

1 **Abundance changes of marsh plant species over 40 years are better**
2 **explained by niche position water level than functional traits**

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20

21 **Abstract**

22 Understanding the factors that determine species' resistance to environmental change is of
23 utmost importance for biodiversity conservation. Here we investigated how the abundances of
24 marshland species are determined by niche properties and functional traits. We re-surveyed
25 150 vegetation plots that were first surveyed in 1973 in order to explore species abundance
26 changes over time. We found that the mean water level in the habitats of most studied species
27 decreased significantly from 1973 to 2012. Nine of 17 target species were identified as
28 abundance decreasing species and the other eight as abundance increasing species. The
29 comparisons of seven plant characteristics (niche position water level, plant height, and five
30 leaf traits) showed that the decreasing species had a significantly higher value of optimum
31 water level and marginally significantly lower leaf N contents and specific leaf area (SLA)
32 than those in increasing species. The stepwise regression analysis showed that optimum water
33 level and leaf N were the best predictors of abundance changes of marsh plant species, as well
34 as that the effect of optimum water level was stronger than that of leaf N. Our findings
35 demonstrated that niche properties may be important for forecasting changes in wetland plant
36 communities over time.

37

38 **Keywords:** species abundance; environmental change; optimum water level; leaf traits;
39 vegetation resurvey; wetland.

40 **Introduction**

41 Environmental changes are altering both the geographical distributions and the abundances of
42 plants worldwide (Beckage *et al.*, 2008; Hughes, 2000; Sturm *et al.*, 2001; Sala *et al.*, 2000;
43 Walther *et al.*, 2002). However, it is difficult to predict how plant communities will respond to
44 these changes because of the species-specific responses which occur among taxa (Grime,
45 1998; Lavorel & Garnier, 2002). Therefore, understanding which particular plant
46 characteristics determine the performance of species under environmental change is of utmost
47 importance for biodiversity conservation as well as for predicting future changes in species
48 distributions under climate change.

49 The responses of species to habitat change primarily depends on their biological and
50 ecological characteristics (Joan *et al.*, 2009; Broennimann *et al.*, 2006). Biological
51 characteristics, e.g., establish new populations, are determined by morphological and
52 physiological traits (e.g., individual size, root depth, mycorrhizae) related to resource
53 acquisition or competitiveness (Lavergne *et al.*, 2004; Van der Veken *et al.*, 2007). Ecological
54 characteristics, such as niche properties, may also be shaped by environmental drivers (e.g.,
55 water availability, temperature) (Devictor *et al.*, 2010; Swihart *et al.*, 2006; Williams *et al.*,
56 2007; Alarcon & Cavieres, 2018). There is a growing interest in the use of functional traits
57 and niche properties of species as indicators of their response capacities in the assessment of
58 the impacts of environment change on plant communities (Foden *et al.*, 2013; Triviño *et al.*,
59 2013; Garcia *et al.*, 2014; Pearson *et al.*, 2014). However, whether these characteristics are
60 predictors of the performance responses of species to temporal environmental changes has

61 rarely been experimentally tested in the field.

62 Several key properties or traits have been proposed as determinants of species responses to
63 environmental change (Soudzilovskaia *et al.*, 2013; Alarcon & Cavieres, 2018; Estrada *et al.*,
64 2015; Broennimann *et al.*, 2006), including niche position, leaf N contents and specific leaf
65 area *et al.*. Meanwhile, many hypotheses have been proposed, for example (1) species with
66 marginal niche position is more sensitive to environmental change than those with middle
67 niche position (Johnson, 1998); (2) species with higher leaf N contents (nitrogen-demanding
68 species) are often comparably winner species (Diekmann *et al.*, 1999); (3) species with higher
69 specific leaf area tended to be loser species compared to winner species (Naaf and Wolf,
70 2011). However, these hypotheses remain poorly explored under other conditions of
71 environmental changes besides climate warming.

72 Over the last several decades, the Sanjiang Plain in Northeast China has undergone
73 pronounced temperature increases and unprecedented land use changes with marked
74 decreases in wetland areas (Liu & Ma, 2002). These changes caused significant changes in
75 species composition and richness (Lou *et al.* 2015). Moreover, our previous studies have
76 identified a significant impact of habitat change on niche properties (Lou *et al.*, 2018) and
77 functional traits (Lou *et al.*, 2012; 2016) of dominant marsh plants. However, these studies
78 mainly focused on either community-level changes or differences in functional traits of
79 individual species. It is not known how the abundance of individual species has responded to
80 habitat change over the recent decades. The studies by Lou *et al.* (2012; 2015; 2016; 2018)
81 provide the basis for exploring how abundance changes of marsh plant species to be related

82 with functional traits and niche properties.

83 This study aimed to investigate the influence of functional traits, niche properties and
84 environmental changes on abundance changes of marsh plant species in Northeast China.
85 Firstly, we identified increasing and decreasing species by comparing abundance of the
86 dominant marshland species between the sampling year 1973 and 2012. Secondly, we tested
87 whether the increasing and decreasing species differed in niche and trait attributes. Thirdly,
88 we quantified the relative importance of niche properties, functional traits and environmental
89 changes.

90 **Materials and methods**

91 **Study area**

92 The Sanjiang Plain in Northeast China is the alluvial plain of the Heilongjiang, Songhua, and
93 Wusuli Rivers. It encompasses a total area of 108,829 km² and has an altitude of mostly <200
94 m a.s.l. (Fig. 1). The climate type of the area is temperate humid and sub-humid continental
95 monsoon climate, with mean annual precipitation of 510-620 mm and mean annual
96 temperature of 2.1-4.5 °C. The vegetation is dominated by four plant communities:
97 permanently flooded emergent marshes (dominant species: *Phragmites australis*, *Carex*
98 *lasiocarpa*, and *Carex pseudocuraica*), seasonally flooded tussock marshes (*Carex*
99 *appendiculata* or *C. meyeriana*), occasionally flooded marsh meadows (*C. appendiculata* and
100 *Calamagrostis angustifolia*), and shrub marsh meadows (*Betula fruticosa*, *Alnus sibirica*,
101 *Salix brachypoda*, and *C. angustifolia*). The soil types include Luvisols, Phaeozems,

102 Cambisols, and Histosols.

103 The study area includes the Sanjiang Plain Marsh Ecological Experimental Station (CERN)
104 and the International Long Term Ecological Research Network (ILTER, [http://](http://data.iter-europe.net/deims/site/iter-eap-cn-29)
105 data.iter-europe.net/deims/site/iter-eap-cn-29). In recent decades, this area has undergone
106 significant climate warming and human reclamation activities (Liu & Ma, 2002) which
107 resulted in drying of the wetland habitats and drastic decreases in marsh areas from more than
108 50,000 km² in the 1940s to 9,100 km² in 2000 (Lou *et al.*, 2015).

109 **Vegetation survey**

110 In July and August of 1973, when the water level was the lowest in the whole growing season
111 (Lou *et al.*, 2016), the first vegetation survey of the Sanjiang Plain was conducted by Zhao
112 Kuiyi, Li Chonghao, Yi Fuke *et al.* (Changchun Institute of Geography, CAS) with the aim of
113 mapping vegetation and describing vegetation types. In this historical study, vegetation was
114 surveyed using sampling plots of 1 m×1 m. For each vascular plant species in each plot, the
115 percentage cover (0-100% vertical projection) was estimated. Furthermore, water level in
116 each plot was measured using a meter stick above the soil surface. In the above-mentioned
117 historical surveys, vegetation plots were not permanently marked, but the positions of the
118 plots were described in great detail so that they could be located again.

119 In July and August of 2012, we resurveyed 70 plots of *Carex lasiocarpa* formations and 80
120 plots of *Carex appendiculata* formations (a total of 150 plots) following the sampling
121 protocols described in Zhao *et al* (1999). The descriptions of the sites and plot locations from

122 the previous surveys (e.g., landform, proximity to river) were carefully studied and all
123 available information was taken into account when we were relocating plots within similar
124 vegetation types. Plots were placed as close as possible to their supposed original locations in
125 each wetland site (estimated spatial errors <10 m). All the plots were located in national or
126 provincial nature reserves, and no human disturbance (such as fire) occurred from 1973 to
127 2012. In 2012, the geographic position of every studied plot was determined using a GPS.
128 Plant nomenclature followed Fu (1995).

129 **Data analyses**

130 Species abundance changes

131 Species abundance indicates the percentage cover on average for all plots where the plant
132 species was present. We calculated species abundance for both 1973 and 2012. If the changes
133 in abundance of a species from 1973 to 2012 were positive, the species was regarded as
134 ‘increasing species’, in the opposite case, the species was regarded as ‘decreasing species’.
135 Only species occurring in at least 15 plots in whether the original sampling or resampling
136 were considered for statistical analyses of species cover ($n = 17$). For each of the 17 species,
137 paired t-test was used to test the significance of the differences in species cover between the
138 two sampling years.

139 Analysis of the drivers of species abundance changes

140 In order to explain the observed differences in abundance between the two periods, we
141 assembled the data on environmental changes and species traits according to their ecology

142 and biology.

143 As Lou *et al.* (2015) found that hydrology is the main factor controlling the changes along the
144 marsh zonation in the study area, we used the change in water level as the indicator of
145 environmental change. For each species in each sampling year, we calculated the average
146 water level in all plots where the species occurred. For each species, the significance of the
147 differences in the water level between the two sampling years was tested by paired t-test, and
148 the change in the water level between the two sampling years was calculated by subtracting
149 the water level value in 1973 from the water level value in 2012.

150 We used niche optimum along the water level gradient as an ecological property. For all the
151 selected species, the responses of each species to water level gradient were fitted by
152 Generalized Additive Models (GAM, Hastie and Tibshirani, 1990). In which, water level and
153 abundance data (represented by percent cover, 0-100%, as a continuous variable) from the
154 field survey in 1973 were used as the explanatory and dependent variable, and the identity and
155 Gaussian were selected as the link function and error term, respectively. The optimum of each
156 species was identified as the value of water level at which abundance of a species had its
157 maximum.

158 For the analysis of biological traits, we measured plant height, leaf area (LA), specific leaf
159 area (SLA), leaf N, P, and N:P ratios from the samples collected in the ten field sites during
160 vegetation surveys in 2012. In each marsh site, aboveground parts of ca. 10 to 20 individuals
161 or ramets per studied species were harvested and taken back to the laboratory. Plant height

162 was measured by ruler. Three healthy mature leaves were obtained from each individual and
163 measured by a leaf area meter (LI3000C). Leaf samples were further dried in a drying oven
164 for 24 h at 70 °C, and their dry weights were measured by analytical balance with the
165 accuracy of 0.0001 g. Phosphorus and Nitrogen concentrations were determined using the
166 molybdenum blue method and the indophenol blue method, respectively, using Skalar
167 Auto-Analyzer. Boxplots were used to remove outliers, following which the mean values of
168 each trait in each studied species were calculated. We evaluated whether decreasing and
169 increasing species differed in their trait attributes using the t-test. We also tried to collect the
170 information on root traits of the studied species, but this task was not completed because of
171 sampling difficulties resulted from the clonality of the studied species in the field. For this
172 reason, root traits were not included in the analysis of biological traits.

173 Finally, we assessed how much of the variation in abundance could be explained by
174 environmental changes and plant ecological and biological properties using a linear model.
175 We conducted a stepwise regression analysis of the changes in abundance, and only
176 significant variables were selected as the predictors. Meanwhile, in order to clearly assess the
177 relationship between each trait or niche parameter and abundance changes, we also conducted
178 a linear regression analysis for each trait or niche parameter with change in cover as the
179 response variable. In addition, we also tested the effect of phylogeny on species abundance
180 changes and the selected significant variables, and found no correlation between them
181 (supporting information I). So the effect of phylogeny was excluded, and phylogeny was not
182 included as an driving factor of species abundance changes.

183 All independent variables were standardized prior to the regression analysis. The statistical
184 analyses were conducted in R version 3.4.1 (R Development Core Team 2010) with the R
185 package mgcv (Wood, 2006).

186 **Results**

187 **Changes in water level in the investigated habitats**

188 General climate conditions during the two sampling years were comparable. Mean daily air
189 temperature and monthly precipitation from January to December in 1973 were similar to
190 those in 2012 (Fig. 2) and were not significantly different (t test: $F=0.481$, $p=0.495$ for mean
191 air temperature; $F=0.072$, $p=0.792$ for monthly precipitation). Mean water level in the 150
192 plots decreased significantly from 9.7 ± 0.69 cm (mean \pm SE) in 1973 to 5.3 ± 0.41 cm in 2012
193 (paired t-test: $t=5.477$, $p<0.001$). Out of the 17 common species, 11 species experienced a
194 significant decline in the mean water level of their habitats of at least 4.5 cm from 1973 to
195 2012, and two species (*Stachys baicalensis* and *Scutellaria baicalensis*) experienced an
196 increase, but it was not significant (Table 1).

197 **Changes in species abundance**

198 The 17 dominant marsh species are all perennials. Of which, nine species decreased in their
199 abundance from 1973 to 2012 and were identified as decreasing species, and eight species
200 increased in their abundance and were identified as increasing species. Average abundance
201 changes between the sampling year 1973 and 2012 among decreasing and increasing species
202 ranged from -12.2% (*Carex pseudocuraica*) to +7.3% (*Carex appendiculata*). Two of the
203 decreasing species (*Menyanthes trifoliata* and *Sanguisorba tenuifolia*) and five of the
204 increasing species (*Lysimachia thyrsoiflora*, *Glyceria spiculosa*, *Equisetum fluviatile*, *Iris*
205 *laevigata*, and *Carex pseudocuraica*) were significant (Fig. 3). The group of decreasing and

206 increasing species were both heterogeneous and were comprised of seven and five families,
207 respectively (supporting information I).

208 **Drivers of species abundance changes**

209 The comparison of seven tested traits between the increasing and decreasing species showed
210 that only the difference in optimum water level was significant (Fig. 4, t-test: $t=3.811$,
211 $p=0.002$). The differences in leaf N and SLA between the increasing and decreasing species
212 were marginally significant (t-test: $t=-1.891$, $p=0.078$; $t=-2.095$, $p=0.054$, respectively; Fig. 4).
213 No significant differences were observed in the other traits (plant height, leaf P, N:P ratios and
214 leaf area) between the increasing and decreasing species (Fig. 4).

215 Optimum water level and leaf N were good individual predictors of abundance change and
216 they were negatively and positively correlated with abundance changes, respectively (Table 2).
217 The best model based on multiple traits explained 68% of the variance and included only
218 optimum water level and leaf N. However, R^2 only marginally increased when leaf N was
219 added as a predictor in the model with niche position water level (Table 2, Fig. 5).

220 **Discussion**

221 In this study, we conducted a novel analysis of the driving factors of species abundance
222 change over time at the local scale. Out of all tested factors, the most important factor for
223 explaining changes in marsh plant abundance was the relative realized optimum position
224 along the water level gradient, and leaf N also had a minor impact. i.e. species with a higher
225 water level optimum and, at the same time, lower leaf N content decreased more dramatically
226 in abundance between 1973 and 2012.

227 The two traits included into the best model (optimum water level and leaf N) represent the
228 environmental tolerance and resource capture capacity of a species, respectively, and these
229 traits explained more than half of the variation in cover change. The explanatory power of the
230 relative realized optimum position along the water level gradient was much greater than that
231 of leaf N. On the one hand, this indicates that the influence of environmental tolerance on
232 species sensitivity is greater than that of biological traits. On the other hand, this is a relatively
233 high value in comparison with those obtained in other studies on abundance dynamics
234 (Soudzilovskaia *et al.*, 2013). This is likely because of the fact that the water level gradient
235 represents a complex gradients (correlation with the other environmental factors, e.g. soil
236 nutrient, Lou *et al.*, 2013) and the effects of the other substrates on species abundance may be
237 integrated into that of water level.

238 The univariate negative correlation between species abundance change and optimum water
239 level (Table 1) indicates that the species with high optimum water level increase their

240 dominance, while the species with low optimum water level decrease their dominance as a
241 consequence of habitats drying. This is consistent with the niche position (or habitat
242 availability) hypothesis and with other studies which assumed that the closer the niche is to
243 the margins of the environmental gradient, the more sensitive the species are to habitat change
244 (Heino & Mendoza, 2016; Williams *et al.*, 2007; Broennimann *et al.*, 2006). This suggests
245 that the potential sensitivity of species to habitat change can, at least partly, be estimated *a*
246 *priori* from their niche characteristics along key environmental gradients, and this was
247 confirmed in another study as well (Thuiller *et al.*, 2005).

248 In the present study, biological traits seemed to play a relatively minor role in the prediction
249 of marsh species abundance changes. Out of the investigated traits, there was a relatively big
250 difference only in leaf N and SLA between the decreasing and increasing species. Leaf N of
251 the increasing species was higher than that of the decreasing species. On the one hand, leaf N
252 is related to leaf growth, and species with high leaf N have generally a rapid growth rate
253 (Reich *et al.*, 2008). Laliberte *et al* (2012) found that species associated with a rapid growth
254 rate become dominant under soil resource addition, and this supports our result based on the
255 fact that the N deposition is serious in study area (Lou *et al.*, 2015). On the other hand, this
256 suggests that the minor importance of leaf N may be a result of its correlation with the
257 optimum water level which was stronger than that of all the other tested traits (supporting
258 information II), i.e., its contribution may be a result of its covariance with the optimum water
259 level. Similarly, SLA of the increasing species was larger than that of the decreasing species,
260 and this is also consistent with the result of Laliberte *et al.* (2012). Moreover, SLA has been

261 proved to impact abundance dynamics in the studies by Soudzilovskaia *et al.* (2013) and
262 Estrada *et al.* (2015). However, this trait had very low explanatory power for abundance
263 changes in our study, most likely because the capacity for rapid growth and competition
264 conferred by SLA is possibly not useful to new ramets regeneration, which is the main way to
265 increase species dominance in wetland communities dominated by colonization.

266 The exclusion of a variety of reproductive traits along with population dispersal may also
267 impact the relationships between biological traits and species abundance changes. The role of
268 reproductive traits in species persistence and colonization has been highlighted by many
269 researchers (Thuiller *et al.*, 2012; Estrada *et al.*, 2015; Pacifici *et al.*, 2017; MacLean &
270 Beissinger, 2017). Most wetland vascular plant species feature clonal reproduction and their
271 clonal growth traits (e.g., tiller number, rhizome biomass, root depth, etc.) were shown to be
272 important for species distribution dynamics at small scales (Purcell *et al.*, 2019; Moor *et al.*,
273 2015; 2017). For example, species with deeper roots are more able to resist habitat changes
274 than shallower-rooted species (Willis, 2017). In the present study, the increased abundance of
275 *Menyanthes trifoliata* may be related to its deep roots. In addition, our approach did not
276 consider intra-specific plasticity or variation of traits, which can be substantial since species
277 traits depend on hydrological heterogeneity (e.g., Kostikova *et al.*, 2013) and are well
278 documented as key mechanisms affecting species resistance to habitat change (Valladares *et*
279 *al.*, 2014; Liancourt *et al.*, 2015).

280 The correlation between niche properties and functional traits (especially life history traits)
281 may interfere with our results. The study carried out by Thuiller *et al.* (2004) confirmed that

282 niche position was related to leaf and flowering traits. In the present study, niche position
283 water level may have been determined by the traits related with flooding conditions, by other
284 adaptations to anoxia, and perhaps by the presence of mycorrhiza at the dry side of the
285 gradient. For example, Purcell *et al.* (2019) demonstrated that fine root traits (such as
286 aerenchyma and dry matter content of fine root) are correlated with flooding duration in
287 ephemeral wetlands. Such traits were not included in this study because of the difficulty in
288 collecting data on these traits. In the follow-up studies, the correlation analysis of niche
289 properties and life history traits related to flooding conditions needs to be carried out.

290 Finally, water level changes was not showed as the variable response for species dominance
291 change in this study, but its role was third next to that of leaf N and optimum water level
292 (Table 2). This demonstrates that water level change is still an important driving factor of
293 vegetation change, and should be strengthened in the future research. As for the driving
294 factors of water level decrease, besides climate warming and drainage mentioned in our
295 previous study (Lou *et al.*, 2015), the impact of land use change needs to be reemphasized
296 here. The area of paddy field in this region increased from 3,200 ha in 1990 to 91,300 ha in
297 2005, and much more groundwater was extracted for irrigation, with the result that the buried
298 depth of groundwater level in this area decreased by 3 m on average (Li *et al.*, 2007).

299 **Conclusions**

300 This study highlighted that the response of species abundance to habitat change depends more
301 on their niche position water level than on their functional traits. It is well known that local

302 abundances of species are related to the extent of their geographical distribution (Brown,
303 1984); thus, niche position water level, and possibly leaf N, should be considered for
304 integration into species distribution models for predicting regional distribution of wetland
305 plants. This study suggested at least three perspectives for further research, concerning: a)
306 disentangling the relative contribution of soil nutrient availability in the complex gradient
307 represented by water level; b) including reproductive and life history traits related with
308 flooding conditions into the driving mechanism of abundance changes of marsh plant species,
309 and c) acquiring a better understanding of site hydrology as it is an important controlling
310 factor of vegetation changes in marsh ecosystems.

311

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317

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465 Appendix A. Supplementary data

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Table 1. Mean water level for 17 dominant species in Sanjiang Plain marsh in the two sampling years. *p*-value was obtained from paired t-test. Species are sorted by their presence in the plots 1973.

Species	Number of plots		Mean water level (cm) (mean \pm SE)		
	1973	2012	1973	2012	<i>p</i>
<i>Carex lasiocarpa</i>	109	101	11.6 \pm 0.83	6.6 \pm 0.53	0.000
<i>Glyceria spiculosa</i>	84	50	13.2 \pm 1.17	6.1 \pm 0.64	0.000
<i>Carex pseudocuraica</i>	58	93	10.8 \pm 1.25	6.3 \pm 0.63	0.003
<i>Lysimachia thyrsoiflora</i>	57	70	9.6 \pm 1.02	5.4 \pm 0.48	0.000
<i>Caltha palustris</i>	56	80	8.6 \pm 0.83	3.8 \pm 0.53	0.000
<i>Equisetum fluviatile</i>	52	57	10.3 \pm 1.11	5.6 \pm 0.61	0.001
<i>Menyanthes trifoliata</i>	50	48	10.4 \pm 1.06	6.4 \pm 0.55	0.005
<i>Iris laevigata</i>	47	38	7.6 \pm 0.86	5.9 \pm 0.54	0.066
<i>Salix myrtilloides</i>	47	47	10.3 \pm 1.06	5.2 \pm 0.72	0.000
<i>Comarum palustre</i>	44	80	8.4 \pm 0.93	7.2 \pm 0.67	0.442
<i>Carex meyeriana</i>	40	44	8.2 \pm 1.0	5.7 \pm 0.86	0.075
<i>Carex appendiculata</i>	38	43	6.9 \pm 0.96	1.4 \pm 0.27	0.000
<i>Calamagrostis angustifolia</i>	31	46	5.5 \pm 0.90	3.1 \pm 0.42	0.025
<i>Sanguisorba tenuifolia</i>	28	22	4.9 \pm 0.77	3.6 \pm 0.59	0.186
<i>Lycopus lucidus</i>	21	51	4.1 \pm 0.95	1.7 \pm 0.48	0.019
<i>Stachys baicalensis</i>	9	19	2.9 \pm 1.01	4.3 \pm 0.64	0.158
<i>Scutellaria baicalensis</i>	4	20	3.3 \pm 0.88	4.7 \pm 1.00	0.608

470 **Table 2.** Results of the regression analyses of abundance changes and plant functional traits. The
 471 ecological trait was the optimum water level, and the biological traits were individual height, leaf N, P,
 472 and N:P, specific leaf area (SLA) and leaf area (LA). Only the variables strongly related to change in
 473 species abundance are shown. OWL, optimum water level; WLC, water level change; N, number of
 474 species; B, regression coefficient.

Response variable	Model	Significant predictors	B	AIC	F	R ² _{adj}	p
Cover change	multiple stepwise regression (n=17)	OWL + Leaf N		87.160	17.82	0.68	< 0.001
		OWL	-3.54				< 0.001
		Leaf N	1.02				0.200
	individual predictor (n=17 for each predictor)	OWL	-3.98	87.222	32.12	0.66	< 0.001
		Leaf N	2.55	101.111	5.814	0.23	0.029
		WLC	1.50	104.951	1.606	0.036	0.224
		Leaf N:P ratio	0.91	106.061	0.556	< 0	0.468
		SLA	0.80	106.205	0.43	< 0	0.524
		Leaf P	0.58	106.436	0.216	< 0	0.648
		Leaf area	0.40	106.56	0.11	< 0	0.749
Height	-0.11	106.67	0.01	< 0	0.93		

476 **Figure legends**

477 **Fig. 1** Distribution of the investigated sampling plots in the wetlands of the Sanjiang Plain,
478 Northeast China.

479 **Fig. 2** The comparison of monthly mean air temperature (a) and monthly precipitation (b) of
480 five national meteorological stations (Fujin, Jiamusi, Baoqing, Hulin and Hegang Station) in
481 study area for the sampling year 1973 and 2012.

482 **Fig. 3** Abundance changes of the 17 most common wetland species in Sanjiang Plain between
483 the sampling year 1973 and 2012.

484 **Fig. 4** Comparison of niche property and functional traits between the decreasing and
485 increasing species. DS: decreasing species; IS: increasing species.

486 **Fig. 5** The relationship between optimum water level, leaf N, and species abundance changes.

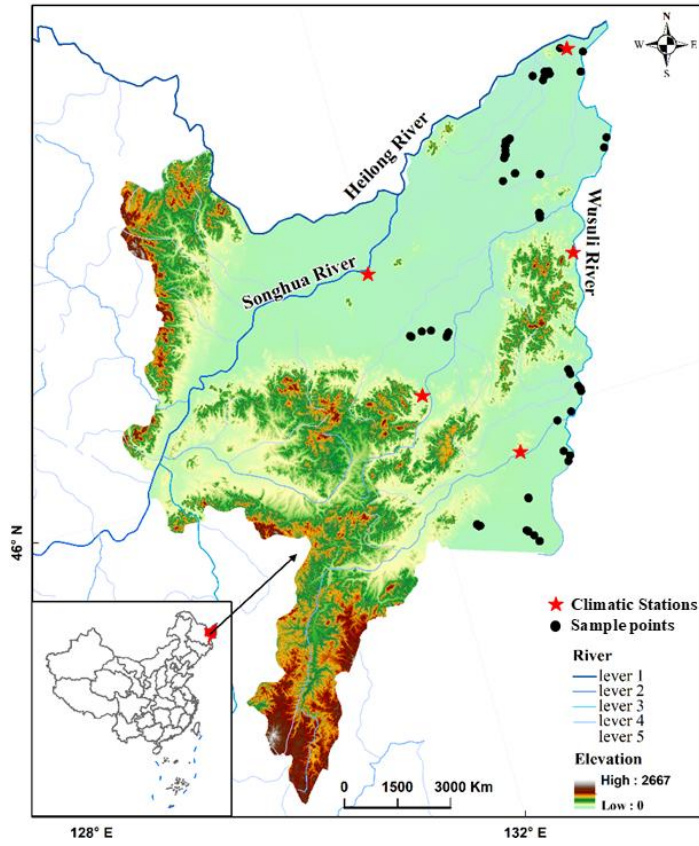


Fig. 1 Distribution of the investigated sampling plots in the wetlands

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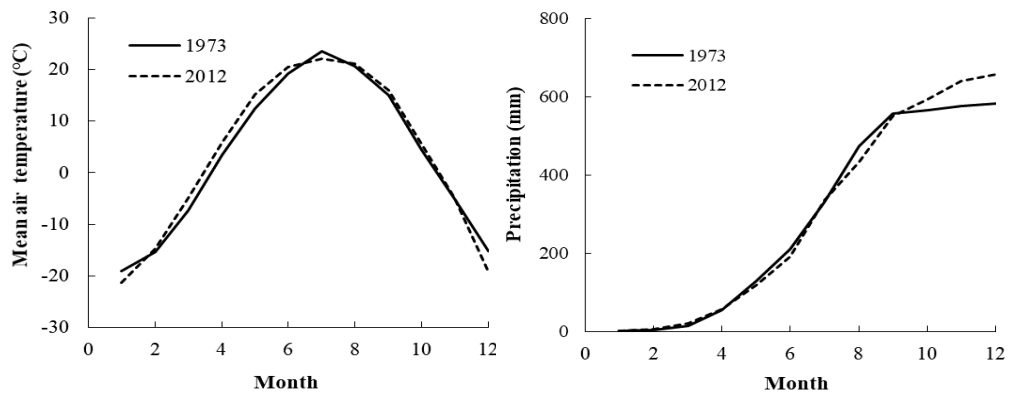


Fig. 2 Monthly mean air temperature (a) and accumulated rainfall in January-December (b) of five national meteorological stations (Fujin, Jiamusi, Baoqing, Hulin and Hegang Station) in study area for the sampling year 1973 and 2012.

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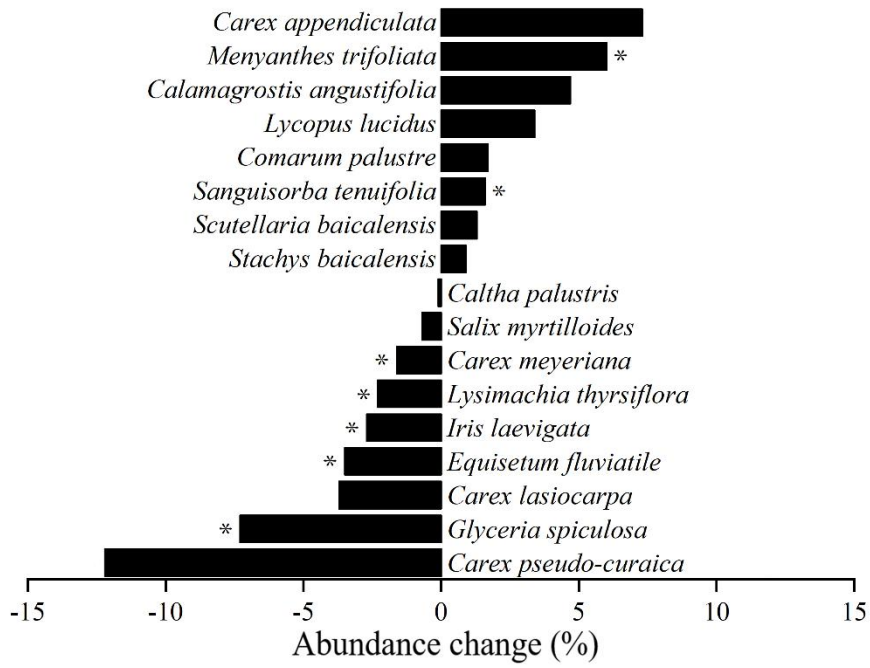


Fig. 3 Abundance changes of the 17 most common wetland species in Sanjiang Plain between the sampling year 1973 and 2012. * indicates significant abundance change based on the paired-t test.

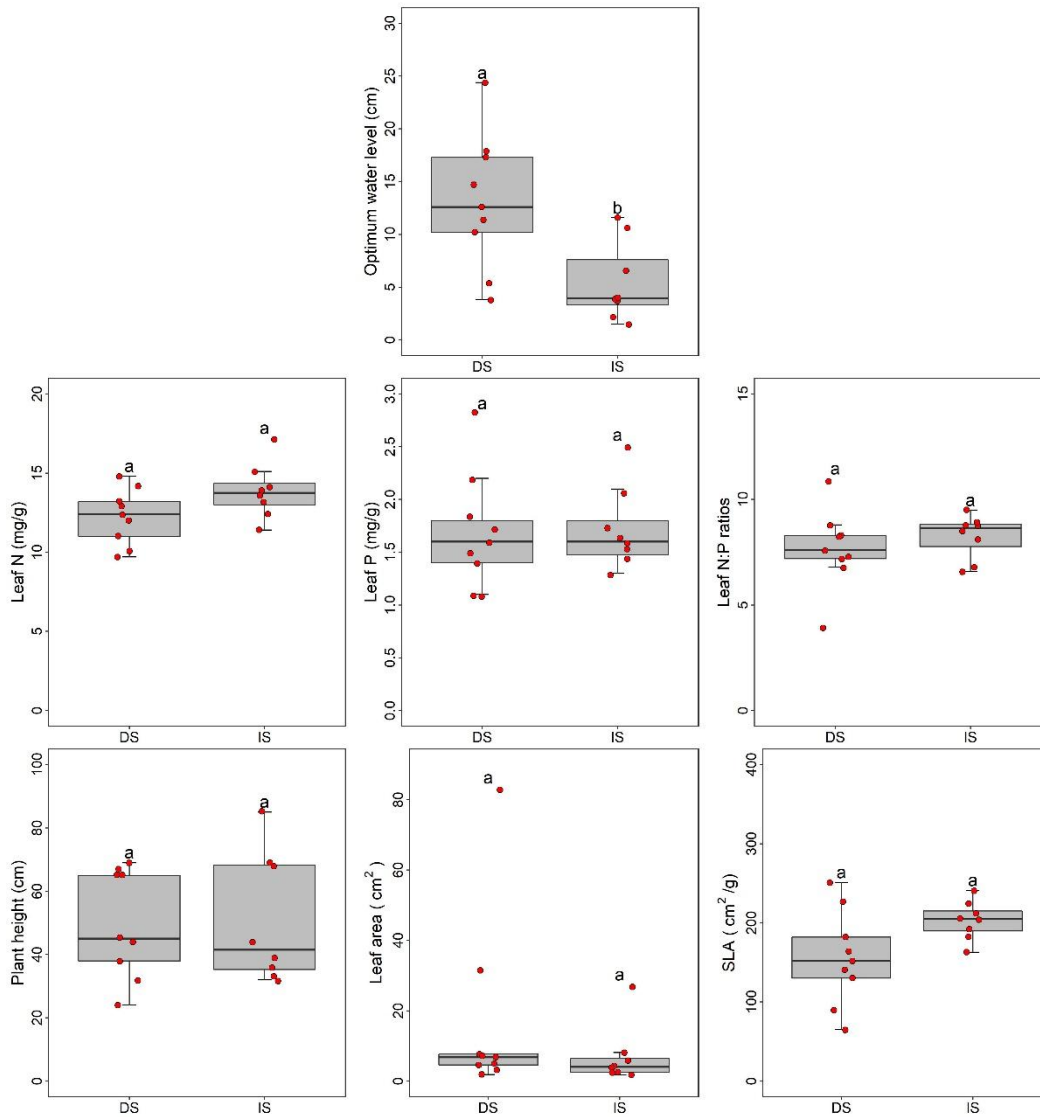


Fig. 4 Comparison of niche property and functional traits between the decreasing and increasing species. DS: decreasing species, n=9; IS: increasing species, n=8. The core boxes of boxplots indicate the interquartile range of data whereas the whisker lines symbolize the centiles 5 and 95, middle black line is the median.

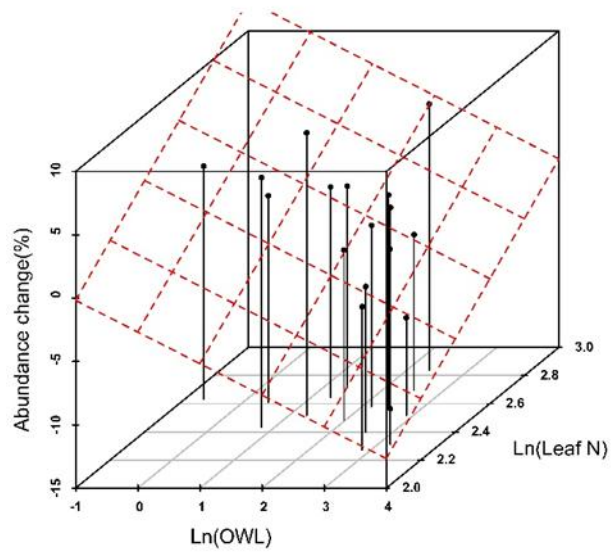


Fig. 5 The relationship between optimum water level, leaf N and species abundance changes (n=17 species).

Supplementary Material

[Click here to download Supplementary Material: supporting information-revision.docx](#)

Conflict of interest statement

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the position presented in, or the review of, the manuscript entitled “ Abundance changes of marsh plants over 40 years are better explained by niche position than functional traits”.

Credit author statement

Yanjing Lou: investigation, data curation, writing, original draft preparation; **Jutta Kapfer:** methodology, reviewing and editing; **Pete Smith:** reviewing and editing; **Ying Liu:** investigation, data analysis, figures. **Ming Jiang and Xianguo Lu:** data collecting and reviewing; **Michael Ashcroft:** reviewing and editing.