorporate their evolutionary relationships into our analyses (Table S1). Combining
163 the conserved *rbcL* and *5.8S* regions with faster-evolving *matK* and noncoding *trnL* and *ITS*
164 regions can help discriminate phylogenetic relationships within and amongst both families
165 and genera (Kynndt *et al.*, 2005). Sequences for each region were aligned using ClustalX
166 v2.1, iterating each step to refine fit (Larkin *et al.*, 2007), and we estimated tree structure and
167 branch lengths using reversible-jump Markov chain Monte Carlo (MCMC) sampling in
168 MrBayes v3.2 (Huelsenbeck *et al.*, 2004; see Methods S1 for full details). We used a
169 majority-rule consensus tree in our analyses, with branch lengths averaged over the trees in
170 the posterior samples containing that branch, as all but 4 of 123 branches were present in
171 >95% of posterior samples.

172

173 *Species occurrences along flooding gradient (P1)*

174 We tested the relative importance of species-specific responses to flooding in driving
175 community assembly. This involved predicting the occurrence of each species in each of the
176 5170 plots given flooding duration, spatial scale (plot, transect and kettlehole), and species
177 identity. Following Ives & Helmus (2011), we accounted for the fact that species can show
178 similar mean occurrences and responses to flooding because they are phylogenetically
179 related. We considered macroevolutionary models of both a Brownian motion, which

180 assumed that unobserved continuously valued traits influenced the probability of occurrence
 181 along our flooding gradient and evolved along our phylogenetic tree through random drift,
 182 and an Ornstein-Uhlenbeck (OU) process, which assumed there was selection towards a
 183 central trait value acting on the unobserved traits that influenced occurrence (see Methods S1
 184 for full details). To test the influence of spatial processes on species occurrence among
 185 transects within each kettlehole $v_{lm}^{(1)}$, we estimated the effect of each transect from a
 186 Gaussian spatial correlation structure equal to $e^{-(\tau\mathbf{D})^2}$, where τ was the strength of the spatial
 187 correlation across all transects and \mathbf{D} was a matrix of pairwise distances among the mid-
 188 points of transects in each kettlehole (Dormann *et al.*, 2007). We then let the presence-
 189 absence of each species j within plot k along transect l at kettlehole site m be drawn from a
 190 Bernoulli distribution with probability p_{jklm} that was equal to:

$$191 \quad \text{logit}(p_{jklm}) = \mu + v_{klm}^{(1)} + v_{lm}^{(1)} + v_m^{(1)} + v_{jl} + v_{jm} + v_j^{(1)} + v_j^{(2)}d_k, \quad (\text{eqn 1})$$

192 where μ was the estimated mean probability of occurrence across all species that varied
 193 according to the sampled plot, transect, and kettlehole with a value of $v_{klm}^{(1)}$, $v_{lm}^{(1)}$, and $v_m^{(1)}$,
 194 respectively, and allowed species to differ in this response among transects and kettleholes
 195 independent of phylogenetic relatedness according to v_{jl} and v_{jm} . Including $v_{klm}^{(1)}$, $v_{lm}^{(1)}$, and
 196 $v_m^{(1)}$ accounted for the fact that the presences-absences of species in the same plot, among
 197 plots on the same transect, and among plots in the same kettlehole were non-independent.
 198 We also let occurrence vary among species because of phylogenetically relatedness.
 199 Relatedness changed mean occurrence according to $v_j^{(1)}$ and influenced the response of each
 200 species $v_j^{(2)}$ to flooding duration d_k . All v terms were sampled from independent zero-mean
 201 normal distributions with estimated standard deviations (SDs) to compare sources of
 202 variation in p_{jklm} .

203 We calculated the relative importance of both continuous effects, such as flooding
 204 duration, and factor levels, such as transect or species identity, using variance components
 205 (VCs) (Qian & Shen, 2007; Hector *et al.*, 2011). Processes such as dispersal limitation and
 206 demographic stochasticity will be associated with spatial and/or residual-level variation, so
 207 we can infer the overall importance of flooding in driving community assembly by
 208 expressing its VC relative to these other factors. We estimated VCs as the SD of each v , with
 209 the SD of the residual error equal to the VC unexplained by our model (Hector *et al.*, 2011).

210

211 *Relating aerenchyma to occurrences along flooding gradient (P2)*

212 We built upon our model in eqn 1 to test whether greater RAV was associated with species
 213 that occupied sites there were flooded for longer periods. This first involved measuring root
 214 aerenchyma as the proportional volume of gas space within roots (Visser & Bögemann,
 215 2003). We focused on the 22 of the 24 most common species in our study, as these could be
 216 readily measured. For each species, we collected an average of 8 individuals (SD = 2) at
 217 regularly-spaced intervals across the flooding gradient in one of our kettleholes immediately
 218 after flooding in February 2013. In the lab, sections ca. 30 mm long were cut from root
 219 apices of each sample and weighed before and after vacuum infiltration with water. The
 220 difference between the two weights measured the mass of the internal air space. We
 221 expressed this mass relative to the mass of infiltrated tissue multiplied by an average specific
 222 weight of infiltrated tissue ($=1.036 \text{ g mL}^{-1}$) to derive percent root porosity. Species-specific
 223 differences in specific weight are sufficiently small that they do not measurably alter root
 224 porosities (Visser & Bögemann, 2003). For each species, we calculated maximum potential
 225 flooding tolerance RAV_{max} as the largest observed RAV. RAV_{max} therefore focused on the
 226 theoretical potential that each species could achieve. Using a population- rather than
 227 individual-level trait also eliminated the confounding effects of within-species variation on
 228 our analyses.

229 We then used the hierarchical modelling approach of Pollock *et al.* (2012) and Jamil
 230 *et al.* (2013) to test how the probability of occurrence of the 22 species with RAV
 231 measurements depended upon the interaction between RAV_{max} and the environment. Our
 232 approach advanced the previous methods by recognizing that species are non-independent
 233 and can show similar responses because of a shared evolutionary history. As in eqn 1, we
 234 predicted occurrence from a Bernoulli distribution with a probability p_{jklm} that depended upon
 235 flooding duration, allowing species to respond differently in each kettlehole site m :

$$236 \quad \text{logit}(p_{jklm}) = \gamma_j + \beta_{j[m]}d_k + v_k^{(2)} + v_l^{(2)} + v_m^{(2)}. \quad (\text{eqn 2})$$

237 The mean probability of occurrence of each species and how it was influenced RAV_{max} was
 238 given by:

$$239 \quad \gamma_j = \gamma^{(1)}_j + \gamma^{(2)}\text{RAV}_{\text{max},j} + v_j^{(3)},$$

240 where $\gamma^{(1)}_j$ estimated species-specific mean occurrences that were not phylogenetically
 241 related, $\gamma^{(2)}$ estimated the extent to which mean occurrence changed with RAV_{max} , and $v_j^{(3)}$
 242 reflected species-specific differences in occurrence that were phylogenetically related and
 243 estimated from pruning the larger 63 species phylogeny (Ives & Helmus, 2011). $v_j^{(3)}$ was
 244 estimated as in eqn 1 by scaling our phylogenetic tree with an estimated SD, thereby allowing
 245 phylogenetic relationships to provide additional information to RAV_{max} about the mean

246 occurrences of species, such as if unmeasured traits with a strong phylogenetic signal
247 influenced species distributions (Ives & Helmus, 2011). As with eqn 1, we also tested
248 whether transforming branch lengths in our phylogenetic tree according to an OU process
249 was a better fit to the observed occurrence data. We tested whether RAV_{\max} influenced
250 species' responses to flooding duration in eqn 2 by expressing a species-specific slope β_j as:

$$251 \quad \beta_j = \beta_1 + \beta_2 RAV_j + v_m^{(3)}.$$

252 We experimentally verified the role of RAV_{\max} in conferring flood tolerance. In a
253 previous experiment, we removed 96 16×16 cm turfs (8 cm depth) from one of the kettlehole
254 sites and submerged them in full sun for 110, 130, 150, and 170 days (Tanentzap *et al.*,
255 2013). Within each turf, we summed the number of times each species intersected one of 50
256 randomly generated coordinates at the start and immediately after each submergence period.
257 We then calculated the maximum potential for each species to mitigate biomass loss from
258 flooding (i.e. flooding tolerance) as the largest change in frequency observed across all pots.
259 Here, we correlated flooding tolerance with RAV_{\max} for 12 species that had both sets of trait
260 measurements using generalised least squares that accounted for phylogenetic relatedness.

261

262 *Pattern and process of aerenchyma evolution (P3)*

263 We tested the null hypothesis that potential flooding tolerance was as different among closely
264 related species as expected by chance. We quantified trait similarity with the K statistic
265 (Blomberg *et al.*, 2003), which captures the observed variance in RAV_{\max} relative to that
266 expected if it had evolved along a phylogenetic tree under a Brownian motion (BM). We
267 compared this to a null distribution for K generated by randomly shuffling the tips of our
268 phylogeny 1,000 times. We rejected our null hypothesis if the observed K was greater than
269 the null distribution >95% of the time. Values greater than expected at random indicate traits
270 are more similar among closely related species than compared with distant relatives, while
271 values smaller than random indicate less similarity among close relatives (Blomberg *et al.*,
272 2003). Critically, K alone cannot identify mechanisms generating trait distributions as similar
273 values arise from multiple evolutionary processes, e.g. strong stabilizing selection or adaptive
274 differentiation that slows over time (Revell *et al.*, 2008).

275 We also sought to identify the process underlying the evolution of potential flooding
276 tolerance across our phylogeny. We first fitted five evolutionary models to the RAV_{\max}
277 observed for each species using maximum-likelihood methods. Three models were based
278 entirely on a BM, whereby genetic drift occurred at a rate σ_B and was either: constant (BM1);
279 varied directionally, on average (BMD); or accelerated or decelerated exponentially over time

280 (ACDC), as might be expected where species radiate adaptively and variation in traits
281 between ancestors and descendants becomes progressively smaller (Harmon *et al.*, 2010).
282 One limitation with the ACDC model is that it may be very difficult to detect without
283 species-rich ($n > 50$) clades at the family- or order-level and traits of extinct ancestors (Slater
284 & Pennell, 2014). The fourth model (OU1) was based on an Ornstein–Uhlenbeck process,
285 where species evolved towards an optimal trait value θ at a rate of α and with random noise
286 from a BM added to this deterministic process (Hansen, 1997). The fifth model was non-
287 evolutionary and assumed traits were normally distributed with no covariance among species
288 (N1). Finally, we also fitted four variants that allowed evolutionary rates and optima to vary
289 between species that were primarily restricted (i.e. obligate) versus unrestricted (i.e.
290 facultative) to ephemeral wetlands (Methods S1). There were strong *a priori* reasons to
291 expect selective regimes differed between obligate and facultative taxa. Specifically, obligate
292 taxa should be pulled towards higher RAV_{\max} (i.e. high θ and α ; low σ_B). Facultative species
293 may instead shift towards a smaller RAV_{\max} (i.e. high α ; low θ and α), because RAV has
294 limited or no adaptive value in drier sites and/or low RAV improves the structural resistance
295 of roots against compaction once soils dry and shrink (Striker *et al.*, 2007).

296 All evolutionary models were estimated with the *R* packages *geiger* and *OUwie*. We
297 compared models with the small-sampled Akaike information criterion (AICc), with smaller
298 values indicating greater support (Burnham & Anderson, 2002). AICc was averaged among
299 character maps for models with variable selective regimes (Methods S1). As AICc is highly
300 sensitive to false negatives depending on the number of taxa and structure of the underlying
301 phylogeny, we also used parametric bootstrapping to detect differences between the two best
302 supported models (Methods S1).

303

304 *Evolutionary relatedness along flooding gradient (P4)*

305 We tested whether communities were more evolutionarily related as flooding increased. In
306 contrast to the generalised linear mixed models described by eqns 1-2, we were interested in
307 testing whether phylogenetic clustering at the community-level increased with flooding rather
308 than simply identifying whether it existed. This analysis also complemented our previous
309 models by focusing on community- rather than individual-level responses.

310 For each plot with >2 species ($n = 2,035$), we calculated the net relatedness index
311 (NRI) as the difference between the mean phylogenetic distance (PD, i.e. branch length in the
312 63 species consensus tree) observed among pairs of individuals within the plot and a mean
313 PD randomly sampled for the same number of species from across the entire phylogeny. The

314 null sampling therefore assumed that all 63 could hypothetically colonise all plots, which was
315 reasonable given the spatial range of our study. The difference between observed and
316 randomly sampled PD was then divided by the SD of the randomly sampled PD and
317 multiplied by -1 to derive NRI. Negative and positive values denote less- and more-closely
318 related communities than expected by chance, respectively, while values of zero are
319 consistent with random assembly. We focused on NRI because it captures clustering from
320 root to terminal nodes, so is more appropriate than other measures of dispersion for
321 phylogenies driven by deep divergences with little intra-family sampling (Webb, 2000).

322 We tested whether NRI within each plot k along transect l at kettlehole m varied with
323 the flooding duration experienced by that plot d_{klm} given normally-distributed error and a
324 mean η_{klm} , which was equal to:

$$325 \quad \eta_{klm} = \beta_3 + \beta_4 d_{klm} + \beta_5 \ln(s_{klm}) + v_{lm} + v_m, \quad (\text{eqn 3})$$

326 where β_3 was the mean NRI across plots, β_4 was the effect of flooding, β_5 was the effect of
327 plot-level species richness, and v_{lm} and v_m accounted for random variation among transects
328 and kettleholes, respectively, and were each $\sim N(0, \sigma_v)$ with separately estimated σ_v 's. β_5 helps
329 control for the fact that the mean of PD can increase while its variance decreases as more
330 species are recorded (Cadotte *et al.*, 2010), potentially inflating NRI.

331

332 *Model estimation and hypothesis testing (P1, P2, and P4)*

333 We fitted all statistical models (eqns 1–3) using MCMC sampling by calling *Stan* v.2.7 from
334 *R* (Stan Development Team, 2015). Four MCMC chains of at least 2,000 iterations were
335 simulated for each model, with a warm-up of 1,000 runs. All regression coefficients (i.e. β 's)
336 and standard deviations (i.e. σ 's) were drawn from uninformative priors that were $\sim N(0, 100)$
337 and $U(0, 100)$, respectively. We used a weakly informative prior for the strength of selection
338 along our phylogeny α of $\sim N(0,1)$. All independent variables were scaled to a mean of 0 and
339 SD of 1 prior to model estimation. Convergence was verified with standard approaches
340 (Methods S1). *R* code to fit a *Stan* model to simulated data is given in Methods S2.

341 For each parameter, we calculated posterior means and 95% credible intervals (CIs)
342 by drawing a subset of at least 1,000 simulations. We did not reject the hypothesis that the
343 interaction between species identity and flooding was a more important driver of species
344 occurrence than flooding on its own (P1, equation 1) if the 95% CI for the difference between
345 the variance component of the interaction and that of flooding was ≥ 0 . Similarly, we rejected
346 null hypotheses of no effect of flooding on aerenchyma volume (P2, equation 2) and flooding
347 on community relatedness (P4, equation 3) if 95% CIs for focal regression coefficients

348 excluded zero. Where we fitted different transformations of our phylogenetic tree, parameter
349 estimates were reported only for the best supported model. Models were compared with the
350 leave-one-out information criterion (LOOIC), which is more accurate than classical
351 information criterion in a Bayesian context yet is interpreted similarly, i.e. smaller values
352 indicate better supported model and we selected the more parsimonious model where
353 differences in LOOIC were <2 (Vehtari *et al.*, 2015).

354

355 **Results**

356 *Species occurrences constrained by tolerance of flooding*

357 Species-specific responses to flooding were an important driver of community assembly,
358 supporting P1 that predicted species occurrences should change differently along a flooding
359 gradient. For example, whilst many species were less likely to occur with increased flooding
360 duration, there was considerable variation in prevalence and some graminoids had strong
361 positive responses (Fig. S2). Consequently, the effect of species identity that allowed close
362 relatives to co-vary and its interaction with flooding duration explained much more variation
363 in the probability of occurrence of individuals than simply the mean effect of flooding (95%
364 CIs for VCs, species \times flooding interaction: 4.8 – 5.5; species identity: 4.0 – 5.0; flooding
365 duration: 0.3 – 0.5; Fig. 1). The model allowing close relatives to co-vary without a clear
366 directional effect was better supported than the model in which all species were concurrently
367 drawn towards a central mean for their probability of occurrence (LOOIC for BM vs OU
368 model: 63768 and 63816, respectively). Differences among species in occurrence across
369 kettlehole sites and transects independent of their phylogenetic relatedness were also
370 relatively small, suggesting that environmental responses that were not evolutionarily
371 conserved were comparatively weak influences over community assembly (95% CIs: 2.3 –
372 2.9 and 1.1 – 1.3, respectively). Site-level variation in species occurrence, reflecting such
373 factors as differences in the regional species pool, and transect- and residual-level variation,
374 presumably associated with stochastic and spatial processes unrelated to flooding, such as
375 dispersal limitation, were also relatively minor (for all, upper 95% CI <1.7 ; Fig. 1). Little
376 variation was similarly explained at the plot-level (95% CI: 0.8 – 0.9).

377 We found that species occurring in sites that were flooded for longer periods had
378 greater root aerenchyma volume as predicted by P2 (95% CI for RAV \times flooding interaction
379 effect β_2 : 0.45 – 0.51). For example, a 20% increase over the observed range of flooding
380 duration from 304 to 507 days submergence reduced the probability of occurrence of species
381 with $<20\%$ RAV_{max} by nearly 9% (Fig. 2). By contrast, species were between 1.3 – 7.7%

382 more likely to occur in these conditions where RAV_{max} exceeded 30% (Fig. 2). Neither
383 RAV_{max} or flooding duration influenced species occurrence on their own (95% CIs for $\gamma^{(2)}$
384 and β_1 : -0.51 – 0.65 and -0.57 – 0.78, respectively), and a model of BM again better
385 supported patterns in occurrence among close relatives ($\Delta LOOIC$ vs OU model: -4.5).
386 Transect- and plot-level variation were also negligible in our model (for both, upper 95% CI
387 of estimated $\sigma < 0.29$) as compared with site- and species-level sources of variation in slopes
388 and intercepts (95% CIs for σ parameters overlapping and ranging between 0.01 – 1.27).
389 Experimental evidence suggested that high RAV_{max} minimized biomass loss during flooding
390 (95% CI for change in frequency with logit-transformed RAV_{max} : 2.4 – 11.3), thereby
391 favouring increased abundance by allowing individuals to exploit gaps created by the loss of
392 species with low RAV_{max} . Species that always lost biomass during flooding (i.e. maximum
393 change in frequency was negative) never had a $RAV_{max} > 25\%$ (Fig. S3). All these results
394 were consistent with those in the larger dataset and implicated RAV_{max} as a mechanism
395 behind the large amount of variation explained by the species \times flooding interaction in Fig. 1.
396

397 *Tolerance to flooding is evolutionarily conserved*

398 We found evidence of non-random selective forces acting upon RAV_{max} , leading to patterns
399 of trait conservatism as predicted by P3. We specifically rejected the null hypothesis that
400 flooding tolerance was as different among relatives as expected by chance. Close relatives
401 were instead more similar in RAV_{max} than distant relatives (observed $K = 0.59$ greater than
402 95% of null distribution between 0.16 – 0.58).

403 Evolutionary models suggested that traits of ancestors were retained in descendants
404 because of physiological constraints that stabilized onto different $RAVs$ optimal for obligate
405 versus facultative wetland taxa (Fig. 3). OU2 was the best supported model based on the
406 qualitative use of AICc and variants of this model (OU2, OU2A, or OU2V) collectively
407 accounted for almost all the support among the candidate set (Table 1). Parameter estimates
408 were also very similar when comparing averages across the 1,000 OU2 fits versus estimates
409 weighted across all three OU2 variants using AICc, whereby optimal RAV_{max} (logit scale)
410 was equal to -0.84 vs -0.83, respectively, for obligate taxa, and -1.38 vs -1.56, respectively,
411 for facultative taxa. Given these similarities, we tested whether support for the OU2 was
412 more likely to arise than expected if trait values were derived under N1, the next best class of
413 evolutionary models (Table 1). Reassuringly, 98.8% of the observed differences between
414 OU2 and N1 across all 1,000 character maps were greater than the upper 95% of values
415 expected had the underlying data been generated by N1, and we always rejected N1 when

416 data were simulated under OU2 (i.e. power of 100% to choose between models with false
417 positive rate of 5%), showing that our phylogeny was sufficiently informative to detect
418 differences in underlying trait models despite its relatively small size. Support for the OU2
419 model held when we compared it to the BMD, which was the next best supported non-OU
420 model based on AICc, as differences between models were always smaller than empirical
421 observations and we had a power of 100% to choose between these when data were simulated
422 under a BMD. Thus, irrespective of whether OU2, OU2A, or OU2V was the best fitting
423 model, there was strong evidence to reject a non-phylogenetic model of trait evolution.

424 Parameter estimates from the model with maximum likelihood across the set of 1,000
425 OU2 fits, each using a different ancestral character map, centred on a relatively high RAV_{max}
426 for obligate wetland species (mean \pm SE: 0.34 ± 0.03). Facultative taxa had a much lower
427 optimum of 0.12 ± 0.04 . The relatively large α (mean \pm SE: 3.4 ± 1.2) and small σ_B ($0.80 \pm$
428 0.53) parameters associated with this model suggested that species were rapidly drawn to
429 their phenotypic optima (Hansen 1997), evolving half this distance in <10% of the total tree
430 length with little confounding BM (95% confidence intervals for random change in RAV_{max}
431 on logit-scale = $-0.51 - 0.51$). Model averaging with AICc across the entire set of OU2
432 models only strengthened these effects ($\alpha = 15.4$; $\sigma_B = 4.3$; optima unchanged).

433

434 *More similar communities as flooding increases*

435 Communities were more closely related than expected by chance as flooding duration
436 increased (Fig. 4), as predicted by P4. The net relatedness index (NRI) of plots increased
437 with flooding duration when calculated from all the species in our phylogeny (95% CI: 0.19 –
438 0.28). This effect was equally strong when we calculated NRI only from the 22 taxa with
439 RAV measurements (95% CI: 0.19 – 0.29, $n = 1,491$ plots), suggesting that our observations
440 across the larger 63-species dataset were consistent with the findings that RAV_{max} determined
441 species occurrences (Fig. 2) and was conserved across the phylogeny (Fig. 3). The increase
442 in NRI across the 63-species dataset was also not simply due to the fact that there were fewer
443 species in communities there were flooded for longer periods of time, and hence fewer long
444 branch lengths, because we accounted for the variation in NRI associated with species
445 richness in our model (95% CI: 0.03 – 0.11). A phylogenetic tree for all 63 study species is
446 given in Supporting Information Fig. S4.

447

448 **Discussion**

449 Our findings support our central hypothesis, which predicts that environmental change should
450 favour increasing phylogenetic relatedness where species' responses to the new conditions
451 are evolutionarily conserved. In our study, a mean of 58% of the variation in occurrence
452 along flooding gradients was explained by species-specific responses that allowed close
453 relatives to vary similarly, implicating evolutionarily conservatism in species' responses (Fig.
454 1). By focusing on a subset of species, we then found that root aerenchyma influenced
455 responses to flooding and was under strong selection towards habitat-specific optima (Figs 2,
456 3, S3). We specifically found that large RAV_{max} was conserved within obligate wetland
457 species that tolerated flooding. This conservatism may explain why communities are more
458 phylogenetically related as flooding increases in our study and potentially many others (e.g.
459 Verdú & Pausas, 2007; Helmus *et al.*, 2010; Ding *et al.*, 2012). Patterns of phylogenetic
460 structure may however also differ across spatial scales. For example, phylogenetic clustering
461 may weaken within a single distributional zone, such as in plots that were never flooded,
462 where competitive interactions can be more important controls over community assembly
463 than environmental barriers to species establishment (Cavender-Bares *et al.*, 2006).

464 We are also among the first to show that aerenchyma modulates species responses to
465 changing flooding regimes in natural ecosystems. Previous studies have focused on
466 experimentally or theoretically demonstrating the role of aerenchyma role in conferring
467 flooding tolerance (Justin & Armstrong, 1987; Sorrell *et al.*, 2000; Mommer *et al.*, 2006; van
468 Bodegom *et al.*, 2008), or have shown that community-weighted mean trait values change
469 along flood gradients (Baastrup-Spohr *et al.*, 2015). Others have related the extent of
470 aerenchyma to the maximum water depths that species occupy (e.g. Brix *et al.*, 1992). Here
471 we used the RAV of individual species to explain their specific changes in occurrence along
472 waterlogging gradients (i.e. Fig. 2). Our results also demonstrate that measuring species
473 responses to flooding with RAV will improve upon the subjective classification of habitat
474 requirements widely used in the aquatic plant literature (Casanova & Brock, 2000).

475 Values of physiological traits enhancing plant survival are likely to be evolutionarily
476 conserved because deviations may prove fatal where environmental filtering is strong. For
477 example, low light availability and gas exchange are major causes of mortality during
478 flooding (Vervuren *et al.*, 2003). Here, we found support for the prediction that selection
479 stabilised around a relatively large RAV_{max} in obligate wetland species because it promoted
480 occupancy of flooded communities. By contrast, RAV may be non-adaptive for facultative
481 taxa that occupy drier sites, leading to smaller values for this taxonomic group. Such strong
482 trait-based control over environmental persistence can help explain why closely related

483 species retain similar levels of RAV_{max} through evolutionary time (Cooper *et al.*, 2010; Crisp
484 & Cook, 2012). Other traits for responding to environmental change may also be under
485 strong selection towards specific trait values over evolutionary timescales (Litsios *et al.*,
486 2014), but it remains unknown whether this process is widespread. Data syntheses suggest
487 that stabilizing selection, for example, is not more common in plants than other forms of
488 selection (Kingsolver & Diamond, 2011); though no explicit response traits were included in
489 these analyses.

490 We cannot exclude competition as a selective force acting upon trait evolution and
491 community assembly. Large RAV_{max} should enhance relative performance and thus resource
492 capture because it allows plants to minimize biomass loss associated with flooding (Fig. S3).
493 As large RAV_{max} is strongly conserved, this will create differences in competitive ability that
494 map onto our phylogeny. Communities can therefore be more closely related than expected
495 by chance, as observed here, because competition is the dominant force driving assembly and
496 closely related species will be less likely to exclude each other given their similar competitive
497 abilities (Mayfield & Levine, 2010). Such a role for competition could explain why species-
498 specific differences unrelated to flooding influenced species occurrence (Fig. 1). However,
499 changes in plant biomass associated with competitive interactions may be negligible relative
500 to the effects of flooding (Lenssen *et al.*, 2004), and many natural disturbances in fact change
501 the relative competitive abilities of species (e.g. Suding & Goldberg, 2001; Fynn *et al.*,
502 2005). Disentangling the primary driver of community assembly may thus need controlled
503 experiments.

504 Our results suggest that local changes in hydrology will influence the relatedness of
505 plant communities elsewhere if levels of RAV are strongly conserved across the tree of life.
506 Existing data suggest that such changes in phylogenetic relatedness may be likely. Across
507 234 species in the Cape reeds family (Restionaceae), Huber & Linder (2012) found that
508 aerenchyma was ancestrally present and regularly gained in wet habitats but never lost.
509 Although we focused on considerably fewer species, null simulations showed that our
510 phylogeny was sufficiently informative to discern similar macroevolutionary processes and
511 our sampling across families targeted the scale at which distinct evolutionary units emerge
512 (Barracough & Humphreys, 2015). The presence of aerenchyma may have in fact been
513 conserved in much of the world's flora given its ancient origins in plants that evolved ca. 300
514 million years ago (Green, 2010). Aerenchyma may have only been lost during the transition
515 from waterlogged to well-drained or drier habitats (e.g. Huber & Linder, 2012), where it may
516 pose a cost to mechanical strength of roots (Striker *et al.*, 2007).

517 Predicting the future responses of phylogenetic structure to global change can help
518 inform efforts to conserve uniquely evolved features, ecological functions, and the long-term
519 capacity of biota to persist and adapt to future change (Winter *et al.*, 2013). Here we have
520 shown that reconstructing the evolution of physiological traits that influence species
521 distributions can help provide insight into patterns of phylogenetic structure. By identifying a
522 key trait associated with reducing biomass loss from environmental change (i.e. RAV_{max}), we
523 predicted contemporary species occurrences, albeit on a local scale, and found that
524 evolutionary conservatism towards high values of this trait should promote phylogenetic
525 clustering across future communities if flooding increases. More generally, our work
526 illustrates the value of reconstructing evolutionary history in order to predict the direction of
527 future change in phylogenetic structure.

528

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539

540 **Author contributinos**

541 A.J.T and W.G.L designed the research, A.J.T and W.G.L performed experiments and
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543

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740

741 **Supporting Information**

742 Additional supporting information may be found in the online version of this article:

743 **Fig. S1** Temporal trends in flooding.

744 **Fig. S2** Species occurrence along flooding gradient.

745 **Fig. S3** Biomass loss during submergence versus root aerenchyma volume.

746 **Fig. S4** Phylogenetic hypothesis for 63 wetland species.

747 **Table S1** Genetic markers for study species.

748 **Table S2** Correlations among measures of flooding regime.

749 **Methods S1** Additional methods.

750 **Methods S2** Stan code for fitting a model with phylogenetic effects.

751

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753 supporting information supplied by the authors. Any queries (other than missing material)
754 should be directed to the New Phytologist Central Office.

755 **Table 1.** Evolutionary models fitted to maximum root aerenchyma volume (RAV_{max})
756 observed for 22 species. Models were based on either: a Brownian motion with drift that was
757 constant (BM1), varied directionally (BMD), accelerated or decelerated exponentially over
758 time (ACDC), or constant at different rates between obligate and facultative wetland species
759 (BM2); an Ornstein–Uhlenbeck process with the same optimal trait value (θ), rate of
760 attraction towards the trait optima (α), and random noise (σ) across all species (OU1), or a
761 different θ (OU2), both θ and α (OU2A), or both θ and σ (OU2V) between obligate and
762 facultative wetland species; or a non-evolutionary process that assumed no covariance among
763 species (N1). Best supported model bolded. AICc weight (w_i) is proportion of support for a
764 model out of given candidate set. *Averaged across 1,000 model fits, each with a different
765 character map.

model	AICc	w_i
OU2*	30.8	0.66
OU2A*	33.5	0.17
OU2V*	33.9	0.14
N1	38.5	0.01
OU1	40.4	0.01
BMD*	41.8	<0.01
BM1	42.3	<0.01
ACDC	42.7	<0.01
BM2	43.8	<0.01

766

767 **Figure Legends**

768 **Fig. 1.** Mean \pm 95% CIs for variance components (standard deviation scale) explaining
769 probability of occurrence of 63 species across 5,170 vegetation plots. Overall, the model
770 correctly classified most observations, as measured by a large proportion of explained cross-
771 validated deviance (= 0.51) and an area under a receiver operating characteristic curve (AUC)
772 of 0.97, which represents the probability that a species presence will be scored higher than an
773 absence. Spp_{phylo} and $Spp_{non-phylo}$ respectively represent species-specific responses that either
774 were or were not phylogenetically-related and these effects were only moderately inter-
775 correlated (absolute Spearman's ρ for all pair-wise comparisons among variance components
776 <0.50).

777
778 **Fig. 2.** Large root porosity increases probability of occurrence as flooding duration lasts
779 longer. We plotted the change in the percent probability of occurrence in 22 species from a
780 20% increase in flooding duration versus their maximum potential root aerenchyma volume,
781 measured as porosity. Solid line is mean model fit and shaded area is 95% CI. Proportion of
782 cross-validated deviance explained and AUC for the overall model were 0.81 and 0.81,
783 respectively.

784
785 **Fig 3.** Phylogram for 22 wetland species with measurements of maximum root aerenchyma
786 volume (RAV_{max}) scaled with symbol size from 10–40%. The phylogram was generated by
787 dropping tips lacking trait data from a Bayesian majority-rule consensus tree estimated for all
788 our 63 study species (Fig. S4). Branch colours are posterior probability (PP) of habitat
789 affinity being either obligate (O, green) or facultative (F, blue) to wetlands.

790
791 **Fig. 4.** Communities are increasingly related as flooding duration increases. For plotting
792 only, points were averages \pm standard error of ca. 250 plot-level observations at the median
793 of each of 8 duration-class bins. Solid line is mean change in net relatedness index (NRI)
794 with flooding duration at mean values of all other predictor variables in eqn 3. Shaded area
795 denotes 95% CI. Lines adjacent to axes denote the positions of flooding duration and NRI
796 within the plotted range.

Explanatory variables

Variance components







