

1 **Title: Can we predict which species win when new habitat becomes**  
2 **available?**

3 **Short title:** Colonising new habitat

4 **Authors:** Miki Nomura<sup>1\*</sup>, Ralf Ohlemüller<sup>1</sup>, William G. Lee<sup>2¶</sup>, Kelvin M. Lloyd<sup>2¶</sup>, Barbara J.  
5 Anderson<sup>2</sup>

6 <sup>1</sup>Department of Geography, University of Otago, PO Box 56, Dunedin, New Zealand

7 <sup>2</sup>Manaaki Whenua Landcare Research, Private bag 1930, Dunedin, New Zealand

8 **Emails:**

9 Miki Nomura; [miki.nomura@postgrad.otago.ac.nz](mailto:miki.nomura@postgrad.otago.ac.nz)

10 Ralf Ohlemüller; [ralf.ohlemuller@otago.ac.nz](mailto:ralf.ohlemuller@otago.ac.nz)

11 William G. Lee; [LeeW@landcareresearch.co.nz](mailto:LeeW@landcareresearch.co.nz)

12 Kelvin M. Lloyd; [LloydK@landcareresearch.co.nz](mailto:LloydK@landcareresearch.co.nz)

13 Barbara J. Anderson; [AndersonB@landcareresearch.co.nz](mailto:AndersonB@landcareresearch.co.nz)

14

15 ¶ These authors contributed equally to this work.

16

17 **Corresponding author\*:** Miki Nomura. Email: [miki.nomura@postgrad.otago.ac.nz](mailto:miki.nomura@postgrad.otago.ac.nz),

18 Telephone: +64 22 6540064, ORCID: 0000-0002-8948-6232

19 **Author contributions;** WGL, RO and BJA conceived the study, MN developed and  
20 conducted the analyses and wrote the first draft of the manuscript. All authors contributed to  
21 the writing and editing of the manuscript.

22

23

## 24 **Abstract**

25 Land cover change is a key component of anthropogenic global environmental change,  
26 contributing to changes in environmental conditions of habitats. These changes can lead to  
27 the redistribution of species and shifts in the functional composition and properties of  
28 ecosystems. Deforestation is globally the most widespread anthropogenically driven land  
29 cover change leading to conversion from closed forest to open non-forest habitat. The  
30 consequences of these functional habitat changes on species distributions are only poorly  
31 understood. This study investigates the relative roles of geographic features, species climatic  
32 niche characteristics and species traits in determining the ability of open-habitat plant species  
33 to take advantage of recently opened habitats. We use current occurrence records of 18  
34 herbaceous, predominantly open-habitat species of the genus *Acaena* (*Rosaceae*) to  
35 determine their prevalence in recently opened habitat. Geographic features of the spatial  
36 distribution of open habitat, species' climatic niche characteristics, and species traits related  
37 to dispersal were tested their correlation with species' prevalence in anthropogenically  
38 opened habitat. While primary open habitat (naturally open) was characterised by cold  
39 climates, secondary open habitat (naturally closed but anthropogenically opened) is  
40 characterised by warmer and wetter conditions. We found high levels of variation in the  
41 prevalence of secondary open habitat among the investigated species indicating differences  
42 between species in their ability to colonise newly opened habitat. For the species  
43 investigated, geographical and climatic niche factors showed generally stronger relationships  
44 with species' prevalence in secondary open habitat than functional traits did. For small  
45 herbaceous species, geographical and environmental factors appear to be more important than  
46 species functional traits for facilitating expansion into secondary open habitats. Our results  
47 suggested that the land cover change might have triggered the shifts of factors controlling

48 open-habitat plant distributions from the competition with forest trees to current  
49 environmental constraints.

50

## 51 **Introduction**

52 Over three quarters of the global land surface have been modified by human activity [1]. In  
53 the last two decades alone, c. one-tenth (3.3 million square km) of global wilderness areas  
54 was lost [2]. Such anthropogenic land cover change affects biodiversity loss from habitat  
55 declines, and therefore can lead to the functions and distributions of species and ecosystems  
56 [3-5]. As the original (or natural) vegetation and physical properties of an area are modified,  
57 the available habitat to species and the environmental conditions will change and affect  
58 which species and ecosystems are found in that area [6].

59 Deforestation is a typical example of anthropogenic land cover change and, at its most basic  
60 level, results in a change from forest habitat to more open, non-forest habitat, usually  
61 scrubland or grassland. Deforestation occurred in many parts of the world following human  
62 settlement (e.g. North America [7], Europe [8] and New Zealand [9]) and is ongoing; 2.3  
63 million square kilometres forest was lost globally between 2000 and 2012 [10]. Species  
64 distributions are strongly dependent on the environmental conditions that define habitat, and  
65 therefore, species are susceptible to land cover change [11-13]. Understanding how species  
66 respond to habitat change is important for predicting how ongoing anthropogenic land cover  
67 change may influence future species assemblages. Here, we investigate the relative  
68 contribution of landscape structure, species climatic niches and species functional traits to  
69 species' expansion into recently opened habitats.

70 The effects of land cover change history on plant distributions have been reported widely in  
71 the world [14-16]. Although the history since pre-human times is not generally available,  
72 New Zealand offers good records of the land use change history since the first human

73 settlement, because a human being settled in the land much later (c. 800 years ago) than other  
74 regions in the world. Habitats which have been available for organisms before and after  
75 anthropogenic activities, primary habitats, and those which became available after  
76 anthropogenic activities, secondary habitats, have different ecosystems. For example, a  
77 primary forest in tropical zones showed marked differences in community structure and  
78 composition from secondary and plantation forests [3]. Therefore, the expansion of secondary  
79 open-habitat following human arrival provides a new ecological opportunity for open habitat  
80 species to expand their range across these recently deforested areas.

81 In this study, we investigate the geographical distribution and climatic niches of 18  
82 herbaceous species in relation to both primary and secondary open habitat in New Zealand.  
83 We assess the relative prevalence of the species in these habitats and determine the  
84 importance of three sets of factors – the geographic features, the species’ climatic niches and  
85 the species’ dispersal traits for expansion into the secondary habitats. Specifically, we address  
86 three questions;

87 1) What are the climatic characteristics of primary and secondary open habitats occupied by  
88 the species?

89 2) What are the current spatial distributions of the species in primary vs. secondary open  
90 habitat?

91 3) What is the relative importance of geographic features of habitat, the species’ climatic  
92 niches and species dispersal traits for expansion into secondary open habitat?

93

## 94 **Material and Methods**

### 95 **Study Species**

96 *Occurrence records* - We used occurrence records and trait data for 18 of 21 species of the  
97 genus *Acaena* occurring in New Zealand (Table S1). Three species were not used in this  
98 study because of the small number of occurrence records (< 5). The genus *Acaena* is a  
99 characteristic herbaceous element of open habitats in New Zealand, with a wide geographical  
100 and environmental range [17]. The genus is confined mostly to the southern hemisphere and  
101 comprises approximately 50 species [18, 19]. Indigenous New Zealand species of *Acaena* are  
102 prostrate, long-lived perennials, representing two main divisions based on contrasting  
103 dispersal features; the presence/absence of barbed spines on their fruits [17]. Of the 18  
104 species selected, 17 species are native to New Zealand and one species (*A. agnipila*) is  
105 introduced from Australia and naturalised [20]. Occurrence records of these species were  
106 compiled from personal observation, surveys and reports (See a reference list in Appendix for  
107 detailed source information) and location information from online databases; New Zealand  
108 Virtual Herbarium (<http://www.virtualherbarium.org.nz>) and New Zealand National  
109 Vegetation Survey (<https://nvs.landcareresearch.co.nz>).

110

## 111 **Pre-human and current land cover data**

112 New Zealand's pre-human land cover was derived from modelled spatial data of potential  
113 suitability of New Zealand's key forest tree species at 100 m grid resolution [21]. Current  
114 land cover was derived from the latest version of the New Zealand land cover polygon data,  
115 'LCDB4' [22]. We converted pre-human and current land cover and a digital elevation model  
116 for the area [23] to rasters on 1km grid resolution using the majority rule in ArcGIS 10.2  
117 [24].

118 In both land cover datasets, land cover classes were amalgamated so that each 1 km grid cell  
119 was assigned to one of three land cover types:

120 1) Native forest: Grid cells with any type of indigenous forest.

121 2) Non-forest: Grid cells with non-forest, open land cover classes, which are potentially  
122 suitable for *Acaena* species, e.g. grasslands, shrublands and gravel areas. These non-forest  
123 grid cells are here referred to as ‘open’ habitat.

124 3) Others: Grid cells with land cover classes that are typically not potential habitats for  
125 *Acaena* species e.g. urban area and waterbodies.

126 For a full list of class conversions from LCDB land cover classes into the three land cover  
127 types used in this study, see Table S2. In addition, the grid cells of current non-forest were  
128 assigned levels of openness, “high” or “low” (Table S2b).

129 In order to quantify the change from forest to open habitat, each 1 km grid cell was assigned  
130 one of the following three categories:

131 I) Primary open habitat: Grid cells that continuously had open habitat, i.e. are non-forest land  
132 cover in pre-human and current times.

133 II) Secondary open habitat: Grid cells that only had open habitat since human arrival, i.e. had  
134 forest land cover in pre-human times and non-forest land cover currently.

135 III) Others: Grid cells that are neither primary nor secondary open habitat.

136 Hereafter, we refer to species occurrence records in primary/secondary open area as  
137 “primary/ secondary open occurrence records”.

138

139 Our principle metric is “species prevalence in secondary open habitat”, which quantifies  
140 effects of anthropogenic land cover change on open habitat species. We calculated the species  
141 prevalence in secondary open habitat as:

142 
$$P_{2open} = \frac{N_{2oor}}{N_{p0or} + N_{2oor}}$$

143 where  $P_{2open}$  is the proportion of secondary open habitat,  $N_{2oor}$  is the number of secondary  
144 open occurrence records and  $N_{p0or}$  is the number of primary open occurrence records.

145 High values reflect that the species has a proportionally high prevalence in secondary open  
146 habitat, which we interpret as high ability to utilise newly opened habitat.

147

## 148 **Current climatic conditions and *Acaena* species climatic niches**

149 Gridded average climate data (1960 - 1990) was retrieved from  
150 <http://www.worldclim.org/current> for four climate variables to quantify climatic conditions  
151 available in New Zealand and species climatic niches: annual mean temperature, minimum  
152 temperature of coldest month, annual precipitation and precipitation seasonality [25].  
153 Environmental analyses were limited to climatic factors, as temperature and precipitation are  
154 likely to be primary driving factors of *Acaena* species distributions at this national spatial  
155 scale [26]. To capture the multi-dimensional climate space, an ordination, Principal  
156 Component Analysis (PCA) [27], was performed on the four climate variables using the  
157 package “stats” in R [28]. The first two ordination axes explained 61.6% and 24.0% of the  
158 variation in the climate data respectively and were here used to delineate New Zealand  
159 climate space and the *Acaena* species’ climatic niches. Hereafter, the first ordination axis is  
160 referred to as the “temperature axis” because it is strongly correlated with temperature  
161 variables and the second axis is referred to as “precipitation axis”. High values on the  
162 temperature axis indicate a cold environment, while high values on the precipitation axis  
163 indicate a dry environment.

164

## 165 **Correlates of prevalence in secondary open habitat**

166 We investigated the relative importance of species geographical, environmental and  
167 functional trait features for facilitating species to move into new open habitat as it became  
168 available following human settlement. The relationship between “species prevalence in

169 secondary open habitat” (response variable) defined above and the following indices  
170 (predictor variables) from the three main groups (Table 1) was tested with a generalized  
171 linear model using the R package “stats” with a normal error function and an identity link.

172 A) Geographical variables:

- 173 1. *Species’ current range size* was calculated as the natural-log-transformed number of  
174 species occurrence records across all habitats.
- 175 2. *Species’ preference for open habitat* was calculated as the proportion of all  
176 occurrence records that are located in open habitat over occurrence records that are in  
177 native forests and open habitats.
- 178 3. *Availability of secondary open habitat*: In order to quantify how much open habitat  
179 has become available in the neighbourhood of primary occurrences, the availability of  
180 secondary open habitat was quantified for each species as follows: for each primary  
181 occurrence (that is, an occurrence record in forest or primary open habitat), the  
182 number of grid cells with secondary open habitat within a  $10 \times 10$  km neighbourhood  
183 around the occurrence record was calculated. Availability of secondary open habitat is  
184 defined as the cumulative total number of secondary open grid cells. Each secondary  
185 open grid cell was not counted more than once when it was located in the  
186 neighbourhood of more than one primary occurrence.
- 187 4. *Mean elevation of current range*: to test whether species occurring at a higher  
188 elevation are more likely to take advantage of newly opened habitats, the mean  
189 elevation of all occurrence records across all habitats was calculated.

190 B) Climatic variables:

- 191 5. *Species climatic niche volume*: Niche volume was estimated as a proxy of climatic  
192 tolerance and was quantified as niche overlap on 2-D space comprising of temperature  
193 and precipitation axes between each species and the entire New Zealand climate



194 space. Niche volume was calculated using Schoener's D index [29] with the "ecospat"  
195 package in R [30]. Schoener's D ranges from 0 to 1 with higher values indicating  
196 larger niche overlap.

197 6. *Niche overlap between primary and secondary open habitat* was quantified as  
198 climatic niche overlap (Schoener's D) between the climatic niches occupied by  
199 primary and secondary open occurrence records of each species. Higher values  
200 indicate higher similarity in climate conditions between occurrence records in primary  
201 and secondary open habitat.

202 7. *Medians of species temperature and precipitation niches*: The median of the  
203 temperature and precipitation axes of the species occurrences across all habitats were  
204 calculated to analyse the individual effects of temperature and precipitation on species  
205 distributions.

206 C) Species trait variables:

207 *Life form – dispersal ability*: We selected two functional traits on the basis of  
208 relevance for the species' ability to shift its range to analyse effects of species  
209 functional traits on species distribution. Each species was assigned one of the three  
210 combinations of life forms and dispersal ability classes; Stoloniferous-Ancistrum  
211 (eleven species), Rhizomatous-Microphyllae (five species) and other combinations  
212 (two species) (Table S3).

213 Based on published information [20], each species was classified as either rhizomatous (five  
214 species) or stoloniferous (eleven species) with two species belonging to other life forms. The  
215 genus *Acaena* has three distinct phylogenetic sections (Pteracaena, Ancistrum and  
216 Microphyllae; Bitter [18]) which are characterised by morphological differences in their  
217 fruits. We used these sections as an index of dispersal ability; Ancistrum has barb-tipped

218 spines which attach the fruits to passing animals and therefore is considered as having higher  
 219 dispersal ability than barbless species in the other two sections.

220

221 **Table 1. Correlates of prevalence for secondary open habitat in the investigated *Acaena***  
 222 **species.**

Groups of factors	Factors tested	Coefficients	SE	p-values
	Intercept	0.85	0.39	0.06
Geography	Species' current range size	-0.48	0.41	0.28
	Preference for open habitat	0.83	0.90	0.39
	Availability of secondary open habitat	1.84	2.20	0.43
	Mean elevation of current range	$-4.2 \times 10^{-4}$	<0.01	0.43
Climatic niche	Species' niche volume	1.93	1.55	0.25
	Niche overlap between primary and secondary open habitat occupied by a species	$-4.6 \times 10^{-3}$	0.39	0.91
	Median of temperature niche	$-5.7 \times 10^{-2}$	0.13	0.68
	Median of precipitation niche	0.23	0.25	0.39
Functional trait	MR	-0.05	0.12	0.70
	O	-0.08	0.17	0.65

223

224 Nine factors from three main groups (Geographical features, climatic niche, functional traits)  
 225 were tested using a multivariate generalized linear model (GLM). Coefficients, SE; standard  
 226 error and p-values of each explanatory variables were derived from the GLM. The results of  
 227 the GLM for “species' life form – dispersal ability” were calculated using the comparisons  
 228 with Stoloniferous-Ancistrum. MR: comparison between Stoloniferous-Ancistrum and  
 229 Microphyllae\_Rhizomatous and O: comparison between Stoloniferous-Ancistrum and other  
 230 types of species' life form and dispersal ability.

231

## 232 **Results**

### 233 **Pre-human and current distribution of open habitat**

234 **Geographical distribution** - Open habitat in the study region increased from 18.4% to  
235 63.4% of the total land area since human arrival in the 13<sup>th</sup> Century AD (Fig. 1 a). Currently,  
236 15.3% of New Zealand's land area is a primary open area, while approximately half (48.1%)  
237 of its current land area is secondary open habitat (Fig. 1 b). 91.0% of the primary open area  
238 and 47.7% of secondary open area are located in the South Island.

239

#### 240 **Figure 1. Forest and open land cover in New Zealand since human settlement at 1km**

241 **grid cell resolution.** (a) Forest (green) and non-forest, open (brown) land cover modelled for  
242 pre-human times in the 13<sup>th</sup> century [21] and observed for current times in 2012 [22]. See  
243 Table S2 for a detailed description of land cover classes. (b) Open areas: Primary open areas  
244 (blue) indicate areas that were forest free prior to and are still open today; secondary open  
245 areas (red) are areas that were forested prior to human settlement but that are currently  
246 characterised by open habitat; others (white) area areas that are currently not open habitat or  
247 are considered unsuitable for our target species (e.g. urban area and waterbodies).

248

249 **Climate** –The climate associated with open habitats in New Zealand have shifted from cold  
250 to warm conditions since the forest clearances following human settlement, however, there  
251 was no clear directional shift along the precipitation axis (Figs. 2, 3 a). The highest  
252 frequency of current open habitat comprising both primary and secondary open habitats  
253 occurred in a warmer and wetter environment (0 – 0.5 in temperature axis and -0.5 – 0 in  
254 precipitation axis) than the pre-human open habitat (2.0 - 3.0 in temperature axis and 2.0 - -

255 1.5 in precipitation axis) (Fig. 2). Note that temperature axis is negatively correlated with  
256 actual temperature. The more of indigenous forests in a warm environment was cleared than  
257 indigenous forests in a cold environment, as shown by the highest frequency of current forest  
258 in a colder environment (0.5 - 1.0 in temperature axis) than secondary open habitats (0 – 0.5  
259 in temperature axis) (Fig. S1)

260

261 **Figure 2. Climate conditions of forest and non-forest, open areas in New Zealand before**  
262 **and after human settlement.** Forests are shown as green dots and open habitats are shown  
263 as brown dots. Figures show the first two axes of a Principal Component Analysis of four  
264 climate variables (see methods) at 1km grid resolution. The total climate space of New  
265 Zealand is shown in dark grey. Schoener's D values indicate the overlap in climate conditions  
266 between forest and non-forest areas.

267

268 **Figure 3. Climate space of primary and secondary open habitat areas (a) and niches of**  
269 ***Acaena* species in currently occupied primary and secondary open habitat (b).**

270 Schoener's D values indicate the climate niche overlap between species' occurrence records  
271 in primary and secondary open areas. "N" is the total number of 1 km grid cells with *Acaena*  
272 occurrences.

273

274

275 ***Acaena* distributions in primary vs secondary open habitat**

276 There were 9944 occurrence records of the 18 *Acaena* species ranging from 9 to 3892 (see Fig.  
277 S2 for each species' distribution and climatic niche). Species of *Acaena* are commonly open-  
278 habitat species, which was reflected in 68.4 % of all occurrence records of the studied species  
279 being found in currently open habitat and 26.6 % in native forest. Furthermore, the numbers of

280 14 species' occurrence records in open habitats were larger than those in forests (Fig. 4). Of all  
281 occurrence records in open habitats, 46.9 % were found in primary open habitat and 53.0 %  
282 were found in secondary open habitat, indicating that *Acaena* occurrence records distribute  
283 almost equally in primary and secondary open habitats. Of all *Acaena* occurrence records,  
284 54.9% are primary occurrences and 36.3% are secondary occurrences, given that secondary  
285 open habitat drove from the pre-human forest. The proportion of occurrence records in  
286 secondary open habitat for any species excluding *A. minor* with no occurrence records in  
287 primary open habitat ranged from 13% (*A. tesca*) to 92% (*A. juvenca*) with an average of 56%  
288 (Table S3). For eight of the 18 studied species, their proportions of secondary open habitat  
289 occupied were > 50%, indicating that they had more of occurrence records in secondary than  
290 in primary open habitat.

291

292 **Figure 4. Proportion of *Acaena* species occurrence records in open (light grey) and**  
293 **forest (dark grey) habitats.** Species are arranged in descending order of proportions of open  
294 habitat. Black dots indicate the proportion of occurrence records in secondary open habitat.

295 See Table S1 for species name codes.

296

## 297 **Correlates of prevalence in secondary open habitat**

298 **Geography** - Current range size across all habitats showed no correlation with the proportion  
299 of secondary open habitat ( $p = 0.28$ ; Fig. 5a; Table 1).

300 On average over the studied 18 *Acaena* species, availability of secondary open habitat was  
301 6.6% of all secondary open area with the maximum was 35% and the minimum was 0.12%.

302 The availability of secondary open habitat showed no correlation with proportions of  
303 secondary open habitat which species currently occupy ( $p = 0.43$ ; Fig. 5b).

304 Preference for open habitat, the proportion of occurrence records in open habitats to forests  
305 and open habitats, ranged from 0.20 to 1 with an average of 0.77. Species preference for open

306 habitats did not show a significant correlation with the proportion of secondary open habitat  
307 currently occupied ( $p = 0.39$ ). Six species with smaller preferences for open habitats than the

308 average over all the studied species ( $< 0.77$ ) all had high proportions of secondary open

309 habitats ( $> 0.5$ ), indicating that species common in primary forests also tend to get into open

310 habitats. The average of temperature niche medians of four strictly open habitat species,

311 species with  $> 0.95$  preference for open habitats, was 1.24. The average was larger than the

312 average of temperature niche medians over all the other species (0.77), indicating that strictly

313 open habitat species typically occur in a colder environment than the climate in which the

314 species common in forest occur.

315 Over the studied 18 species, the average elevation of all occurrence records was 741 m, the

316 maximum was 1220 m and the minimum was 38 m. Mean elevation of the species occurrence

317 records was unrelated to the proportions of secondary open habitat ( $p = 0.43$ ; Table 1). Mean

318 elevations of species with a high preference for open habitats ( $> 0.75$ ) were generally high

319 (average; 902 m), indicating that species occurring at a high elevation generally were more

320 likely to occur in open habitats.

321

322 **Figure 5. Prevalence of secondary open habitats for *Acaena* species in New Zealand and**  
323 **its relationship with species current range size across all habitats, availability of**  
324 **secondary open habitat adjacent to current *Acaena* species distribution and species'**  
325 **niche volume across all habitats derived from climate parameters. See Table S1 for**  
326 species name codes.

327

328 **Climate** – Compared to primary open habitat, *Acaena* distributions in secondary open habitat  
329 covered larger climate spaces and showed a shift into warmer climates (Fig. 3 b). However,  
330 there was no significant relationship between the species' niche medians on the temperature  
331 nor precipitation axes and the proportion of secondary open habitats currently occupied by  
332 the species (Median of temperature axis;  $p = 0.68$ . Median of precipitation axis;  $p = 0.40$ .  
333 Table S3).

334 Species climatic niche volume across all habitats ranged from 0.05 to 0.40 (mean; 0.21)  
335 (Table S3). Climate niche volume was not significantly correlated with the proportion of  
336 secondary open habitat currently occupied by the species ( $p = 0.25$ ).

337 Over the investigated 18 species, the average niche overlap between primary and secondary  
338 open habitats was low at 0.22, indicating the climates of primary and secondary open habitats  
339 occupied by the species were generally not very similar. The maximum niche overlap  
340 between primary and secondary open habitats was 0.58 (*A. novae zelandiae*) and the  
341 minimum was 0 (*A. microphylla* var. *microphylla*, *A. saccaticupula* and *A. tesca*) (Table S3).

342 Species niche overlap between primary and secondary open habitats was not significantly  
343 related to the proportion of secondary open habitat occupied ( $p = 0.91$ ).

344

345 **Figure 3. Climate space of primary and secondary open habitat areas and niches of**  
346 ***Acaena* species in currently occupied primary and secondary open habitats.** Schoener's  
347 D values indicate the climatic niche overlap between species' occurrence records in primary  
348 and secondary open areas. "N" is the total number of 1 km grid cells with *Acaena*  
349 occurrences.  
350  
351 **Species functional traits** – There was no significant difference in proportions of secondary  
352 open habitat occupied by species among the three different types of functional traits. The mean  
353 of proportions of secondary open habitat over Stoloniferous - Ancistrum species was 62.6%,  
354 the mean over Rhizomatous - Microphyllae species was 46.2% and the mean over species with  
355 the other type was 45.1%  
356



## 357 **Discussion**

358 We investigated the climate conditions of pre-human and current open habitat and the  
359 prevalence of species from an open-habitat genus (*Acaena*) in secondary, i.e. recently opened  
360 habitat. We quantified the relative importance of three sets of factors – geographic features,  
361 species' climatic niches and the species' dispersal traits for the ability of species to utilise  
362 secondary open habitat. Our main findings are; 1) the majority of current open habitat  
363 comprising of primary and secondary open habitat is characterised by warmer climate  
364 conditions than pre-human open habitat. 2) Secondary open habitat is generally warmer than  
365 primary open habitat. 3) The prevalence in secondary open habitat varies among studied  
366 species, however, none of the measures of geographic features, climatic niche and functional  
367 traits was significant predictors of species prevalence in the deforested, secondary open  
368 habitat. Nevertheless, geographical and climatic niche factors showed stronger relationships  
369 with the species' prevalence in secondary open habitat than functional traits associated with  
370 dispersal.

371

## 372 **Pre-human and current distribution of open habitats and the** 373 **current distribution of open habitat plants**

374 Since the first human settlement, c. 60% of the original, pre-human forest habitat, was  
375 transformed to open habitat in New Zealand [31]. Our results showed that the majority of  
376 current open habitats are located in low-lying warm and dry areas, in comparison with the  
377 pre-human open habitats. Pre-human open habitats were restricted to relatively small areas,  
378 mostly in the alpine areas above the natural tree line, in wetlands and riverbeds, in frosted  
379 valley floors or in dry low-lying inland areas, which generally have cold environments [32].  
380 Low-altitude regions with warm climate were especially vulnerable to fire and are often best

381 suited and easily accessed for agricultural conversions in New Zealand and elsewhere that  
382 deforestation happens (e.g. tropical forest [33, 34] and Latin America [35]). Therefore, open  
383 habitats in the world should have experienced the climatic shift to warmer conditions due to  
384 human activity.

385

## 386 **The relative importance of factors driving prevalence for** 387 **secondary open habitat**

### 388 **Geography**

#### 389 1. Current range size across all habitats

390 Current range size across all habitats of *Acaena* species did not show significant correlation  
391 with the proportion of secondary open habitat occupied. Range limits can be set by climate,  
392 topography, soils and biotic interaction [36]. The factors controlling the current range limit of  
393 *Acaena* in secondary habitat are likely different from those in pre-human open habitats. It is  
394 likely that pre-human open-habitats reflected very limited climate space as they were  
395 restricted to alpine area where trees did not naturally occur [32], therefore climate of pre-  
396 human open habitat could have been insufficient for some species to realize their potential  
397 climatic niche fully, indicating that competition with forest trees was the main driver of open-  
398 habitat plant distributions in pre-human time. However, current drivers appear to vary  
399 depending on species, because the environments in secondary open habitats have broadened  
400 due to anthropogenic forest clearances, and therefore, currently available climate conditions  
401 allow open-habitat plants to obtain more of their potential climatic niche than those which  
402 they occupied before the forest clearance.

#### 403 2. Availability of secondary open habitat

404 When new habitat becomes available for colonisation, species whose primary occurrences  
405 have more of the new habitats nearby can have advantages for expansion of their distribution  
406 into the new habitats [37]. The positive influence of historical habitat availability on  
407 grassland species richness was found in Estonian islands [38] and wood cricket populations  
408 in the UK were mainly found in woodland fragments situated closely to another occupied site  
409 [39]. However, the positive influence of habitat availability on species re-distribution was not  
410 supported by our study, in which the availability of secondary open habitat was unrelated to  
411 the proportion of secondary open habitat occupied by the species (Fig. 5b). Our method to  
412 quantify the availability of secondary open habitat did not consider possible dispersal  
413 distance (1 – 1500 m from parent plants [40]) and geographical barriers, e.g. high mountains  
414 and glacier. Glaciers worked as barriers for habitat expansion of arctic-alpine plants from the  
415 Last Glacial Maximum to date [41]. Dispersal ability is discussed further in “Species  
416 functional traits”.

### 417 3. Habitat characteristics

418 Characteristics of current habitats can explain prevalence in specific habitats. Although  
419 *Acaena* species are generally open-habitat species, some species can occur within forests and  
420 in edge habitats between forests and open habitat (e.g. *A. anserinifolia*) [17]. In terms of their  
421 current distribution, species with a high preference for open habitats seem to be restricted in  
422 more open habitats (e.g. grasslands), while species with a low preference for open habitats  
423 tend to occur in less open habitat (e.g. shrublands) frequently (Fig. S3). Both grasslands and  
424 shrublands were considered open habitats in our study, however, they have different levels of  
425 openness. Species with a low preference for open habitat should be shade-tolerant, indicating  
426 that the species would survive in less open habitat.

427 In general, species occurring mainly at higher elevations occupy smaller areas of secondary  
428 open habitat, which was indicated by the negative relationship between means of elevation of

429 current range and proportions of secondary open habitat (Table 1). This appears to represent  
430 specialisation to colder conditions, and therefore, indicates more restrictions on the species  
431 expansion into secondary open habitats. For instance, species whose primary habitat was  
432 restricted to the alpine/montane area and/or colder regions showed very small proportions of  
433 secondary open habitat (e.g. *A. saccaticupula* and *A. tesca*).

#### 434 **Environmental space**

435 Species with larger climatic niche volumes did not have significantly greater occupancy in  
436 secondary open habitats (Table 1). This result is against the idea that niche breadths predict  
437 geographical range size [42]. However, temperature niches of *Acaena* species were generally  
438 a better predictor of species geographical range expansion than precipitation. Species that  
439 mostly occur in cold primary open area ( $> 0$  of temperature axis) tend to occupy a small  
440 proportion of secondary open habitat (e.g. *A. saccaticupula* and *A. tesca*). Deforestation in  
441 New Zealand expanded substantial open habitats in warmer climates, however, had small  
442 impacts on extending the availability of these habitats across rainfall gradients.

#### 443 **Species functional traits**

444 Functional traits associated with regeneration and dispersal are critical for establishing  
445 populations in new habitats [40]. Laanisto, Sammuli [43] showed a strong relationship  
446 between distribution change and functional traits across 736 species in diverse genera. Barb-  
447 spined *Acaena* species (species in *Ancistrum* section) generally showed broad geographical  
448 ranges and habitat distributions (Fig. S2) and have higher adherence to animals than barb-less  
449 species [44, 45]. However, life form and dispersal ability of *Acaena* did not show any  
450 relationships with species prevalence of secondary habitats. This result supports Lloyd, Lee  
451 [46] showing no consistent trait differences between common and rare species and could be  
452 attributed to far greater dispersal efficiency following the human arrival with the introduction  
453 of many small mammals, stock, particularly sheep and cattle, and granivorous birds [47]. The

454 difference of dispersal ability tested in our study was just an improvement of an adhesive  
455 feature of seeds to animals, which does not change dispersal types. In addition, the frequent  
456 occurrences of *Acaena* beside roads and tracks reported by Lloyd, Lee [46] indicate that  
457 human transport has established novel pathways for the spread of *Acaena*, as well as for alien  
458 species all over the world [48].

## 459 **Mechanism of realized niche change**

460 Some of *Acaena* species have obtained new climatic niche with obtaining secondary open  
461 habitat. There are two possible mechanisms of how *Acaena* obtained new climatic niche:

462 1) Niche evolution; species of *Acaena* from forest and primary open habitats adapted to the  
463 new habitats created by deforestation, expanding environmental tolerance and range.

464 2) Competitive release; species of *Acaena* were released from the competition with forest  
465 plant species, which triggered the expansion of *Acaena* distribution into newly opened  
466 habitats.

### 467 1. Niche evolution

468 Niche conservatism constrains the environmental expansion and diversification of species  
469 because of inherent restrictions in adaptive plasticity [49]. However, niche evolution along  
470 specific climatic parameters is poorly understood. The evolution rates of potential  
471 environmental niches appear variable. Petitpierre, Kueffer [50] showed that change of  
472 climatic niche through emigration into new habitats is uncommon for terrestrial plants and  
473 Wasof, Lenoir [51] showed that niche can be conserved up to  $10^4$  years. On the other hand,  
474 Early and Sax [52] showed that a large proportion of species' naturalized distributions  
475 occurred outside the climatic conditions occupied in their native ranges.

### 476 2. Competitive release

477 Change of land cover can have drastic and rapid effects on species distribution. Realized  
478 environmental niche can change on the change of non-climatic factors [e.g. species traits and  
479 land use; 53, 54, 55], if they play a strong role in limiting species' native distributions. Land  
480 cover change can destroy habitats of some species, however, it can let other species to shift  
481 their habitat into new habitats by releasing them from competitions. Species expansion  
482 through release from competition has been found in animals where a reduced predator  
483 community contributed to modern fishers' range expansion [56]. The competitive release is a  
484 more realistic mechanism for the change in species prevalence in open habitat than the  
485 evolution of *Acaena* species' climatic niche, because evolutionary processes of adaptations to  
486 new environments generally take a long time.

487 Although some species traits can change in a shorter period (e.g. change of timing of  
488 phenological events as the reaction to climate change [57]), evolutionary change of species  
489 traits (e.g. morphological change) generally requires significantly more time. Therefore, the  
490 time since when *Acaena* species have obtained their new climatic niche (c. 800 years)  
491 appears too short for them to evolve their climatic niches.

492 The response of *Acaena* species to new habitats and climates in our study suggests that  
493 species will exhibit varying distributional shifts as the climate warms. The most vulnerable  
494 *Acaena* species would be those restricted to colder montane/alpine habitats, where  
495 physiological specialisation can restrict options in a warming world. This indicates that  
496 global warming could lead to habitat loss and elevational range shifts of species restricted to  
497 colder montane/alpine habitats as the upward elevational range shifts which have been  
498 reported globally [58, 59].

## 499 **Limitations**

500 Our study is based on the land cover data on 1 km grid resolution which can be too coarse  
501 scale for measuring ecological processes. Moreover, a single land cover class was assigned to  
502 each grid, homogenising any fine-scale habitat diversity.

503 Plant response to environmental change can take decades or longer [60]. However, it is likely  
504 that the herbaceous studied species have attained equilibrium with the new climate regime  
505 after 800 years from the human arrival, because this time frame is much longer than lags in  
506 climate response reported in other studies [e.g. 40, 59, 61, 62]

507

## 508 **Conclusions**

509 Land cover change is a key component of global environmental change driving the  
510 redistribution of species as a consequence of human activity. Change from closed forest to  
511 open habitat is a typical feature of anthropogenic environmental change providing new and  
512 more area suitable for open-habitat species. The climate conditions of current open habitats in  
513 New Zealand are warmer than pre-human times, because forests in warm lowland were  
514 cleared for hunting and agricultural purposes. Thus, anthropogenic activity has opened new  
515 parts of the available climate space for open-habitat species. Our result suggested that open-  
516 habitat species could have occupied only parts of their potential climate space at the LGM,  
517 because they were kept out of climatically suitable areas through competition with trees.

518 Whereas at the present, open-habitat species possibly occupy larger parts of their  
519 climatically-suitable areas than those at the LGM because these areas have been made tree-  
520 free by humans. We found that overall geographical and environmental factors were more  
521 important than species functional traits for potentially facilitating expansion into secondary  
522 habitats.

523

## 524 **Acknowledgements**

525 We thank J.B. Steel for species observation data and occurrence records.

526

527

528



## References

1. Elith J, Kearney M, Phillips S. The art of modelling range-shifting species. *Methods in Ecology and Evolution*. 2010;1(4):330-42.
2. Watson JEM, Shanahan DF, Di Marco M, Allan J, Laurance WF, Sanderson EW, et al. Catastrophic Declines in Wilderness Areas Undermine Global Environment Targets. *Curr Biol*. 2016;26(21):2929-34.
3. Barlow J, Gardner TA, Araujo IS, Avila-Pires TC, Bonaldo AB, Costa JE, et al. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*. 2007;104(47):18555-60.
4. Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, et al. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*. 2011;478(7369):378-+.
5. Newbold T, Hudson LN, Arnell AP, Contu S, De Palma A, Ferrier S, et al. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science*. 2016;353(6296):288-91.
6. Guo FY, Lenoir J, Bonebrake TC. Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications*. 2018;9.
7. Keeley JE. Native American impacts on fire regimes of the California coastal ranges. *J Biogeogr*. 2002;29(3):303-20.
8. Kaplan JO, Krumhardt KM, Zimmermann N. The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews*. 2009;28(27–28):3016-34.
9. Ewers RM, Kliskey AD, Walker S, Rutledge D, Harding JS, Didham RK. Past and future trajectories of forest loss in New Zealand. *Biol Conserv*. 2006;133(3):312-25.
10. Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, et al. High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*. 2013;342(6160):850-3.
11. Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, et al. The importance of land-use legacies to ecology and conservation. *Bioscience*. 2003;53(1):77-88.
12. Ewers RM, Didham RK, Pearse WD, Lefebvre V, Rosa IMD, Carreiras JMB, et al. Using landscape history to predict biodiversity patterns in fragmented landscapes. *Ecol Lett*. 2013;16(10):1221-33.
13. Thuiller W, Gueguen M, Georges D, Bonet R, Chalmandrier L, Garraud L, et al. Are different facets of plant diversity well protected against climate and land cover changes? A test study in the French Alps. *Ecography*. 2014;37(12):1254-66.
14. Brown KA, Parks KE, Bethell CA, Johnson SE, Mulligan M. Predicting Plant Diversity Patterns in Madagascar: Understanding the Effects of Climate and Land Cover Change in a Biodiversity Hotspot. *Plos One*. 2015;10(4).
15. Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, et al. Global consequences of land use. *Science*. 2005;309(5734):570-4.
16. Mosher ES, Silander JA, Latimer AM. The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. *Biol Invasions*. 2009;11(10):2317-28.
17. Lee WG, Macmillan BH, Partridge TR, Lister R, Lloyd KM. Fruit features in relation to the ecology and distribution of *Acaena* (Rosaceae) species in New Zealand. *N Z J Ecol*. 2001;25(1):17-27.
18. Bitter G. Die Gattung *Acaena*. Vorstudien zu einer Monographie. Stuttgart, Germany: E. Schweizerbart; 1910. 1-336 p.
19. Grondona E. Las especies argentinas del género *Acaena* (Rosaceae) 1964. 209-342 p.
20. Webb CJ, Sykes WR, Garnock-Jones PJ. Flora of New Zealand. Christchurch, New Zealand: Botany Division, Department of Scientific and Industrial Research; 1988.
21. Leathwick J, McGlone M, Walker S. NEW ZEALAND'S POTENTIAL VEGETATION PATTERN. 2004.

22. Landcare Research Informatics team. LCDB v4.1 - Land Cover Database version 4.1, Mainland New Zealand. 4.1 ed2015.
23. Columbus J. An assessment of fractal interpolation for deriving Digital Elevation Models (DEM): University of Otago; 2011.
24. Environmental Systems Research Institute. ArcGIS Desktop: Release 10.2. 2013.
25. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol*. 2005;25(15):1965-78.
26. Pearson RG, Dawson TP. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob Ecol Biogeogr*. 2003;12(5):361-71.
27. Venables WN, Ripley BD. *Modern applied statistics with S*. Springer-Verlag; 2002.
28. R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing; 2016.
29. Schoener TW. NONSYNCHRONOUS SPATIAL OVERLAP OF LIZARDS IN PATCHY HABITATS. *Ecology*. 1970;51(3):408-18.
30. Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, et al. Measuring ecological niche overlap from occurrence and spatial environmental data. *Glob Ecol Biogeogr*. 2012;21(4):481-97.
31. McWethy DB, Wilmshurst JM, Whitlock C, Wood JR, McGlone MS. A High-Resolution Chronology of Rapid Forest Transitions following Polynesian Arrival in New Zealand. *Plos One*. 2014;9(11):9.
32. Perry GLW, Wilmshurst JM, McGlone MS. Ecology and long-term history of fire in New Zealand. *N Z J Ecol*. 2014;38(2):157-76.
33. Curran LM, Trigg SN, McDonald AK, Astiani D, Hardiono YM, Siregar P, et al. Lowland forest loss in protected areas of Indonesian Borneo. *Science*. 2004;303(5660):1000-3.
34. Lawton RO, Nair US, Pielke RA, Welch RM. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science*. 2001;294(5542):584-7.
35. Dirzo R, Garcia MC. RATES OF DEFORESTATION IN LOS-TUXTLAS, A NEOTROPICAL AREA IN SOUTHEAST MEXICO. *Conserv Biol*. 1992;6(1):84-90.
36. Pearson RG, Stanton JC, Shoemaker KT, Aiello-Lammens ME, Ersts PJ, Horning N, et al. Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*. 2014;4(3):217-21.
37. Holbrook SJ, Forrester GE, Schmitt RJ. Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia*. 2000;122(1):109-20.
38. Gazol A, Tamme R, Takkis K, Kasari L, Saar L, Helm A, et al. Landscape- and small-scale determinants of grassland species diversity: direct and indirect influences. *Ecography*. 2012;35(10):944-51.
39. Brouwers NC, Newton AC. The influence of habitat availability and landscape structure on the distribution of wood cricket (*Nemobius sylvestris*) on the Isle of Wight, UK. *Landscape Ecology*. 2009;24(2):199-212.
40. Corlett RT, Westcott DA. Will plant movements keep up with climate change? *Trends Ecol Evol*. 2013;28(8):482-8.
41. Eidesen PB, Ehrich D, Bakkestuen V, Alsos IG, Gilg O, Taberlet P, et al. Genetic roadmap of the Arctic: plant dispersal highways, traffic barriers and capitals of diversity. *New Phytologist*. 2013;200(3):898-910.
42. Slatyer RA, Hirst M, Sexton JP. Niche breadth predicts geographical range size: a general ecological pattern. *Ecol Lett*. 2013;16(8):1104-14.
43. Laanisto L, Sammuli M, Kull T, Macek P, Hutchings MJ. Trait-based analysis of decline in plant species ranges during the 20th century: a regional comparison between the UK and Estonia. *Glob Change Biol*. 2015;21(7):2726-38.
44. Shmida A, Ellner S. SEED DISPERSAL ON PASTORAL GRAZERS IN OPEN MEDITERRANEAN CHAPARRAL, ISRAEL. *Israel Journal of Botany*. 1983;32(3):147-59.

45. Carlquist S, Pauly Q. EXPERIMENTAL STUDIES ON EPIZOOCHOROUS DISPERSAL IN CALIFORNIAN USA PLANTS. *Aliso*. 1985;11(2):167-78.
46. Lloyd KM, Lee WG, Wilson JB. Growth and reproduction of New Zealand *Acaena* (Rosaceae) species in relation to rarity and commonness. *N Z J Ecol*. 2002;26(2):149-60.
47. Walker S, Wilson DJ, Norbury G, Monks A, Tanentzap AJ. Effects of secondary shrublands on bird, lizard and invertebrate faunas in a dryland landscape. *N Z J Ecol*. 2014;38(2):242-56.
48. Hulme PE. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*. 2009;46(1):10-8.
49. Martiny AC, Treseder K, Pusch G. Phylogenetic conservatism of functional traits in microorganisms. *Isme Journal*. 2013;7(4):830-8.
50. Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A. Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders. *Science*. 2012;335(6074):1344-8.
51. Wasof S, Lenoir J, Aarrestad PA, Alsos IG, Armbruster WS, Austrheim G, et al. Disjunct populations of European vascular plant species keep the same climatic niches. *Glob Ecol Biogeogr*. 2015;24(12):1401-12.
52. Early R, Sax DF. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Glob Ecol Biogeogr*. 2014;23(12):1356-65.
53. Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, et al. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews*. 2013;88(1):15-30.
54. Luoto M, Virkkala R, Heikkinen RK. The role of land cover in bioclimatic models depends on spatial resolution. *Glob Ecol Biogeogr*. 2007;16(1):34-42.
55. Van der Veken S, Bellemare J, Verheyen K, Hermy M. Life-history traits are correlated with geographical distribution patterns of western European forest herb species. *J Biogeogr*. 2007;34(10):1723-35.
56. LaPoint SD, Belant JL, Kays RW. Mesopredator release facilitates range expansion in fisher. *Animal Conservation*. 2015;18(1):50-61.
57. Ibanez I, Primack RB, Miller-Rushing AJ, Ellwood E, Higuchi H, Lee SD, et al. Forecasting phenology under global warming. *Philos Trans R Soc B-Biol Sci*. 2010;365(1555):3247-60.
58. Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H. A significant upward shift in plant species optimum elevation during the 20th century. *Science*. 2008;320(5884):1768-71.
59. Chen IC, Hill JK, Ohlemuller R, Roy DB, Thomas CD. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*. 2011;333(6045):1024-6.
60. Harrison SP, Goni MFS. Global patterns of vegetation response to millennial-scale variability and rapid climate change during the last glacial period. *Quaternary Science Reviews*. 2010;29(21-22):2957-80.
61. Ash JD, Givnish TJ, Waller DM. Tracking lags in historical plant species' shifts in relation to regional climate change. *Glob Change Biol*. 2017;23(3):1305-15.
62. Bertrand R, Lenoir J, Piedallu C, Riofrio-Dillon G, de Ruffray P, Vidal C, et al. Changes in plant community composition lag behind climate warming in lowland forests. *Nature*. 2011;479(7374):517-20.

## Supporting information

**Figure S1. Climate space of forest (green) and secondary open habitats (blue) in New Zealand after human settlement.** All the figures show climate space of New Zealand as darker grey background. Climate space of native forests (top left) and open habitat (bottom left) areas are shown respectively. The centre figures show climate space of the two habitats together. The histograms on the right side show numbers of 1 km grid cells along temperature (top) and precipitation (right) axes.

**Figure S2. Maps and climate space of primary (blue) and secondary (red) occurrences of *Acaena* species.** “N” in the legend of maps shows the number of occurrences in primary and secondary open area. The total climate space of New Zealand is shown in dark grey.

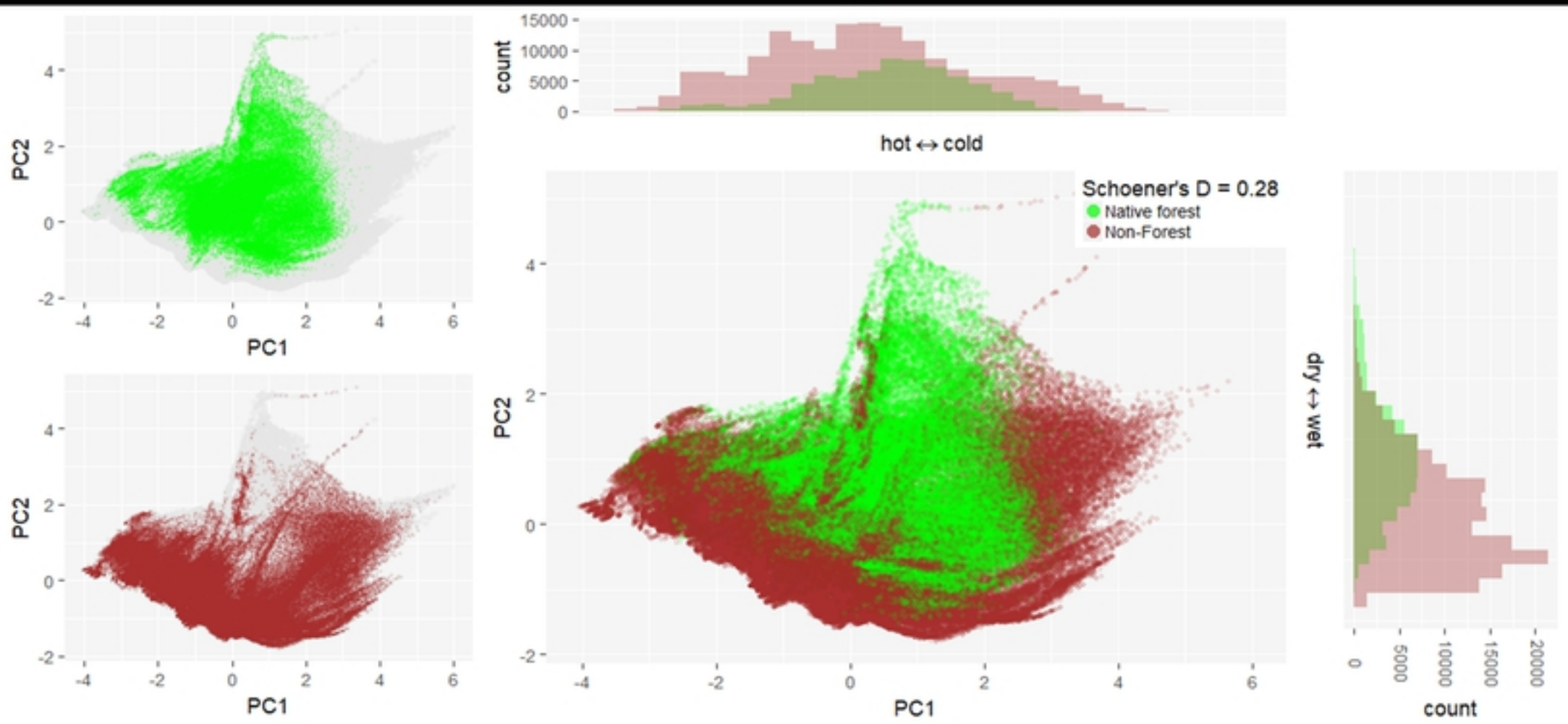
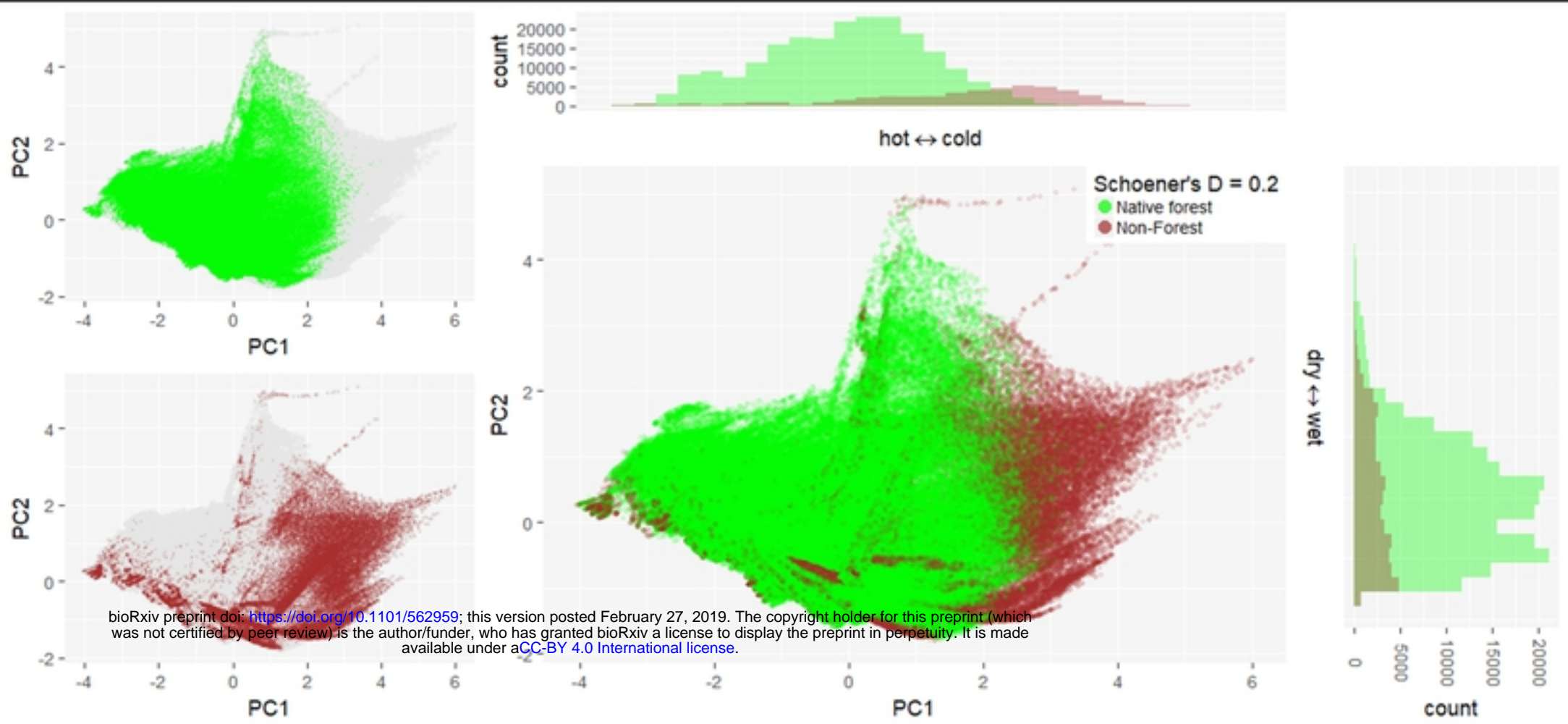
**Figure S3. Proportion of *Acaena* species occurrences in LCDB land cover classes and proportion of secondary open habitat.** LCDB land cover classes were coloured by a habitat type and levels of openness; open habitat with low openness (blue gradient colours), open habitat with high openness (yellow gradient colours) and forests (green gradient colours). Black points on bars show species’ proportion of secondary open habitat. Proportion of secondary open habitat for *A.minor* (“MIN” in the figure) is 1 due to no occurrence records in primary open habitat. Bars were sorted in descending order of preference for open habitat. Species name codes are shown in Table S1.

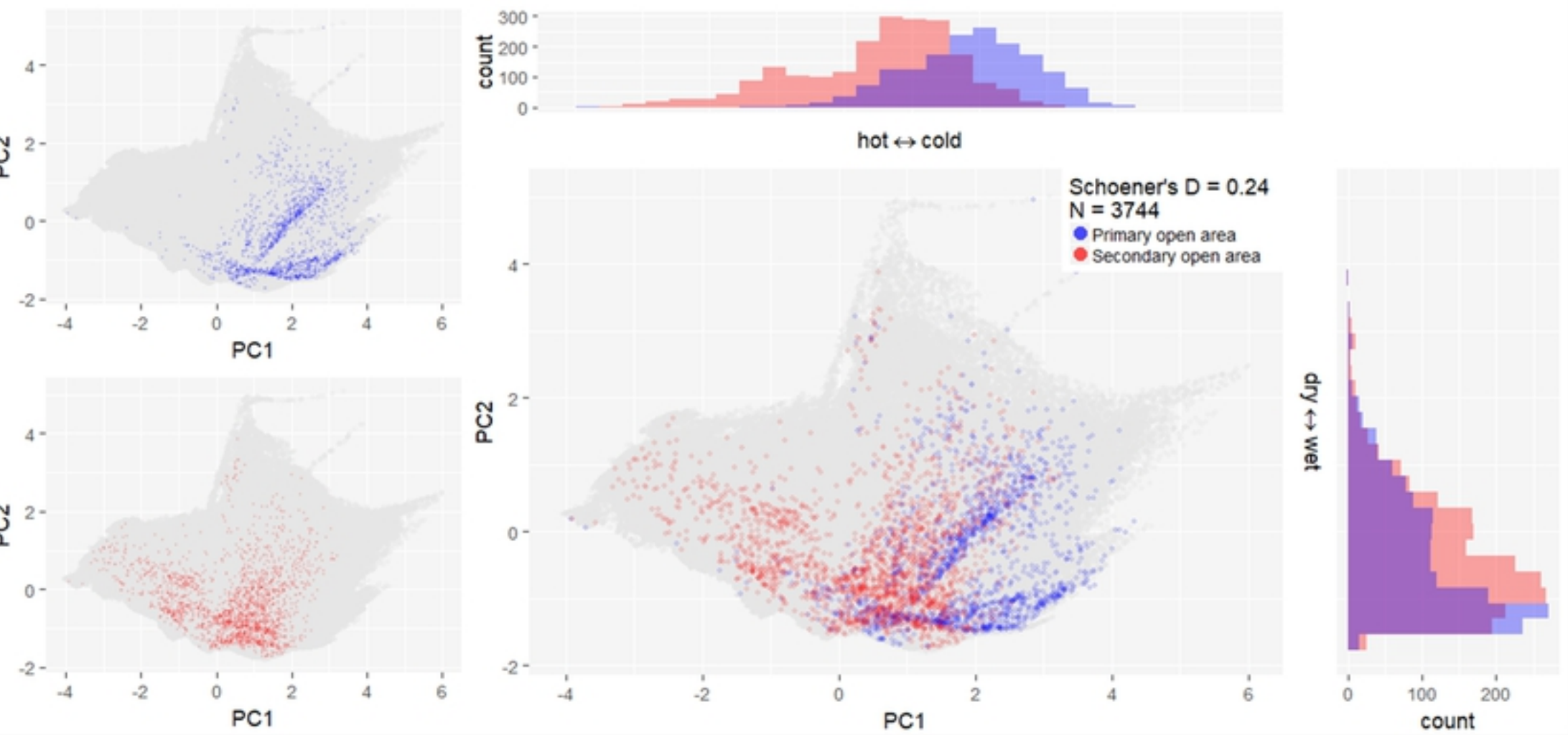
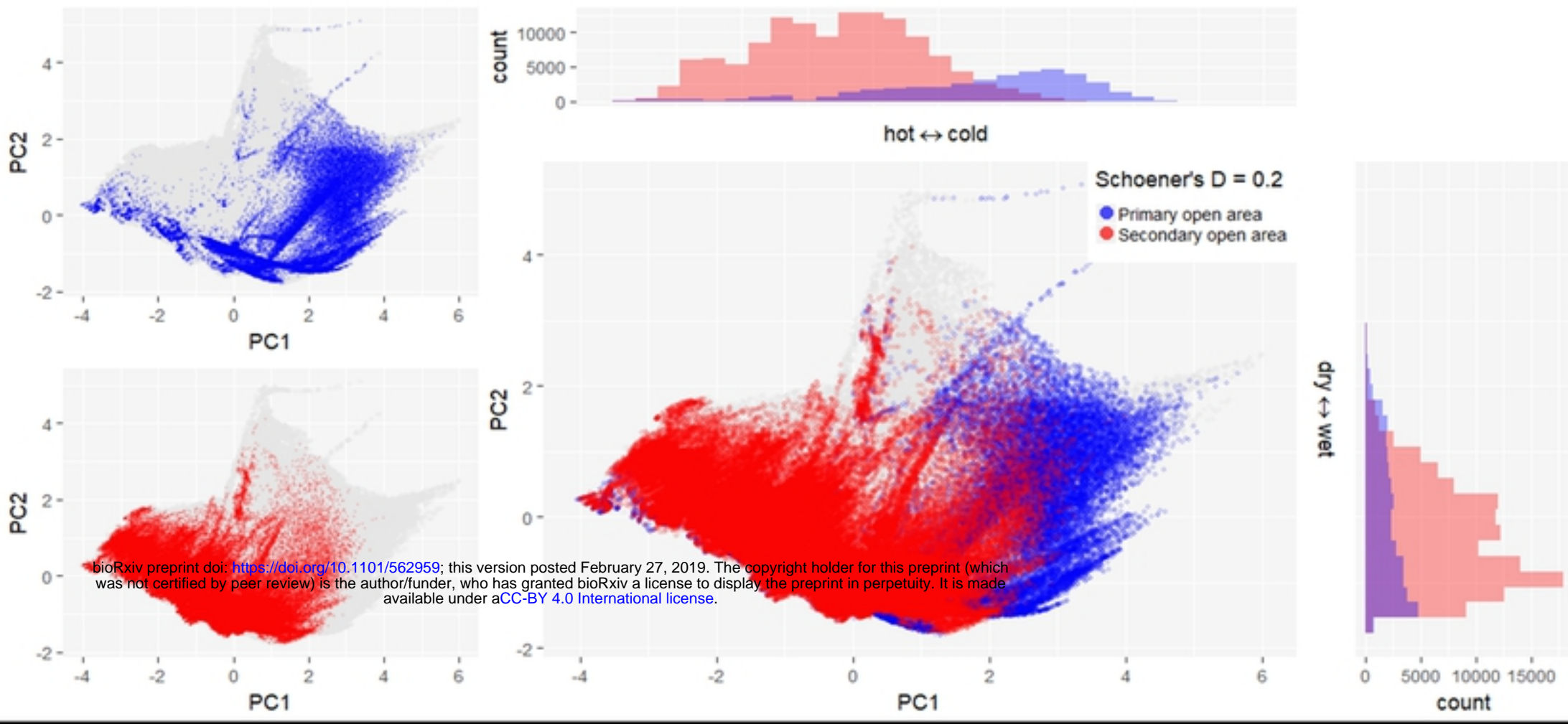
**Table S1. List of species and their number of occurrence records and habitats.**

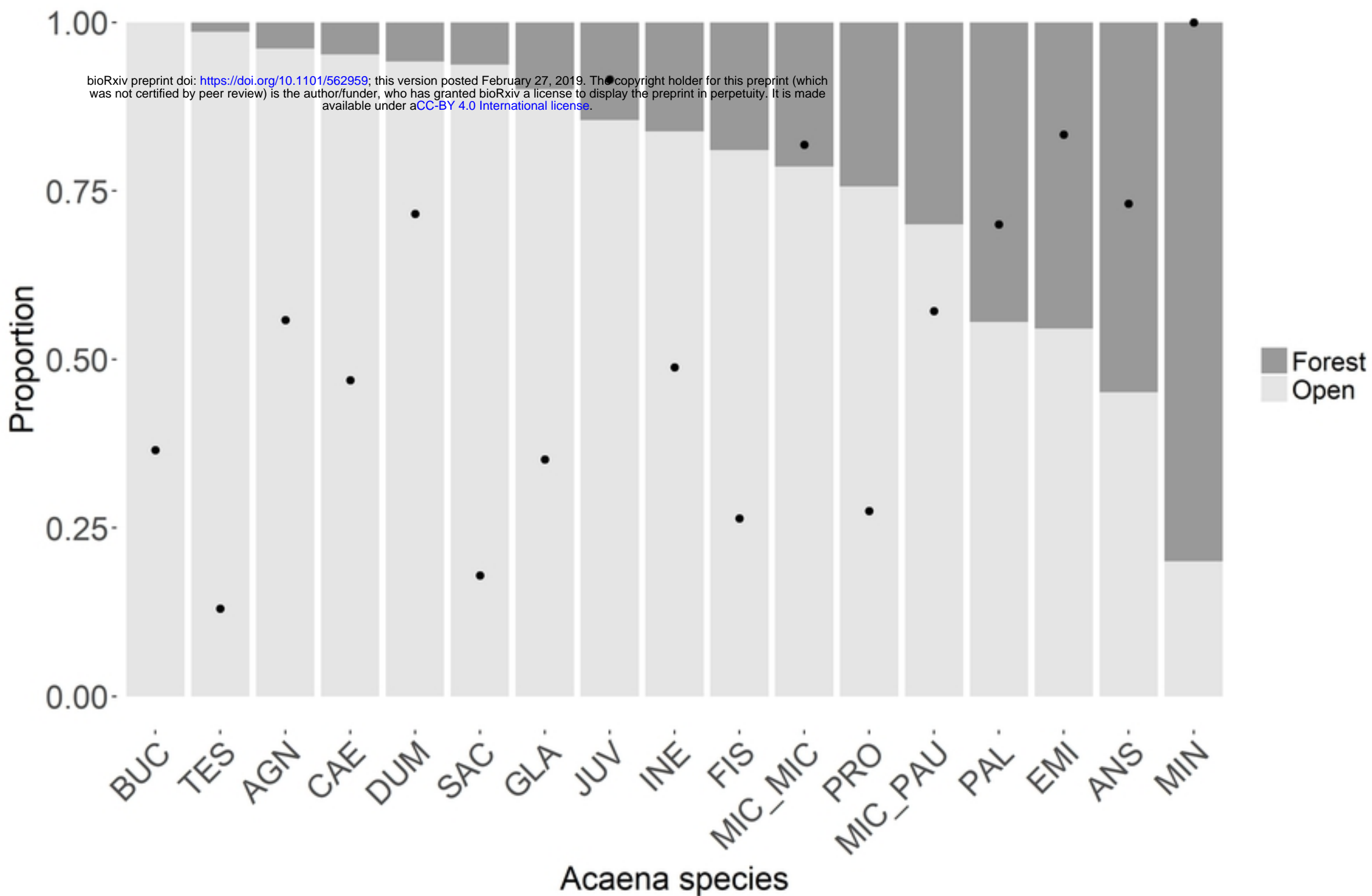
**Table S2. List of land cover classes in original pre-human and current land cover data and classes after conversion to 1 km grid cell data.**

**Table S3. List of analyzed variables; proportion of secondary open habitat and 9 environmental predictors.** SO: Proportion of secondary open habitat, the number of secondary open occurrence records divided by the number of primary and secondary open occurrence records. Niche overlap; values of Schoener’s D showing climate niche overlap between primary open occurrence records and secondary open occurrence records

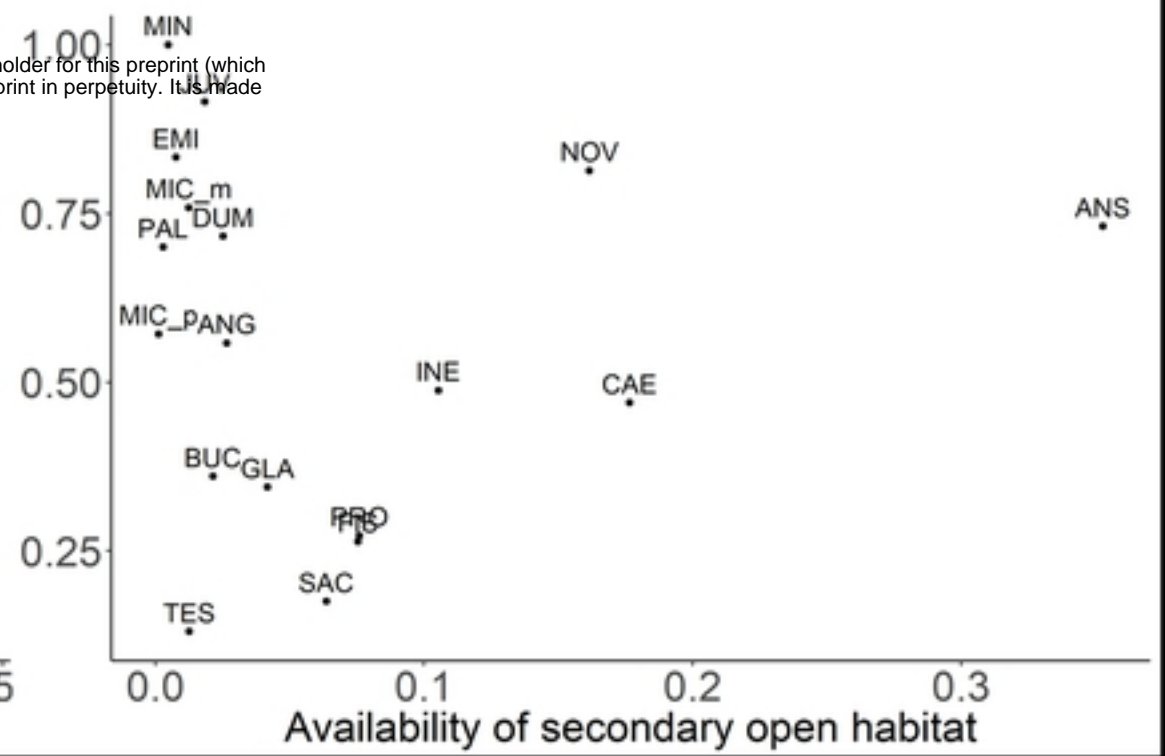
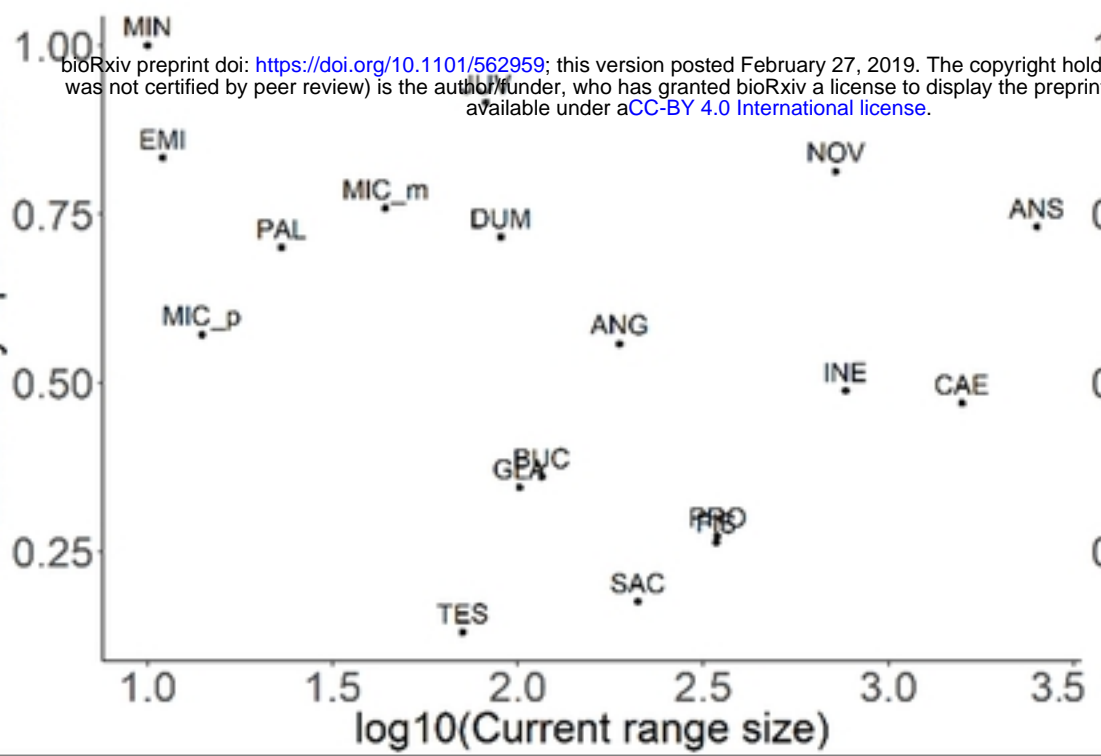
**Reference list of surveys and reports**



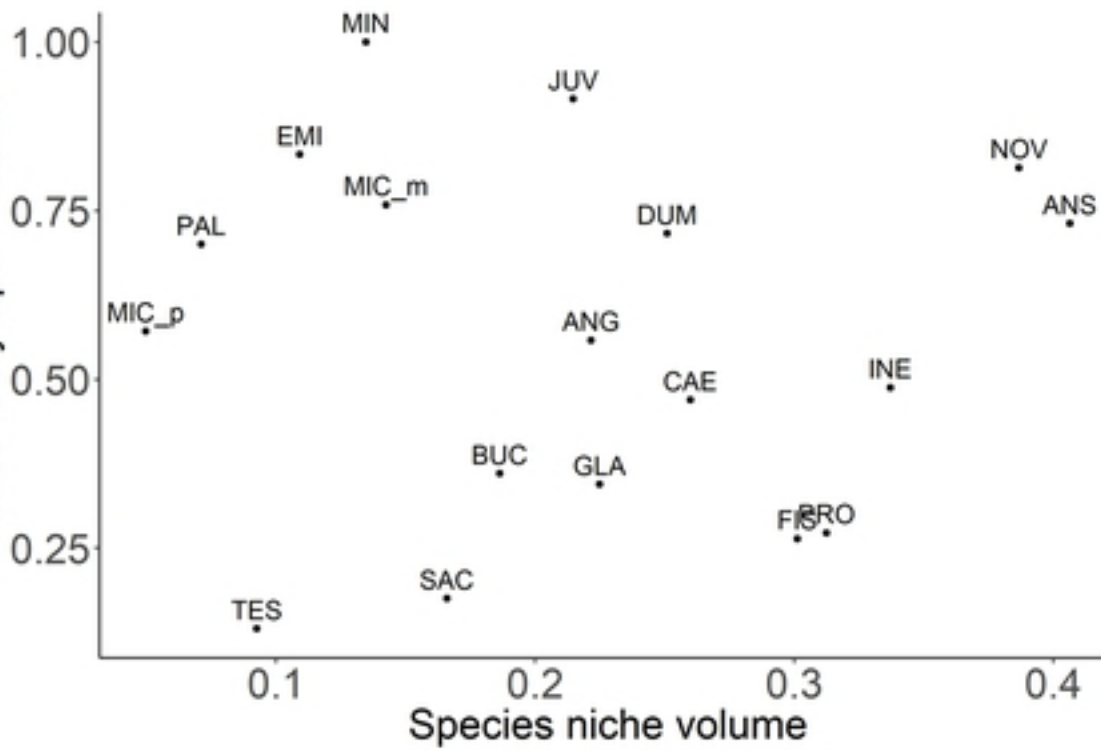




Proportion of occurrence records  
in secondary open habitat



Proportion of occurrence records  
in secondary open habitat





bioRxiv preprint doi: <https://doi.org/10.1101/32959>; this version posted February 27, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

