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3 **Reconstructing geographical parthenogenesis: effects of niche differentiation and**  
4 **reproductive mode on Holocene range expansion of an alpine plant**

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60

61 **ABSTRACT**

62 Asexual taxa often have larger ranges than their sexual ancestors, particularly in areas  
63 affected by Pleistocene glaciations. The reasons of this 'geographical parthenogenesis' are  
64 contentious, with expansion of the ecological niche or colonization advantages of  
65 uniparental reproduction assumed most important in case of plants. Here, we parameterized  
66 a spread model for the alpine buttercup *Ranunculus kuepferi* and reconstructed the joint  
67 Holocene range expansion of its sexual and apomictic cytotype across the European Alps  
68 under different simulation settings. We found that, rather than niche broadening or a higher  
69 migration rate, a shift of the apomict's niche towards colder conditions *per se* was crucial as  
70 it facilitated overcoming of topographical barriers, a factor likely relevant for many alpine  
71 apomicts. More generally, our simulations suggest potentially strong interacting effects of  
72 niche differentiation and reproductive modes on range formation of related sexual and  
73 asexual taxa arising from their differential sensitivity to minority cytotype disadvantage.

74

## 75 INTRODUCTION

76 Asexual species often occupy larger geographical ranges than their sexual relatives and  
77 extend farther towards cold environments (e.g. Bierzychudek 1985; van Dijk 2003; Lowry &  
78 Lester 2006; Randle *et al.* 2009). This long-recognized phenomenon has been coined  
79 'geographical parthenogenesis' (Vandel 1928) and is puzzling because it suggests an  
80 advantage of asexuality that is at odds with the prevalence of sexual reproduction in animals  
81 and plants (Maynard Smith 1978; Kearney 2003; Schaefer *et al.* 2006). The processes  
82 underlying this biogeographic peculiarity are still contentious (e.g. Kearney 2005; Hörandl  
83 2006, 2011). In plants, where asexual reproduction via seeds is called apomixis, two  
84 processes have been emphasized as particularly crucial to explain the success of apomictic  
85 lineages (Hörandl 2006): (i) a broadening of the ecological niche, and (ii) uniparental  
86 reproduction.

87 In flowering plants, a switch to apomixis is commonly associated with the formation of  
88 polyploid cytotypes (Comai 2005). As niche differentiation has long been considered  
89 prerequisite to the establishment of polyploids (Levin 1975, 2003), apomictic (polyploid) taxa  
90 are expected to have environmental tolerances or requirements that are distinct from those  
91 of their diploid and sexual ancestors. In particular, their niches may not only differ but also  
92 be wider than those of the ancestral species because, first, polyploidization is often  
93 associated with a gain of genotypic diversity and genome flexibility (Comai 2005; Kearney  
94 2005), and, second, recurrent establishment of asexual cytotypes from the same parent  
95 species can generate a swarm of ecologically distinct genotypes protected against erosion by  
96 gene flow (Frozen Niche Variation Model, Vrijenhoek 1984, 1994; Peck *et al.* 1998;  
97 Vrijenhoek & Parker 2009). However, this view has been challenged by recent studies  
98 suggesting that neither shifts of niche optima nor a broadening of the niche necessarily

99 accompany the establishment of polyploid cytotypes (Theodoridis *et al.* 2013; Glennon *et al.*  
100 2014; Kirchheimer *et al.* 2016).

101 An alternative line of reasoning for explaining geographical parthenogenesis focuses on the  
102 colonizing advantages of uniparental reproduction: asexuality involves independence of  
103 mating partners. As a consequence, a long-distance dispersal event for a single propagule is  
104 theoretically sufficient for the foundation of a new population ahead of a migrating front,  
105 causing Allee effects to be less influential in slowing range expansion (Baker's law, Stebbins  
106 1950; Baker 1967). Indeed, self-fertility has recently been shown to increase range size  
107 across a number of plant families (Grossenbacher *et al.* 2015). Apomictic plant species are  
108 self-fertile, but usually evolve from self-incompatible diploid outcrossers (Hörandl 2010).  
109 Thus, uniparentally reproducing apomicts commonly have biparentally reproducing sexual  
110 relatives making Baker's law a plausible mechanism for the emergence of geographical  
111 parthenogenesis.

112 The pros and cons of explaining geographical parthenogenesis by these two underlying  
113 ecological processes have been discussed in several reviews (Kearney 2005; Hörandl 2006;  
114 Hörandl *et al.* 2008; Morgan-Richards *et al.* 2010). In particular, Hörandl (2006) concluded  
115 that causality is probably complex and that determinants may interact with each other and  
116 with the environment. However, these considerations remain largely speculative. What is  
117 lacking so far is a study that explicitly evaluates the relative contribution of the two  
118 processes and their possible interaction to the emergence of range size differences in a  
119 particular pair or group of plant species.

120 Here, we undertake such an attempt based on simulations of the Holocene range dynamics  
121 of a diploid sexual plant and its tetraploid and apomictic relative. We focus on *Ranunculus*  
122 *kuepferi* Greuter & Burdet, an alpine buttercup with pronounced geographical

123 parthenogenesis in the European Alps (Cosendai *et al.* 2013): diploid populations are  
124 restricted to the southwestern fringes of the Alps while tetraploid populations extend over  
125 nearly the entire Alpine chain (see Fig. 1). In a previous study, we found evidence that  
126 tetraploids have niche optima that shifted towards colder conditions whereas their niche  
127 breadth decreased rather than increased as compared to diploids (Kirchheimer *et al.* 2016).  
128 Here, we use a spatially and temporarily explicit plant spread model to simulate the  
129 Holocene range expansion of both cytotypes from their putative glacial refugia. The model is  
130 based on empirical measurements of parameters and a reconstruction of the study area's  
131 Holocene climatic history and treeline fluctuations. For the simulations, we switch the  
132 cytotypes' ecological niches and reproductive modes in a factorial design and account for  
133 possible minority cytotype disadvantages (Levin 1975) where populations occur in sympatry.  
134 This simulation experiment allows evaluating the relative importance of niche differentiation  
135 or uniparental reproduction in determining the pronounced range size difference between  
136 cytotypes and how these processes interacted with each other and with the changing  
137 environment.

138

## 139 **MATERIAL AND METHODS**

### 140 ***Species***

141 *Ranunculus kuepferi* is a small, perennial herb growing in various types of grasslands at  
142 elevations between 1300 – 2800 m. The white flowers are insect-pollinated and produce c. 5  
143 – 30 achenes, which serve as diaspores (Müller-Schneider 1986). For more details on species  
144 traits see Table S1 in Supporting Information.

145 Diploid populations of *R. kuepferi* have survived the Last Glacial Maximum (LGM) in spatially  
146 scattered sites at the south-western fringes of the European Alps (Burnier *et al.* 2009).

147 Molecular data suggested that the tetraploid cytotype has most likely emerged from  
148 repeated autopolyploidization (Cosendai *et al.* 2011; Cosendai *et al.* 2013). Here we  
149 conducted a molecular dating showing that tetraploids originated during the Late  
150 Pleistocene or the early Holocene, while diploids are much older (see Appendix S1 and Fig.  
151 S1).

152 While diploids are predominantly sexual outcrossers, tetraploids mainly reproduce by  
153 pseudogamous apomixis. Rare cases of apomictic diploids have been documented and  
154 tetraploids are, in principle, capable of sexual seed production (Schinkel *et al.* 2016; Schinkel  
155 *et al.* 2017). Nevertheless, diploid asexual and tetraploid sexual populations have never been  
156 observed in the field. Some populations in the restricted geographical contact zone are  
157 mixed and triploid as well as pentaploid individuals occur (Cosendai & Hörandl 2010;  
158 Schinkel *et al.* 2016).

### 159 **Study area**

160 We simulated the post-glacial re-colonization of the European Alps (43.6 – 47.9°N latitude,  
161 4.9 – 15.6°E longitude; elevations ranging from sea-level to 4,810 m a.s.l.) by both sexual and  
162 asexual lineages of *R. kuepferi*. The study area was represented by a two-dimensional raster  
163 with a spatial resolution of 100 x 100 m<sup>2</sup> (individual cells of the raster are called sites  
164 henceforth).

165 Maps of the area's climate history (mean, minimum and maximum monthly temperatures  
166 and monthly precipitation sums) back to 10 kyr BP were taken from Maiorano *et al.* (2013),  
167 who had downscaled a global climate time series simulated by the HadCM3 atmosphere-  
168 ocean general circulation model (Singarayer & Valdes 2010) to a spatial resolution of 100 x  
169 100 m<sup>2</sup> (see Espindola *et al.* 2012; Maiorano *et al.* 2013 for downscaling methods). We



170 refined the original 1-kyr temporal resolution of these data to 100 years' time steps by linear  
171 interpolation.

172 *Ranunculus kuepferi* is a grassland species. We hence modelled a spatially explicit time series  
173 of treeline fluctuations across the entire study area to produce a temporarily dynamic mask  
174 of sites that are unsuitable to *R. kuepferi*. The reconstruction was based on the assumption  
175 that the (potential) treeline position is changing with climatic conditions and additionally  
176 accounted for the gradual re-forestation of the Alps during the first millennia of the  
177 simulation period and for the landuse-driven lowering of the treeline during the last  
178 millennia (see Appendix S1 for details).

### 179 **Modelling framework**

180 We simulated the range dynamics of *R. kuepferi* using the modelling framework CATS  
181 (Dullinger *et al.* 2012; Hülber *et al.* 2016). CATS simulates the annual change in species'  
182 occupancy and abundance at each site of a study area. Local populations are represented by  
183 stage-structured cohorts (seeds, juveniles and adults) with annual dynamics determined by  
184 processes of stasis and transition within and among these cohorts (seed yield, seed banking,  
185 germination, juvenile survival, maturation, fecundity; further on summarized as  
186 demographic rates). The demographic rates, and hence the annual seed yield as their joint  
187 outcome, differ at each site and year of simulation according to: (1) climatic/environmental  
188 suitability as predicted by a species distribution model (SDM); and (2) the density (= number  
189 of individuals) of the local population. Under constant environmental conditions, minor  
190 fluctuations of species ranges arise from stochastic events implemented in demographic and  
191 dispersal simulation routines. Under changing conditions, range dynamics result from the  
192 impact of changing environmental suitability, i.e. altered SDM predictions, on the local

193 demographic rates and the subsequent growth or decline of populations, eventual extinction  
194 from no longer suitable sites, or dispersal-mediated establishment at newly suitable sites.

195 ***Parameterization data – SDMs, demography, dispersal***

196 The SDMs used to project changes in the environmental suitability of individual sites for each  
197 cytotype were calibrated and validated with empirical data representing their current  
198 distribution. These data were sampled in 2013 and 2014 and contain 102 plots of 100 x 100  
199 m<sup>2</sup> spread across the entire Alpine range of the species (cf. Kirchheimer *et al.* 2016). Twenty-  
200 three of these populations were purely diploid, 60 purely tetraploid and 19, all from a  
201 narrow contact zone in France, contained individuals of both cytotypes (and occasionally tri-  
202 and pentaploids in addition; Schinkel *et al.* 2016). We coupled these presence data with field  
203 absences (i.e. confirmed true absences for the species *R. kuepferi* sensu lato, and hence also  
204 for both cytotypes) at 8239 non-forest plots extracted from the Alps vegetation database  
205 (Lenoir *et al.* 2012). These plots were also distributed across the entire Alps and cover  
206 elevations between 1000 and 3400 m a.s.l., i.e. they bracket the elevational range of *R.*  
207 *kuepferi*. The combined dataset was then used to parameterize four different algorithms:  
208 Generalized Linear Models (GLM); Generalized Additive Models (GAM); Boosted Regression  
209 Trees (GBM); and Random Forests (RF). Parameterization was performed separately for the  
210 diploid and the tetraploid cytotypes as well as for the merged occurrences of both cytotypes  
211 (i.e. for *R. kuepferi* sensu lato). The four algorithms used provide high to very high  
212 discrimination ability with presence-absence data and are known to be computationally  
213 efficient (e.g. Elith *et al.* 2006). For all models, we used the same set of seven predictor  
214 variables: three bioclimatic variables derived from monthly mean temperatures and  
215 precipitation; one soil variable (percentage of calcareous bedrock material); one variable  
216 indicating site-specific solar radiation income; and two variables describing terrain

217 topography (slope inclination and curvature, see Appendix S1 for details). Models were  
218 validated by calculating the area under the receiver operating curve (AUC), based on a 10-  
219 fold cross-validation (Van Houwelingen & Le Cessie 1990) on the calibration data set.  
220 Weighted means of occurrence probabilities projected by the four modelling techniques  
221 ('ensemble projections') were then used as a measure of each 100 m x 100 m<sup>2</sup> site's  
222 suitability for each cytotype as well as for *R. kuepferi* s.l. (i.e. the two cytotypes in  
223 combination). Weights were determined by the AUC scores of the individual modelling  
224 techniques (see Table S2). After computing the same three bioclimatic variables for the  
225 historical climatic time series, ensemble projections were produced for each 100 years' time  
226 slice provided by the reconstructed climate maps. For the years in-between, site suitability  
227 was linearly interpolated. The result hence was an annual time series of 10,000 suitability  
228 maps per cytotype as well as for *R. kuepferi* s.l. (i.e. the two cytotypes in combination).

### 229 ***Demographic modelling and pollinator competition***

230 The suitability of a site in a particular year was translated into the cytotype's local population  
231 dynamics by relating demographic rates as sigmoidal functions to SDM projections.

232 Demographic rates were thereby constrained between zero and a maximum value extracted  
233 from field data (or, in some cases, estimated, Table S1). In addition, germination and juvenile  
234 survival were modelled as density dependent, i.e. their rates decline with the growth of the  
235 local adult population (Appendix S1).

236 The annual seed yield of a population at a certain site (and year) was calculated as the  
237 product of the population size and two demographic rates: flowering frequency and seed  
238 number per individual. For the sexually reproducing, diploid and outcrossing cytotype, at  
239 least two adult individuals were required for seed set. In case of mixed diploid and tetraploid  
240 populations, we moreover introduced a mechanism to represent the effect of pollinator

241 competition on the diploids, i.e. we computed the probability of pollen transfer from other  
242 diploid individuals. We thereby assumed a pollinating insect to consecutively visit 5 – 10 *R.*  
243 *kuepferi* individuals (exact number chosen randomly within that range at each site) and  
244 calculated the probability that these 5 – 10 visits included at least two diploid individuals  
245 from a binomial distribution with parameter  $p$  (the probability of a diploid individual per  
246 single visit) equal to the proportion of diploids in the entire (mixed) population of the site.  
247 The potential seed yield of the site's diploid population was then multiplied by  $p$  to reduce  
248 the seed yield in response to the encroachment of tetraploids. We did not implement a  
249 similar cross-pollination effect on the apomictic tetraploids. In fact, tetraploids need pollen  
250 for endosperm fertilization ('pseudogamous apomixis'). However, they can use self-pollen  
251 for this purpose (Cosendai *et al.* 2013).

### 252 ***Seed dispersal***

253 Wind is assumed to be the main dispersal vector of *R. kuepferi* diaspores (Müller-Schneider  
254 1986). However, as most species are likely polychorous (Nathan *et al.* 2008), and as  
255 especially large herbivores transport the seeds of many herbs (e.g. Vellend *et al.* 2003), we  
256 combined dispersal functions for four different processes likely to transport diaspores over  
257 longer distances: by wind, within the furs and guts of large herbivores, respectively, and by  
258 an unspecified long distance dispersal (LDD) vector. Wind dispersal was modelled by means  
259 of the analytical WALD kernel (Katul *et al.* 2005). Exo- and endozoochorous kernels were  
260 parameterized on the basis of correlated random walk simulations for the most frequent  
261 large herbivore in the study area, the chamois (*Rupicapra rupicapra* L.). Rare LDD events  
262 were accounted for by distributing 0.1 % of a population's seed yield randomly within a  
263 radius of 50 km. For details on seed dispersal functions see Appendix S1.

### 264 ***Simulation set-up***

265 To identify the relative effects of niche differentiation and mode of reproduction (plus their  
266 possible interaction effect) on the Holocene range development of the two cytotypes, we  
267 ran a factorial design of simulations with two variables: niche (two levels: own niche vs.  
268 common niche of *R. kuepferi* s. l.) and reproductive mode (three levels: own mode – both  
269 sexual – both asexual). To account for (pollinator) competition among cytotypes, simulations  
270 were run simultaneously for both cytotypes. For each factorial combination, three replicate  
271 simulations were run. We refrained from a larger number of replicates as results did not vary  
272 substantially and computing efforts per replicate were extremely high.

273 The initial distribution of each of the two cytotypes, i.e. the sites set as occupied in the first  
274 year of simulation (10 kyr BP), was restricted to the regions assumed to comprise the glacial  
275 refugia of the species in the south-western Alps (Burnier *et al.* 2009). We identified regions  
276 of particular high suitability at 10 kyr BP within a radius of 10 km around each documented  
277 population (12 diploid and 12 tetraploid populations, Fig. 2). Each site within these regions  
278 was assumed to be inhabited by a population of half of the site's carrying capacity. We  
279 started simulations in 10 kyr BP as the available climatic reconstructions are limited to this  
280 period. However, in most areas of the Alps, the main deglaciation did not take place before  
281 the end of the Younger Dryas, i.e. between 11.9 and 10.5 kyr BP (Darnault *et al.* 2012). Even  
282 if distribution ranges of both cytotypes in the southwestern Alps may already have been  
283 larger than we assumed, it is hence highly unlikely that the tetraploid cytotype had emerged  
284 and moved out of the most southwestern Alps before 10 kyr BP.

### 285 ***Statistical analyses of the simulations' outputs***

286 From the final result of each simulation run, i.e. the cytotype distributions reached in the last  
287 simulation year, we calculated the convex-hull around the diploid and tetraploid distribution  
288 ranges, respectively. The convex-hull is the smallest convex area that contains all sites where

289 the respective cytotype is present and was calculated using the *convexhull* function in the R-  
290 package 'siar' (version 4.2, Parnell *et al.* 2013). Areas outside the Alpine chain were removed  
291 from the resulting hulls.

292 For each simulation run, we then divided the resulting convex hull area of the tetraploids by  
293 the convex hull area of the diploids. The log of this ratio was subtracted from the log of the  
294 same ratio applied to the actual distribution of the two cytotypes. This index hence  
295 measures how precisely the simulations recapture the observed range size ratio of the two  
296 cytotypes. We subsequently used this metric as the response variable in a linear regression  
297 with niche, reproductive mode and their interaction as predictors. The variance explained by  
298 these factors was computed from their respective partial  $R^2$  values. As a back-up, we  
299 additionally calculated and inspected  $\Delta AIC_c$  values of the candidate models using the *aictab*  
300 function of the R-package 'AICmodAVG' (version 2.1-1, Mazerolle 2013).

301

## 302 **RESULTS**

### 303 ***Species distribution models (SDMs)***

304 Evaluation scores of SDMs indicate reasonable model projections for both cytotypes as well  
305 as for *R. kuepferi* s.l. (cross-validated AUC 0.76 – 0.85, see Table S2). Niche differences  
306 among the two cytotypes (see Kirchheimer *et al.* 2016) translate into different predictions of  
307 potential geographical ranges (compare blue pixels in Fig. 2 and Fig.S2). In particular, the  
308 preference for cooler temperatures shifts the potential range of the tetraploid to higher  
309 elevations (mean elevation of diploids:  $2,367 \pm 279$  m a.s.l.; tetraploids:  $2,527 \pm 349$  m a.s.l.).  
310 Across the last 10 kyr, potential ranges fluctuated pronouncedly for both cytotypes (Fig. 2).  
311 Initially (10 kyr BP), its size was about equal for both cytotypes (c. 1200 km<sup>2</sup>). Towards 5 kyr  
312 BP it decreased markedly, for diploids in particular (c. 600 km). During the last millennium, it

313 sharply increased again for diploids (c. 1500 km<sup>2</sup>), but further decreased for tetraploids (c.  
314 700 km<sup>2</sup>). These dynamics are partly driven by the relatively modest climatic changes during  
315 the last 10 kyr BP (Figs. S3, S4). More importantly, potential ranges overlap to different  
316 degrees with forest cover during the last 10 kyr. This overlap is stronger for the diploids  
317 which prefer warmer conditions and hence have a higher share of suitable habitats below  
318 the climatic treeline (compare brown pixels in Fig. 2). As a consequence, their potential  
319 range shrinks sharply with the rise of the treeline during the first two millennia, but  
320 increases again with the human-driven lowering of the treeline during the most recent  
321 millennia.

322 Apart from differences in size and its fluctuations over time, the geography of potential  
323 ranges also differs among the two cytotypes. While suitable sites concentrate in the central  
324 parts of the Alps for both cytotypes, their density in large parts of the western Alps is much  
325 lower for diploids than for tetraploids (Fig. 2). Hence, putative ice age refugia and current  
326 areas with high environmental suitability and potentially high abundance are separated by a  
327 pronounced gap, especially in case of diploids.

328 Surprisingly, at first glance, the modelled niche of *R. kuepferi* s. l. is narrower than the one of  
329 the two cytotypes. However, as the two cytotypes have overlapping niches, their  
330 combination accentuates the niche space suitable to both cytotypes relative to the niche  
331 space suitable to only one of them, resulting in a narrower probability distribution across the  
332 respective environmental gradient(s). As a consequence, the projected potential range of *R.*  
333 *kuepferi* s.l. is smaller than those of the individual cytotypes or intermediate between them  
334 (Fig. 2). The geographical distribution of these suitable sites, however, is closer to those of  
335 the tetraploids, likely because tetraploids are more frequent in the dataset used for  
336 parameterizing the SDMs.

### 337 ***Simulation of range dynamics***

338 When running the simulation models with each cytotype's own niche and reproductive  
339 mode, simulations slightly overestimated the empirical distribution ranges of both cytotypes,  
340 but recaptured the ratio of the two distribution ranges quite accurately (Fig. 3a, b, Fig. 4).

341 Accounting for niche differentiation among cytotypes, but assuming that both cytotypes had  
342 the same reproductive mode, did not change these results (Fig. 3c, d, Fig. 4). Independent of  
343 the reproductive mode, the cytotype with the 'tetraploid niche' successfully spreads across  
344 much of the Alps while the cytotype with the 'diploid niche' remains restricted to the  
345 southwestern refugia.

346 Nevertheless, reproductive modes were relevant for simulation results. When the two  
347 cytotypes were assumed to share a common niche of *R. kuepferi* s.l. (Fig. 2) but to keep their  
348 own reproductive modes, simulations overemphasized observed range differences. While  
349 tetraploids re-captured their currently realized range, diploids were confined to an area even  
350 smaller (Fig. 3e). Additional simulations where both cytotypes share the tetraploid niche  
351 (instead of the one of *R. kuepferi* s. l.) delivered very similar results (Fig. S5b). When both  
352 cytotypes were assigned the diploid niche, the asexually reproducing one remained  
353 restricted to the southwestern Alps while the sexually reproducing one went extinct (Fig.  
354 S5a). Taken together, simulations that neglect niche differentiation, but account for  
355 differences in the reproductive mode hence bias observed range size ratios in favour of the  
356 asexual cytotype.

357 Finally, assigning both cytotypes the same niche (of *R. kuepferi* s.l.) and reproductive mode  
358 delivered contrasting results. If both cytotypes are assumed to reproduce asexually, they  
359 both spread across the Alps (Fig 3f) and colonize approximately equal ranges. If both  
360 cytotypes are meant to reproduce sexually, however, the diploid is expanding across the



361 Alps while the tetraploid gets stuck in the western Alps (Fig. 3g). As, in this set-up, the two  
362 cytotypes are assumed to be identical with respect to niche and reproductive mode, and  
363 demographic and dispersal parameters are very similar (Table S1), this result suggests a  
364 potentially important role of priority effects and competition for range formation (as  
365 discussed below).

366 Variance partitioning and the AIC-based evaluation summarize these results: they  
367 consistently suggest that both niche differentiation and differences in reproductive modes  
368 have important and independent effects on simulation outcomes, with niche differentiation  
369 being slightly more influential (Table 1). Moreover, they highlight the importance of the  
370 interaction effect among the two factors which explains about half of the total variance of  
371 the simulation results.

372

## 373 **DISCUSSION**

374 Taken together, our results underline the complex causation of geographical  
375 parthenogenesis (Hörandl 2006). Both processes considered in our simulations can have  
376 significant independent and strong interacting (Table 1) consequences for the development  
377 of ranges in sexual and asexual *R. kuepferi*. The observed range size difference is apparently  
378 determined primarily by niche differentiation, as assigning the cytotypes their own niches  
379 reproduces current range size ratios and range positions quite accurately, independent of  
380 assumed reproductive modes. This niche differentiation opened migration pathways to the  
381 more cold-adapted tetraploid cytotype which were not available to the diploid cytotype.  
382 Eastward expansion of the latter was hence impossible even if simulations assumed that it  
383 would be able to reproduce uniparentally. However, niche differentiation is not a generic  
384 prerequisite (or consequence) of the emergence of (polyploid) apomicts in plants (Glennon

385 *et al.* 2014). Assuming that such differentiation did not happen, as in our simulation design,  
386 is hence likely appropriate for other cases of geographical parthenogenesis. For such cases,  
387 our results suggest a potentially strong effect of the separation of reproductive modes on  
388 the differentiation of the cytotype's range sizes: while under assumed identical reproductive  
389 modes (and the identical niche of *R. kuepferi* s.l.) either both cytotypes or only the sexual  
390 one was able to expand across the Alps, implementing a switch to apomixis on the side of  
391 the tetraploids turns simulation results around and even overemphasizes the superiority of  
392 the tetraploid asexual cytotype.

### 393 ***Geographical parthenogenesis in R. kuepferi***

394 The dominant effect of niche differentiation on the current geographical parthenogenesis in  
395 *R. kuepferi* is surprising at first glance because the tetraploid's niche is not broader than the  
396 one of the diploid (Kirchheimer *et al.* 2016) and its potential range is smaller. Rather than  
397 niche breadth, differences in niche position have hence obviously been responsible for the  
398 emergence of vastly different ranges. In particular, tetraploids' preference for colder  
399 conditions entailed that post-glacial re-encroachment of forests into the Alps interfered  
400 more with the area suitable to diploids than to tetraploids. In addition, the peculiar  
401 topography of the Alps was apparently crucial. The western Alps represent an area of  
402 pronounced topographical complexity owing to particularly high elevations interspersed  
403 with deep glacial valleys. This complexity constituted an efficient barrier to the post-glacial  
404 recolonization of the Alps from marginal refugia for many alpine species (Merxmüller 1952).  
405 As a consequence, the area currently represents the most prominent 'break zone' in the  
406 distribution of both species and alleles in the European Alps (Thiel-Egenter *et al.* 2011, Fig.  
407 2). The tetraploid cytotype of *R. kuepferi* has a higher density of suitable sites in this area  
408 because its niche expands further into the regionally prevailing cool and humid conditions

409 (Kirchheimer *et al.* 2016). By contrast, nearly all sites climatically suitable to diploids in the  
410 area are below the treeline, which is particularly high in this region due to pronounced  
411 climatic continentality (Ozenda 1985).  
412 Our results do not support a primary role of faster migration ability (Baker's Law) in  
413 generating geographical parthenogenesis in *R. kuepferi*. Sexual outcrossers were simulated  
414 to spread across the entire Alps as did apomicts with the 'appropriate' niche. This does not,  
415 of course, mean that spread rates are independent of the reproductive mode, but that the  
416 past 10 kyr were long enough to allow even outcrossing *R. kuepferi* to recolonize most parts  
417 of the Alps if suitable stepping stones had been available. Indeed, many widespread Alpine  
418 species are outcrossers (Schroeter 1908; Körner 2003), even at the highest elevations  
419 (Hörandl 2011). Sexual plants hence obviously managed a sufficiently rapid range expansion  
420 throughout the Alps despite being dependent on the co-occurrence of mating partners.

#### 421 ***Geographical parthenogenesis beyond R. kuepferi***

422 A characteristic feature of geographical parthenogenesis is that ranges of asexual taxa are  
423 not only larger but also often extend further into cold environments that have been  
424 glaciated during the Pleistocene (Bierzychudek 1985). A shift of niche positions towards  
425 cooler conditions appears hence frequently linked to this biogeographic phenomenon. In  
426 apomict plants, this shift is likely mediated by bypassing meiosis and becoming independent  
427 of pollinators, two features that confer advantages in cold climates. However, this shift has  
428 so far primarily been seen as evidence of niche broadening that subsequently enabled range  
429 expansion (Hörandl 2006). In contrast, our results for *R. kuepferi* suggest that a preference  
430 for cooler conditions *per se* may have been responsible for greater distributional success of  
431 asexual lineages. As geographical parthenogenesis is particularly frequent in alpine floras  
432 (Asker & Jerling 1992, other alpine taxa of the European Alps include e.g. *Alchemilla spp.*,

433 *Hieracium spp., Nardus stricta, Pilosella spp., Poa alpina, Taraxacum spp.*, Hörandl 2011) *R.*  
434 *kuepferi* is unlikely a special case. For all these non-forest species, adaptations to cool  
435 conditions have increased the permeability of mountain landscapes during the Holocene  
436 because they helped escaping the rising treeline and facilitated migration across higher  
437 mountain ranges. Additional support for this assumption comes from the biogeography of  
438 narrow range endemics: among vascular plants of the Austrian Alps such endemics are most  
439 frequent at subalpine elevations and decline rapidly in the mid and upper alpine belts (Essl  
440 *et al.* 2009). Postglacial recolonization of the Alps from marginal refugia was hence obviously  
441 easier for species adapted to high than to intermediate elevations.

442 Our simulations also suggest, however, that fixing any ‘main’ mechanism responsible for  
443 geographical parthenogenesis is difficult or impossible because subtle differences can  
444 completely reverse biogeographic patterns. The fundamentally different results illustrated in  
445 Figs. 3f and 3g are particularly instructive in this respect and illustrate the potential  
446 importance that differentiation of reproductive modes can have for the emergence of  
447 geographical parthenogenesis. In both cases, the two cytotypes are assumed to have  
448 identical reproduction modes and a niche that allows colonization of the full species’ range  
449 (= the niche of *R. kuepferi* s. l.). They only differ in the assumed exact position of initial  
450 populations in the southwestern Alps at the simulation start in 10 kyr BP. These minor  
451 differences are irrelevant as long as both cytotypes are assumed to reproduce asexually, but  
452 result in major range size differences if they are assumed to be sexual outcrossers. In this  
453 latter case, the sensitivity of sexually reproducing taxa to minority cytotype disadvantage  
454 obviously amplifies priority effects: differences in positions of initial populations give one of  
455 the cytotypes a head start. The other cytotype hence has to migrate through ‘occupied  
456 terrain’ which greatly delays its own spread (see Appendix S2). For any ‘real’ case of

457 geographical parthenogenesis the implication is (i) that a switch to apomixis immunizes the  
458 asexual cytotype against the disadvantage of necessarily being the minority cytotype  
459 initially, and any consequent priority effects; and (ii) that asexual populations can establish  
460 'biotic barriers' to their sexual relatives and potentially constrain their distribution, even if  
461 niches would allow for a much broader range. In light of these results, niche differentiation  
462 appears not only a means for the establishment of the 'derived' cytotype, but may also  
463 facilitate the survival of the ancestral one (Fig. S5).

#### 464 **Conclusions**

465 Taken together, our results suggest that in *R. kuepferi*, and probably in other taxa of  
466 temperate mountain ranges, the distributional advantage of asexuality is determined by a  
467 complex interaction between the plants and their abiotic and biotic environment. Loss of sex  
468 (Bomblies *et al.* 2015; Mirzaghaderi & Hörandl 2016) and the concomitant polyploidization  
469 (Bierzychudek 1985; Brochmann *et al.* 2004; Comai 2005) likely foster tolerance of cooler  
470 conditions. Tolerance to cooler conditions facilitates re-immigration into (previously  
471 glaciated) mountain ranges because it helps overcoming high elevation barriers. In addition,  
472 loss of sex confers competitive advantages to asexual lineages that can modify or even  
473 reverse the distributional consequences of priority effects and enable asexual populations to  
474 block further migration of their sexual relatives. These findings do not imply that niche  
475 broadening and colonization advantages of uniparental reproduction, the main mechanisms  
476 behind geographical parthenogenesis of plants discussed so far, are unimportant. They  
477 suggest, however, that at least in temperate mountains, niche shifts towards cooler  
478 conditions and competitive advantages of asexuality may even be more important to  
479 understand geographical parthenogenesis.

480

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487

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624 **SUPPORTING INFORMATION**

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626 at Wiley Online Library ([www.ecologyletters.com](http://www.ecologyletters.com)).

627

628 **TABLES**

629 **Table 1** Adjusted  $R^2$  and  $AIC_c$  values of linear regression models explaining simulation results  
 630 by the two factors explored (Reproduction with levels own –sexual – asexual; Niche with  
 631 levels own – common niche of *R. kuepferi* s.l.), and their interaction, respectively. The  
 632 response variable was the difference between simulated and observed (log-transformed)  
 633 range size ratios of the two cytotypes as presented in Fig. 3#.  $AIC_c$  is the Akaike Information  
 634 Criterion corrected for small sample size, calculated following Burnham & Anderson (2002).

<b>Terms</b>	<b>Adj. <math>R^2</math></b>	<b><math>AIC_c</math></b>
Reproduction	0.23	71.0
Niche	0.30	66.9
Reproduction + Niche	0.59	46.5
Reproduction * Niche	0.98	15.7

635

636

637 **FIGURE LEGENDS**

638

639 **Figure 1** Current distribution of the two cytotypes of *R. kuepferi*. Red and blue dots  
640 represent sampled populations of diploids and tetraploids, respectively. Surrounding convex-  
641 hull areas are coloured correspondingly. Areas outside the Alpine chain were removed from  
642 the hulls.

643

644 **Figure 2** Potential ranges of the two cytotypes of *R. kuepferi*, and of *R. kuepferi* s.l. in the  
645 European Alps (grey) at five different times. Coloured sites are those which are climatically  
646 suitable and either above (blue) or below (brown) the treeline at the respective time.  
647 Crosses mark the geographical positions of the initial populations, i.e. those sites assumed to  
648 be occupied at the start of the simulations (10 kyr BP). Polygons in the 'current' row  
649 represent the main break zone in Alpine species distributions identified in Thiel-Egenter *et*  
650 *al.* (2011). To improve visibility, maps have been resampled to a resolution of 1 x 1 km<sup>2</sup> with  
651 all cells containing at least on suitable 100 m x 100 m<sup>2</sup> site coloured appropriately. See Fig.  
652 S2 for an original resolution map.

653

654 **Figure 3:** Convex-hull areas around the observed current distribution of the two cytotypes of  
655 *R. kuepferi* (a) and around the current distributions simulated under the assumption that  
656 cytotypes have their specific climatic niches (b-d) or the merged niche of both cytotypes (e-  
657 g); and that they have their specific reproduction mode (b, e) or that both cytotypes are  
658 either apomicts (c, f) or sexual outcrossers (d, g). Each panel represents the result of a  
659 randomly selected replicate from the respective simulation setting. Background shading

660 indicates sites (= raster cells) occupied by the species at the end of the simulation period.

661 Areas outside the Alpine chain were removed from the hulls.

662

663 **Figure 4** Convex-hull area ratios of the two cytotypes resulting from simulations under the 2

664 \* 3 factorial combinations of the cytotypes' niche (own N vs common N of *R. kuepferi* s. l.)

665 and reproductive modes (own R – sexual R – asexual R). Each dot represents one replicate

666 simulation run. Values were calculated by dividing the convex hull area of the tetraploids by

667 the convex hull area of the diploids. The log of this ratio was subtracted from the log of the

668 same ratio applied to the real ranges of the two cytotypes. A value of 0 hence implies that

669 simulated and real ratios do not differ.

670