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# Plant colonization and survival along a hydrological gradient: demography and niche dynamics

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Author Contributions: CD, AM and AB conceived and designed the investigations. AM measured plant abundance. CD modelled the data. CD and AB wrote the manuscript.

## 1 **Abstract**

2 Predicting the effect of a changing environment, e.g. caused by climate change, on realized niche dynamics  
3 and, consequently, biodiversity is a challenging scientific question that needs to be addressed. One  
4 promising approach is to use estimated demographic parameters for predicting plant abundance and  
5 occurrence probabilities. Using longitudinal pin-point cover data sampled along a hydrological gradient in  
6 the Marais poitevin grasslands, France, the effect of the gradient on the demographic probabilities of  
7 colonization and survival was estimated. The estimated probabilities and calculated elasticities of survival  
8 and colonization covaried with the observed cover of the different species along the hydrological gradient.  
9 For example, the flooding tolerant grass *A. stolonifera* showed a positive response in both colonization and  
10 survival to flooding, and the hydrological gradient is clearly the most likely explanation for the occurrence  
11 pattern observed for *A. stolonifera*. The results suggest that knowledge on the processes of colonization  
12 and survival of the individual species along the hydrological gradient is sufficient for at least a qualitative  
13 understanding of species occurrences along the gradient. The results support the hypothesis that  
14 colonization has a predominant role for determining the ecological success along the hydrological gradient  
15 compared to survival. Importantly, the study suggests that it may be possible to predict the realized niche  
16 of different species from demographic studies. This is encouraging for the important endeavor of predicting  
17 realized niche dynamics.

18

19 **Keywords:** flooding gradient, niche dynamics, plant abundance, plant cover, plant demography

20

## 21 **Introduction**

22 Different plant species are adapted to different water availability regimes, and competition from  
23 neighboring plants has been shown to control plant species occurrence and abundance (Araya et al. 2011;  
24 Grace and Wetzel 1981; Silvertown et al. 1999). In a demonstration of the effect of competition on species  
25 abundance along a hydrological gradient, Ellenberg (1952) sowed six meadow grass species in single species  
26 stands and in mixtures evenly across an experimental water table gradient. The experiment demonstrated  
27 that all species, when grown in monoculture, showed a peak in biomass production at an intermediate  
28 water-table depth, whereas when species competed with each other, the niche overlap was significantly  
29 reduced due to species segregating along the water table gradient (Silvertown et al. 1999). This difference  
30 between plant species occurrences in single species stands and mixtures of naturally found species along a  
31 hydrological gradient is an example of the difference between the fundamental and the realized niche,  
32 respectively (Hutchinson 1957).

33 The ecological success of plant species is typically described by the observed change in plant abundance. In  
34 order to more fully understand changes in plant abundance and make ecological predictions of the effects  
35 of environmental gradients, it is necessary to investigate and quantify the underlying ecological processes.  
36 In principle, this means that all the different interactions between the species in the plant community need  
37 to be investigated (Damgaard 2003), but this is typically an exceedingly demanding task in multi-species  
38 plant communities and, instead, we investigate how the vital rates of the most common species, when  
39 competing with other species, are affected by an environmental gradient (Harper 1977). The realized niche  
40 dynamics of a plant species along an environmental gradient are a function of both the environmental  
41 gradient and competitive effects of other species along the gradient. Predicting realized niche dynamics has  
42 been demonstrated to be useful in addressing both basic and applied ecological questions; e.g. for

43 predicting species distribution with climatic change (Maiorano et al. 2013), for predicting species response  
44 to land use changes (Bomhard et al. 2005), and methodological issue for a better detection and sampling of  
45 rare populations (Guisan et al. 2006).

46 In this study, we assume that the vital rates measured *in situ* in natural plant communities along a gradient  
47 summarize the effect of both the gradient and interspecific interactions on the examined species, i.e.  
48 provide information on the dynamics of the species realized niche along the gradient. This connection  
49 between the Hutchinson realized niche and demography was first pointed out by Maguire (1973), who  
50 modeled niche space as functions of demographic parameters.

51 Generally, we expect that the local probability of occurrence is a function of the demographic parameters  
52 (Thuiller et al. 2014) and, more specifically, that it increases with the probability of colonization and  
53 decreases with the probability of mortality. Thuiller et al. (2014) analysed how demographic parameters  
54 relate to occurrence probability in trees and hypothesized that these relationships vary with competitive  
55 ability, but generally call for the need for empirical data that relate demographic parameters to occurrence  
56 probabilities. Furthermore, demographic processes have been increasingly used in spatio-temporal  
57 modeling of plant populations (Normand et al. 2014). This is motivated by the notion that changes in the  
58 probabilities of colonization and mortality may be the driving changes in species ranges. Furthermore, a  
59 demographic approach to understanding and predicting species' range dynamics has the advantage of  
60 being rooted in ecological theory (reviewed in Normand et al. 2014), and has been shown to improve  
61 predictive ability as it includes plasticity and local adaptation (Morin and Thuiller 2009).

62 Typically, colonization and survival probabilities are estimated from demographic data of individual plants.  
63 However, in many natural plant communities dominated by perennial plants, e.g. grasslands, it is often  
64 difficult to distinguish individual plants due to their vegetative growth pattern and, consequently, to obtain  
65 reliable demographic data. Instead, it is possible to measure "colonization" and "survival" by considering  
66 species turnover at a specific spatial point (Damgaard et al. 2011; Damgaard et al. 2013). If a species was

67 present at time  $t$  at a specific spatial point, but absent at time  $t + 1$ , we may loosely speak of a mortality  
68 event, and if a species is absent from a specific pin-position at time  $t$  and present at time  $t + 1$ , we may  
69 loosely speak of a colonization event (Damgaard et al. 2011; Damgaard et al. 2013). We have chosen to use  
70 the term “colonization” rather than “recruitment”, since the event is defined by a novel occurrence in  
71 space (Adler et al. 2006; Adler et al. 2009). However, in the interpretation of the results it is important to  
72 remember that the concepts of colonization and mortality have a different meaning than usual in  
73 demographic studies where individuals are clearly recognized. The used terminology is more accurate for  
74 some plant species than others; for perennial plant species that spread clonally by forming well-defined  
75 ramets, the concepts of colonization and mortality at a specific spatial point make apparent biological  
76 sense, whereas for species with more variable sizes, the concepts are inadequate descriptions of the  
77 underlying biological causes of a change in plant abundance. Bearing this issue of terminology in mind, we  
78 may generally assert that the cover of a plant species increases with colonization and decreases with  
79 mortality.

80 The aim of this study is to apply a demographic method that is suitable for multi-species communities,  
81 where it is not feasible to measure all interspecific interactions, in order to characterize the ecological  
82 processes that determine the width and segregation of the realized niches along a hydrological gradient.  
83 More specifically, we will measure the demographic processes, survival and colonization of naturally  
84 occurring perennial plant species along a hydrological gradient in Atlantic wet grasslands in France. The  
85 estimated demographic parameters will be compared to the observed probability of occurrence along the  
86 hydrological gradient, and the relative importance of survival and colonization in determining the  
87 occurrence probability along the hydrological gradient will be assessed and discussed. Finally, the  
88 application of the suggested method for estimating demographic parameters will be discussed and  
89 compared to the standard matrix demographic method.

## 90 **Methods**

### 91 **Field site**

92 The study was conducted on grazed wet grasslands situated in the Marais poitevin on the French Atlantic  
93 coast (46°28 N; 1°13 W). The climate is mild Atlantic with an average excess of precipitation over  
94 evapotranspiration in winter of 220 mm and a water deficit in summer of about 300–350 mm (Amiaud et  
95 al. 1998). The grasslands in the Marais poitevin are characterized by an elevation gradient with a range of  
96 45 cm and a consequential flooding gradient varying in duration and water depth. Depending on the  
97 rainfall, the flooding starts in October and the grasslands generally start to dry out in June, although some  
98 years as early as in April (Amiaud et al. 1998).

99  
100 The studied grasslands had a long term grazing history consisting of continuous grazing from the end of  
101 April to December with low stocking rate. This grazing disturbance and the consequent reduced importance  
102 of competitive interactions most likely act as filters on the regional species pool. In the studied plots,  
103 grazing was prevented during the two years the demographic study was carried out, but it was assessed  
104 that this period without grazing was too short to have caused significant changes in the plant community  
105 structure.

### 106 **Hydrological gradient and SEV**

107 Water is an essential and often limiting resource for plant growth, and insufficient water availability leads  
108 to decrease of transpiration and photosynthesis and, ultimately, to wilting and death. However, water may  
109 also be in excess, and waterlogging occurs when a large proportion of the pore spaces in the soil are  
110 occupied by water. This means the diffusion of oxygen and gas exchange between the soil, plants and  
111 atmosphere is limited. The result of this is decreased root growth and functioning, which negatively affects  
112 plant growth and survival (Araya and Garcia-Baquero 2014).

113 In accordance with Gowing et al. (1998) and Stewart et al. (1998), we quantified the stress related to soil  
114 aeration-shortage and drought at each plot by the SEV method, which has been shown to quantify the  
115 trade-off between species' tolerance of aeration stress and tolerances of soil drying stress (Araya et al.  
116 2011; Silvertown et al. 1999). The aeration shortage was measured by the Sum Exceedance Value above a  
117 reference threshold (aeration SEV) and the water shortage as the Sum Exceedance Value below a reference  
118 threshold (drought SEV), which depend on the physical properties of the soil (Gowing et al. 1998). A high  
119 aeration SEV indicates that plant roots are likely to be flooded and a high drought SEV indicates that plants  
120 will probably experience water-shortage. Both SEV parameters, expressed in  $\text{cm day}^{-1}$ , were derived from  
121 the water-table depth level monitored at hourly intervals from March to October using level logger sensors  
122 (Solinst LTC Levellogger Junior model 3001). The aeration SEV was calculated as the cumulative difference  
123 between the water table depth and the reference level at which the plants were expected to be stressed by  
124 limited oxygen (Gowing et al. 1998). The aeration reference threshold was calculated as the water table  
125 depth that corresponds to 10% air-filled soil porosity, inducing an insufficient oxygen diffusion to supply  
126 roots demand, and corresponds to -0.191 m. The drought reference threshold was taken as 0.5 m tension  
127 in the root zone at 100 mm depth (Gowing et al. 1998) and corresponds to a water table of -0.42 m.

128  
129 The water level was found to be driven by elevation and, accordingly, both the aeration SEV and drought  
130 SEV correlated closely to the duration of flooding (Pearson correlation,  $r=0.862$ ,  $P<0.0001$ ). The aeration  
131 SEV was found to vary from 0.3 and  $12.8 \text{ cm day}^{-1}$ , a similar range as in British alluvial grasslands  
132 (Silvertown et al. 1999). The drought SEV varied between 28.3 and  $45.4 \text{ cm day}^{-1}$ , which is somewhat dryer  
133 conditions than in the British alluvial grasslands due to the very clay-rich soil and the relatively large rainfall  
134 deficit during summer.

135  
136 Since aeration SEV and drought SEV were highly correlated, the following demographic analysis was only  
137 performed for one of the two SEV measures, i.e. aeration SEV.

## 138 **Plant species**

139 The vegetation at the site varies in composition along the hydrological gradient (Amiaud et al. 1998) and is  
140 dominated by grasses and sedges except after local heavy grazing episodes, where dicots may become  
141 transiently abundant (Marion et al. 2010). The flats, which are never flooded, present a mesophilous (M)  
142 plant community characterized by grasses and sedges such as *Cynosurus cristatus*, *Lolium perenne*, *Elytrigia*  
143 *repens* and *Carex divisa*. Flooding duration and water levels are variable on the intermediate slopes, from  
144 one to three months a year. The soil may be saline on the slopes and have salt-tolerant vegetation with a  
145 meso-hygrophilous (MH) plant community of sedges and grasses such as *Juncus gerardi*, *Alopecurus*  
146 *bulbosus* and *Hordeum marinum*. The depressions are flooded from winter to early spring, with a maximal  
147 water depth attaining 30–40 cm. They have a hygrophilous (H) plant community comprising flood-tolerant  
148 species such as *Agrostis stolonifera*, *Glyceria fluitans* and *Eleocharis palustris*.

149  
150 In this analysis, we estimated the demographic parameters of six abundant perennial species with variable  
151 clonal growth forms (see Benot et al. 2009; Klimešová and Klimeš 2006) and *in situ* distribution along the  
152 elevation gradient. *Agrostis stolonifera*, which is a stoloniferous tussock forming species, is distributed all  
153 along the elevation gradient, but more frequent in flooded locations, *Cynosurus cristatus* and the  
154 stoloniferous *Lolium perenne* are tussock forming mesophilous species, and the tussock forming *Hordeum*  
155 *secalinum* occurs both in the mesophilous and meso-hygrophilous vegetation. *Poa trivialis*, which is a  
156 stoloniferous tussock forming species, is found in both the mesophilous and the hygrophilous vegetation,  
157 and the tussock forming *Carex divisa* is found all over the elevation gradient (Marion et al. 2010). For all the  
158 studied species, the fundamental niche and realized niche were previously found to be shaped by the  
159 aeration SEV or flooding duration (Merlin 2012; Violle et al. 2011).

## 160 **Plant abundance measures**

161 Seventy permanent plots were placed along two elevation transects with a distance of 20 cm between  
162 plots. The cover of all the species in the plots was determined by the pin-point method: along both  
163 diagonals of the 25 x 25cm large plots, a pin was inserted every 4 cm for a total of 17 points per plot, and all  
164 the species that were touched by the pin were recorded. The abundance of the plant species was also  
165 measured by the vertical density, i.e. the number of times that a species touched each of the 17 pins in the  
166 pinpoint frame. The vertical density appeared to be integrative of the biomass growth of species during the  
167 growing season (Damgaard et al. 2009). The vertical density was used to order the different plant species  
168 according to abundance.

169

170 The abundance measurements were made on 23-29 October, 2008, 3-12 June, 2009, and 19-20 October,  
171 2009. The main demographic analysis was made on the change in plant cover during an entire year, i.e. the  
172 pin-point data from October, 2008, was compared with the pin-point data from October, 2009. However, in  
173 order to study whether the importance of the demographic processes differed during winter flooding or  
174 during the spring-summer dry out period, we also compared the pin-point data from October, 2008, with  
175 the data from June, 2009, and the pin-point data from June, 2009, with the data from October, 2009,  
176 respectively.

## 177 **Demographic model**

178 Here, we consider absence-presence data of species *A* from successive recordings from the same pin-point  
179 position. There are four possible transition events and corresponding probabilities between the successive  
180 recordings (Table 1). These transition probabilities depend on i) the probability ( $p$ ) that plant species *A* is  
181 present at time  $t$  (i.e. the cover of species *A* at time  $t$  Damgaard 2009), ii) survival; the probability that plant  
182 species *A* is present at the pin-point position both at time  $t$  and time  $t+1$ , iii) colonization; the probability

183 that plant species A is absent at the pin-point position at time  $t$ , but present at time  $t+1$ . The possibility of a  
 184 combined mortality and colonization is ignored.

185 As a generalization of the method developed in Damgaard et al. (2011; 2013), the probability of  
 186 colonization,  $c(z)$ , and survival,  $s(z)$ , are here assumed to be linear functions of an environmental gradient,  
 187  $z$ ,

$$188 \quad c(z) = c_0 + c_z z \quad (1a),$$

$$189 \quad s(z) = s_0 + s_z z \quad (1b).$$

190 The maximum likelihood estimates of the four parameters of colonization and survival (eqn. 1) were  
 191 estimated from the pin-point data by the four possible events of two successive recordings ( $X_1, X_2, X_3, X_4$ )  
 192 and their transition probabilities (Table 1) by maximizing the likelihood function of the multinomial

193 distribution, and where the probability that species A is present at time  $t$  is estimated as,  $p = \frac{X_1 + X_3}{n}$ ,

$$194 \quad L(c_0, c_z, s_0, s_z) = \prod_{i=1}^n \frac{(X_1 + X_2 + X_3 + X_4)!}{X_1! X_2! X_3! X_4!} p_{X_1}^{X_1} p_{X_2}^{X_2} p_{X_3}^{X_3} p_{X_4}^{X_4} \quad (2),$$

195 where  $p_{X_i}$  are defined in Table 1.

196 The change in the probability of species A being present from year  $t$  to  $t+1$  is denoted by  $\pi$  and is defined  
 197 as the ratio between the probability,  $p'$ , that species A is present at time  $t+1$  and the probability,  $p$ , that  
 198 species A is present at time  $t$ ,

$$199 \quad \pi = \frac{p'}{p} = \frac{p_{X_1} + p_{X_4}}{p_{X_1} + p_{X_3}} = \frac{c(z)}{p} + s(z) - c(z)s(z) \quad (3).$$

200 If  $\pi < 1$ , then the probability of species A being present, i.e. the cover of species A, decreases, and if  
 201  $\pi > 1$ , then the cover of species A increases. The change in cover over time is a function of the  
 202 colonization probability, the survival probability and the environmental gradient.

203 The relative sensitivity of the change in cover to the survival and colonization processes was determined by  
 204 an elasticity analysis. That is, following Damgaard et al. (2011; 2013), the elasticity of  $\pi$  was assumed to be  
 205 a function of colonization and survival,

$$206 \frac{c(z)}{\pi} \frac{\partial \pi}{\partial c(z)} = \frac{c - (p c(z)s(z))}{c + (p s(z)) - (p c(z)s(z))} \quad (4a),$$

$$207 \frac{s(z)}{\pi} \frac{\partial \pi}{\partial s(z)} = 1 - \frac{c(z)}{c + (p s(z)) - (1 - p)} \quad (4b).$$

208 Note than in the present application, where the species composition is allowed to vary along the  
 209 hydrological gradient, the effect of the hydrological gradient on the demographic parameters cannot be  
 210 separated from the possible changed competitive effect of the altered species composition.

## 211 Estimation procedure

212 The Bayesian joint posterior distribution of the four parameters of interest ( $s_0, s_z, c_0, c_z$ ) was estimated  
 213 using a Bayesian MCMC algorithm (Metropolis-Hastings) for each of the species using likelihood function (2)  
 214 and assuming that the prior distributions of the probabilities  $c(z)$  and  $s(z)$  were between zero and one.

215 The MCMC iterations converged relatively quickly to a stable joint posterior distribution (results not  
 216 shown), and the estimations were made from 100,000 iterations with a lag phase of 10,000 iterations.

217 Judged from the plotted MCMC iterations, there was some covariance between the parameters that  
 218 modelled the intercept and the slope in (1a) and (1b), respectively, but there was no covariance between  
 219 the two parameters that modelled colonization (1a) and survival (1b), i.e. the effects of hydrology on  
 220 colonization and survival was separated in the fitting procedure. The distribution of the elasticity of

221 colonization and survival (4) was calculated from the joint posterior distribution of the parameters and the  
222 mean elasticity was normalized to one.

223 All calculations were done using Mathematica version 10 (Wolfram 2015).

## 224 **Results**

225 The marginal posterior distributions of the four parameters of interest ( $S_0, S_{SE}, C_0, C_{SE}$ ) are summarized in  
226 Table 2 for the six most abundant species. For *A. stolonifera*, which was the species with the highest  
227 abundance across the hydrological gradient, both the colonization and survival probabilities increased  
228 significantly with aeration SEV. For the three species that followed next in order of overall abundance, *C.*  
229 *cristatus*, *L. perenne* and *H. secalinum*, the colonization probabilities decreased significantly with increasing  
230 aeration SEV. For the two least abundant species, *C. divisa* and *P. trivialis*, the hydrological gradient was not  
231 found to have a significant effect on the colonization and survival probabilities. However, since the  
232 statistical power of the analysis is an increasing function of the number of discriminating demographic  
233 events, the latter negative results may be attributed to lack of statistical power.

234 The dependency of the colonization and survival probabilities with the hydrological gradient matched the  
235 occurrence pattern for the four most abundant species along the hydrological gradient, where *A.*  
236 *stolonifera* was the only species that increased in cover with increasing SEV (Fig. 1).

237 The relative sensitivity of the change in cover of the six most abundant species to the survival and  
238 colonization processes was determined by an elasticity analysis (Fig. 2). The elasticities are functions of the  
239 initial cover and the hydrological gradient (eqn. 4), and generally and as expected, the importance of the  
240 colonization process for a change in cover decreased with increasing initial cover. Furthermore, *A.*  
241 *stolonifera* differed qualitatively from the other species, i.e. the importance of colonization increased with  
242 aeration SEV for *A. stolonifera*, whereas the importance of colonization decreased with SEV for the other  
243 species.

244 In order to study whether the importance of the demographic processes differed during winter flooding or  
245 within the spring-summer period, we also compared the pin-point data from October, 2008, with the data  
246 from June, 2009, and the pin-point data from June, 2009, with the data from October, 2009. The marginal  
247 posterior distributions of the four parameters of interest ( $S_0, S_2, C_0, C_2$ ) for both winter flooding or within  
248 the spring-summer period were qualitatively similar to the posterior distributions reported for the whole  
249 year in Table 2, except that there was no significant effect of flooding on the colonization probability of *H.*  
250 *secalinum* (results not shown).

## 251 **Discussion**

### 252 **Effect of hydrological gradient**

253 In the Marais poitevin grasslands, it has previously been shown that the flooding pattern is related to  
254 occurrence probabilities, i.e. Violle et al. (2011) showed that the occurrence pattern of 27 out of 37 species  
255 responded significantly to the elevation (flooding) gradient. Here, we have estimated the demographic  
256 parameters of six of the most abundant perennial species and found that there was a consistent pattern  
257 between the estimated probabilities and calculated elasticities of survival and colonization as well as the  
258 observed cover of the different species along the hydrological gradient. The flooding tolerant grass *A.*  
259 *stolonifera*, which is most abundant when flooding is prolonged, showed a positive response in both  
260 colonization and survival to flooding and/or differing competitive effects of the changed species  
261 composition and differed qualitatively in all aspects from the other species. Accordingly, the hydrological  
262 gradient is clearly the most likely explanation for the occurrence pattern observed for *A. stolonifera* versus  
263 the other commonly observed species.

264 Demographic processes can be affected by hydrology and competition and, consequently, that hydrology  
265 affects the ecological success of different plant species along the hydrological gradient in wet fertile  
266 grasslands (Li et al. 2015; Lytle and Merritt 2004; Merlin et al. 2015; Scanga 2014). In a meta-analysis,

267 Silvertown et al. (2015) showed that response to hydrological conditions is widespread (found in 43 out of  
268 48 studies) and occur in a “remarkably wide range of terrestrial environments ranging from arid to wet”.  
269 This suggests that the methods presented here generally may be used to predict the effect of a changing  
270 water regime in most grasslands communities or, possibly, the effect of other environmental drivers in  
271 grasslands communities (Harpole and Tilman 2006; Stevens et al. 2004).

## 272 **Predicting the realized niche**

273 Generally, we expect that the local probability of occurrence increases with the probability of colonization  
274 and decreases with the probability of mortality. In this study, we found that the dependency of the  
275 colonization and survival probabilities along the hydrological gradient matched the occurrence pattern for  
276 the four most abundant species along the hydrological gradient. This result indicates that knowledge of the  
277 processes of colonization and survival of the individual species along the hydrological gradient is sufficient  
278 for at least a qualitative understanding of species occurrences along the environmental gradient. Since it is  
279 the underlying assumption of this study that if the vital rates are measured *in situ* in natural plant  
280 communities along a gradient, then these vital rates will summarize the effect of both the environmental  
281 gradient and interspecific interactions on the examined species (Maguire 1973; Normand et al. 2014;  
282 Thuiller et al. 2014), we conclude that it may be possible to predict the realized niche along an  
283 environmental gradient from demographic studies. This is encouraging for the important endeavor of  
284 predicting realized niche dynamics in a changing climate (reviewed in Normand et al. 2014). The results are  
285 also in agreement with Adler et al. (2010), who found that demographic rates responding to niche  
286 dimension were rather stable and did not fluctuate across years.

287 In the study by Thuiller et al. (2014), the relationships between vital rates and occurrence probability were  
288 less clear than in our study, and they argue that this may be due to variable competitive effects. Indeed, the  
289 drawback of this and most other demographic studies is that the population ecological effect of variable  
290 abundance and interspecific competition is not taken into account as in a proper population ecological

291 realistic empirical competition model of the effect of the environmental gradient on the plant community  
292 dynamics (Damgaard 2011; Merlin et al. 2015). However, demographic population models may be the best  
293 alternative to simple species distribution modelling in many multi-species plant communities where it is not  
294 feasible to measure all relevant plant-plant interactions (see also Wisz et al. 2013). It is, thus, interesting to  
295 assess the generality of the present finding, and we agree with Thuiller et al. (2014) that: “Despite the  
296 foundational nature of these ideas, quantitative assessments of the relationship between range-wide  
297 demographic performance and occurrence probability have not been made. This assessment is needed  
298 both to improve our conceptual understanding of species, niches and ranges and to develop reliable  
299 mechanistic models of species geographic distributions that incorporate demography and species  
300 interactions.”

301 Furthermore, the results obtained are also ecologically meaningful due to explicit quantification of the  
302 niche dimension investigated, here flooding, as advocated by Smith et al. (2005) and suggested by  
303 Silvertown et al. (1999). The method also follows the suggestion of several authors to characterize the  
304 realized hydrological niche of each species and to build process-based models (e.g. Bartholomeus et al.  
305 2011; Silvertown et al. 2015), which is motivated by the fact that a demographic approach of understanding  
306 and predicting species’ range dynamics has the advantage of being rooted in ecological theory (reviewed in  
307 Normand et al. 2014). More specifically, the method allows an assessment of which suite of life history  
308 traits that affect either colonization or survival is most important for determining the width of the realized  
309 niche.

### 310 **Colonization vs. survival**

311 The obtained results support the view that colonization has a predominant role for determining the  
312 ecological success along the hydrological gradient compared to survival. In the dense vegetation cover,  
313 where the importance of competition remains high throughout the flooding gradient, colonization ability  
314 appears to be the most important parameter for the ecological success of perennial plant (Li et al. 2015;

315 Lytle and Merritt 2004; Merlin et al. 2015; Scanga 2014). These results are further corroborated by the  
316 finding of Chu and Adler (2015), who demonstrated the importance of the recruitment process for species  
317 niche space and fluctuation-independent coexistence for iteroparous herbs of open habitats. However, it is  
318 important to remember that the estimated colonization and survival probabilities as well as the connected  
319 elasticities are calculated from repeated pin-point cover data and, as mentioned before, the used  
320 terminology of colonization and survival is more accurate for some plant species than others.

321 More generally, the present findings suggest that the range of realized niches primarily is determined by  
322 the ability of a species to colonize new resource space in competition with other species rather than  
323 securing survival at an already colonized resource space. This finding is related to the seed limitation  
324 hypothesis, i.e. that many plant species are limited by colonization (Rees et al. 2001; Turnbull et al. 2000).  
325 Likewise, Adler et al. (2010) demonstrated that the recruitment process is more important than both  
326 survival and growth processes in determining niche differences. They hypothesized that pathogens and  
327 natural enemies have relatively strong effects during recruitment and mediate coexistence mainly at this  
328 stage of recruitment.

329 The importance of dispersal traits for the ecological success of plant species has previously been  
330 demonstrated by (e.g. de la Riva et al. 2011), and Schulze et al. (2012) showed that clonal growth is more  
331 important than sexual reproduction for determining population growth. In the Marais poitevin grasslands,  
332 the colonization process is dominated by clonal propagation; *C. cristatus*, *L. perenne*, *H. secalinum* and *A.*  
333 *stolonifera* provide numerous fast growing ramets (Benot et al. 2013), eventually supported by nutrients  
334 and carbohydrates provided from older better rooted ramets (Oborny et al. 2001). On the other hand, in  
335 the absence of clonal vegetation growth/propagation, Jäkäläniemi et al. (2005) showed that survival had a  
336 relatively large impact on patch dynamics.

### 337 **Estimating demographic parameters**

338 In order to make general predictions from demographic studies, it is important that they are not  
339 taxonomically biased; and this may be a problem in most traditional plant demographic studies, since  
340 certain plant morphologies, such as clearly distinct individuals, flowers and seeds are more readily  
341 measured and integrated into a matrix population model. For comparison, in the COMPADRE database of  
342 matrix population models there are 316 records of Poaceae out of 6242 total plant records, which probably  
343 is an underrepresentation of the family compared to its ecological role. In fact, one advantage of the used  
344 demographic method of space occupancy is that it is not taxonomically biased, since all pin-point  
345 measurements of the different species are performed at the same time.

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351

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Table 1. The four possible events of two successive recordings of presence-absence data and their

transition probabilities.  $p = \frac{X_1 + X_3}{n}$ ;  $s(z) = s_0 + s_z z$  and  $c(z) = c_0 + c_z z$ . The variables are explained in the text.

Event	Description	Transition probability
$X_1: A_t, A_{t+1}$	Species A was present in year $t$ and was also present in year $t+1$	$p( s(z) + c(z) ( 1 - s(z) ) )$
$X_2: \text{not } A_t, \text{not } A_{t+1}$	Species A was not present in year $t$ and was also not present in year $t+1$	$( 1 - p ) ( 1 - c(z) )$
$X_3: A_t, \text{not } A_{t+1}$	Species A was present in year $t$ but was not present in year $t+1$ (indicates a possible mortality event)	$p( 1 - p ) ( 1 - c(z) )$
$X_4: \text{not } A_t, A_{t+1}$	Species A was not present in year $t$ but was present in year $t+1$ (indicates a possible event of colonization event)	$( 1 - p ) c(z)$

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Table 2. Marginal posterior distributions (percentiles) of colonization and survival probabilities of the six most common species.  $s(z) = s_0 + s_z z$  and  $c(z) = c_0 + c_z z$ . The probability that the effect of the hydrological gradient on  $s_z$  or  $c_z$ , is greater than zero is also shown (note that significant departures from zero includes both  $P(> 0) < 0.05$  and  $P(> 0) > 0.95$ ). The species are ordered in decreasing abundance across the hydrological gradient. The variables are explained in the text.

Species	$s_0$			$s_z$				$c_0$			$c_z$			
	2.5%	50%	97.5%	2.5%	50%	97.5%	P(> 0)	2.5%	50%	97.5%	2.5%	50%	97.5%	P(> 0)
<i>Agrostis stolonifera</i>	0.333	0.473	0.604	-0.002	0.022	0.039	<b>0.965</b>	0.394	0.455	0.510	0.021	0.033	0.040	<b>1.000</b>
<i>Cynosurus cristatus</i>	0.042	0.117	0.192	-0.011	-0.001	0.020	0.425	0.072	0.112	0.161	-0.010	-0.006	0.001	<b>0.033</b>
<i>Lolium perenne</i>	0.048	0.238	0.457	-0.029	-0.009	0.019	0.232	0.226	0.278	0.336	-0.022	-0.018	-0.012	<b>0.000</b>
<i>Hordeum secalinum</i>	0.004	0.114	0.455	-0.017	0.007	0.052	0.728	0.167	0.247	0.346	-0.022	-0.014	-0.002	<b>0.014</b>
<i>Carex divisa</i>	0.004	0.086	0.284	-0.008	0.024	0.054	0.921	0.063	0.108	0.168	-0.006	0.002	0.012	0.681
<i>Poa trivialis</i>	0.003	0.066	0.365	-0.019	0.012	0.056	0.766	0.112	0.194	0.308	-0.019	-0.008	0.010	0.172

1 Figure Legends

2 Fig. 1. The cover of the six most common species along the hydrological gradient (aeration SEV) is shown  
3 for the first year (1 = 100% cover). The fitted line is the model (constant, exponential, or sigmoid) that was  
4 best supported by the pin-point cover data (lowest AIC). The best fitting models were a) *A. stolonifera*:  
5 exponential; b) *C. cristatus*: sigmoid; c) *L. perenne*: exponential; d) *H. secalinum*: constant; e) *C. divisa*:  
6 sigmoid; f) *P. trivialis*: exponential

7 Fig. 2. Elasticity of survival and colonization of the six most common species at varying initial cover (solid  
8 blue:  $p = 0.01$  , dotted black:  $p = 0.1$  , dashed green:  $p = 0.5$  , dotted-dashed red:  $p = 0.9$  . Note that  
9 the two elasticities sum to one. If the lines increase (decrease) with aeration SEV then the relative  
10 importance of survival increases (decreases) with aeration SEV. Color version of this figure is available  
11 online.

Fig. 1

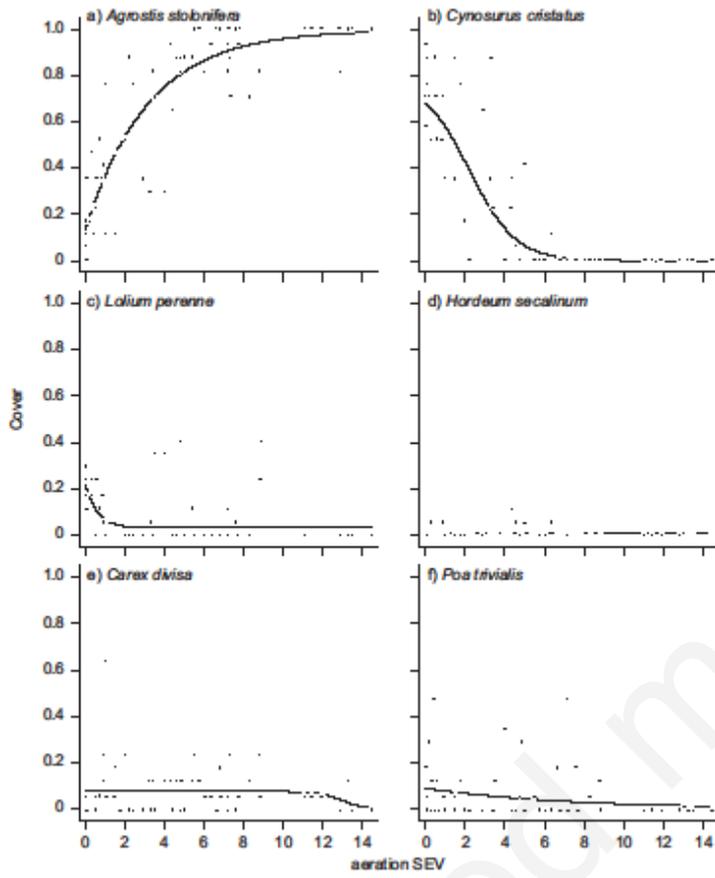


Fig. 2

