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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Abstract

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

Introduction

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

The responses of species to habitat change primarily depends on their biological and ecological characteristics (Joan *et al*., 2009; Broennimann *et al*., 2006). Biological characteristics, e.g., establish new populations, are determined by morphological and physiological traits (e.g., individual size, root depth, mycorrhizae) related to resource acquisition or competitiveness (Lavergne *et al*., 2004; Van der Veken *et al*., 2007). Ecological characteristics, such as niche properties, may also be shaped by environmental drivers (e.g., water availability, temperature) (Devictor *et al*., 2010; Swihart *et al*., 2006; Williams *et al*., 2007; Alarcon & Cavieres, 2018). There is a growing interest in the use of functional traits and niche properties of species as indicators of their response capacities in the assessment of the impacts of environment change on plant communities (Foden *et al*., 2013; Triviño *et al*., 2013; Garcia *et al*., 2014; Pearson *et al*., 2014). However, whether these characteristics are 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 km^2 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://

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 km^2 in the 1940s to 9,100 km^2 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).

Results

Changes in water level in the investigated habitats

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

Changes in species abundance

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

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).

Discussion

220

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.

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465 Appendix A. Supplementary data

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468

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 ± SE)		
	1973	2012	1973	2012	p
Carex lasiocarpa	109	101	**11.6 ± 0.83**	**6.6 ± 0.53**	**0.000**
Glyceria spiculosa	**84**	**50**	**13.2 ± 1.17**	**6.1 ± 0.64**	**0.000**
Carex pseudocuraica	**58**	**93**	**10.8 ± 1.25**	**6.3 ± 0.63**	**0.003**
Lysimachia thyrsiflora	57	70	**9.6 ± 1.02**	**5.4 ± 0.48**	**0.000**
Caltha palustris	**56**	**80**	**8.6 ± 0.83**	**3.8 ± 0.53**	**0.000**
Equisetum fluviatile	52	57	**10.3 ± 1.11**	**5.6 ± 0.61**	**0.001**
Menyanthes trifoliata	50	48	**10.4 ± 1.06**	**6.4 ± 0.55**	**0.005**
Iris laevigata	47	38	7.6 ± 0.86	5.9 ± 0.54	0.066
Salix myrtilloides	47	47	**10.3 ± 1.06**	**5.2 ± 0.72**	**0.000**
Comarum palustre	**44**	**80**	8.4 ± 0.93	7.2 ± 0.67	0.442
Carex meyeriana	40	44	8.2 ± 1.0	5.7 ± 0.86	0.075
Carex appendiculata	38	43	**6.9 ± 0.96**	**1.4 ± 0.27**	**0.000**
Calamagrostis angustifolia	31	46	**5.5 ± 0.90**	**3.1 ± 0.42**	**0.025**
Sanguisorba tenuifolia	28	22	4.9 ± 0.77	3.6 ± 0.59	0.186
Lycopus lucidus	**21**	**51**	**4.1 ± 0.95**	**1.7 ± 0.48**	**0.019**
Stachys baicalensis	9	19	2.9 ± 1.01	4.3 ± 0.64	0.158
Scutellaria baicalensis	**4**	**20**	3.3 ± 0.88	4.7 ± 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.
475

| 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

Figure legends

Fig. 1 Distribution of the investigated sampling plots in the wetlands of the Sanjiang Plain,

Northeast China.

Fig. 2 The comparison of monthly mean air temperature (a) and monthly precipitation (b) of

five national meteorological stations (Fujin, Jiamusi, Baoqing, Hulin and Hegang Station) in

study area for the sampling year 1973 and 2012.

Fig. 3 Abundance changes of the 17 most common wetland species in Sanjiang Plain between

the sampling year 1973 and 2012.

Fig. 4 Comparison of niche property and functional traits between the decreasing and

increasing species. DS: decreasing species; IS: increasing species.

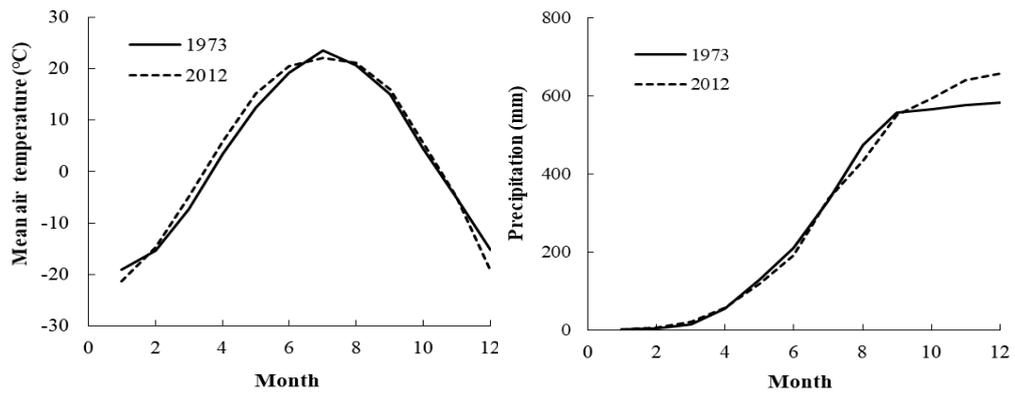**Fig. 5** The relationship between optimum water level, leaf N, and species abundance changes.
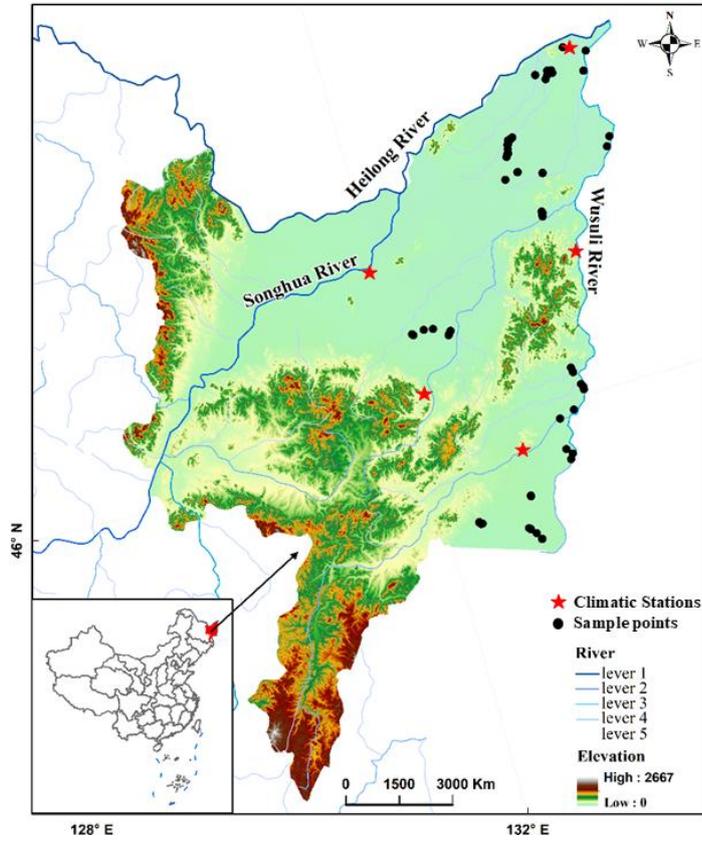
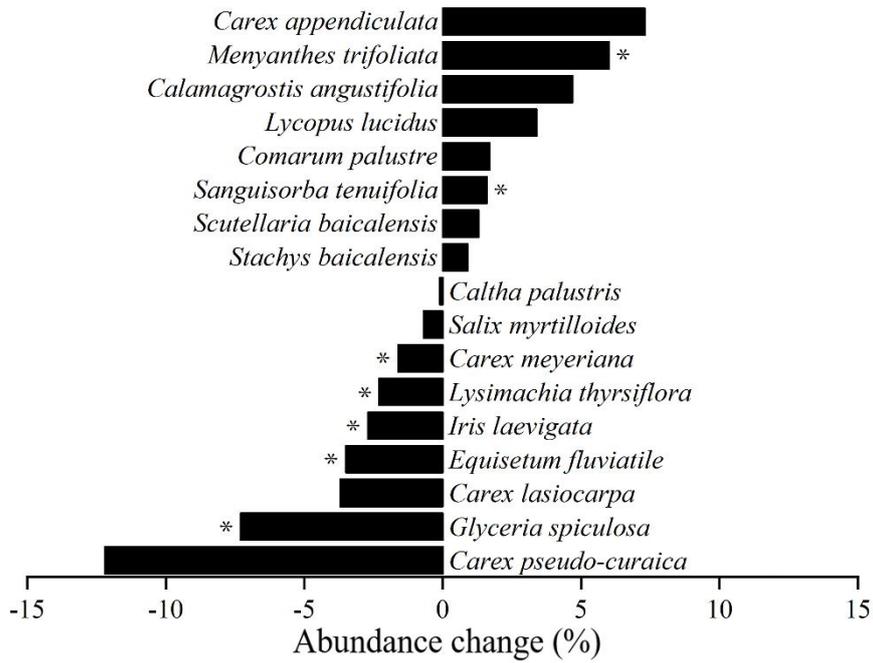**Fig. 1** Distribution of the investigated sampling plots in the wetlands

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.

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.
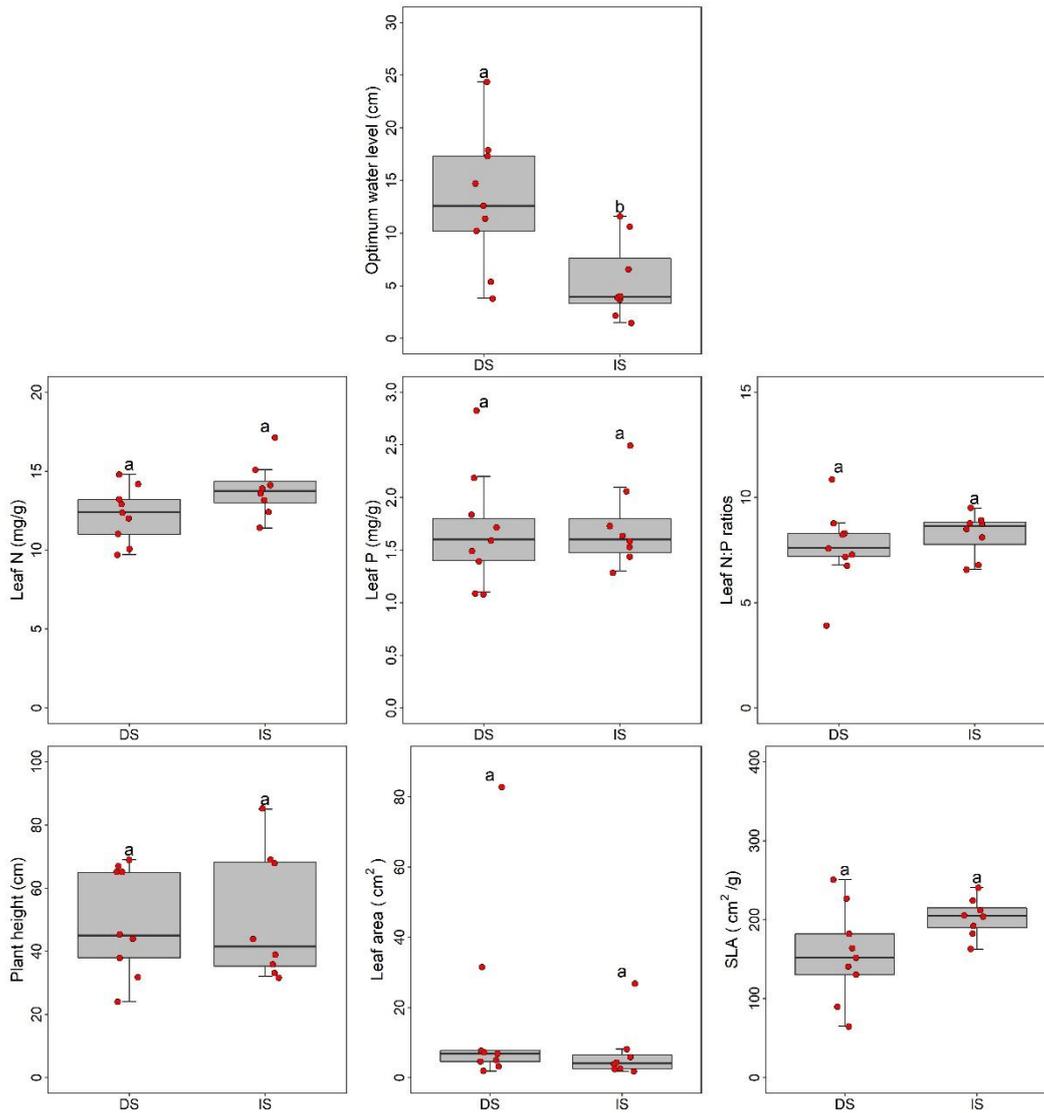
Fig. 4 Comparison of niche property and functional traits between the decreasing and increasing species. DS: decreasing species, n=9; IS: increasing species, n=8. The core boxes of boxplots indicate the interquartile range of data whereas the whisker lines symbolize the centiles 5 and 95, middle black line is the median.
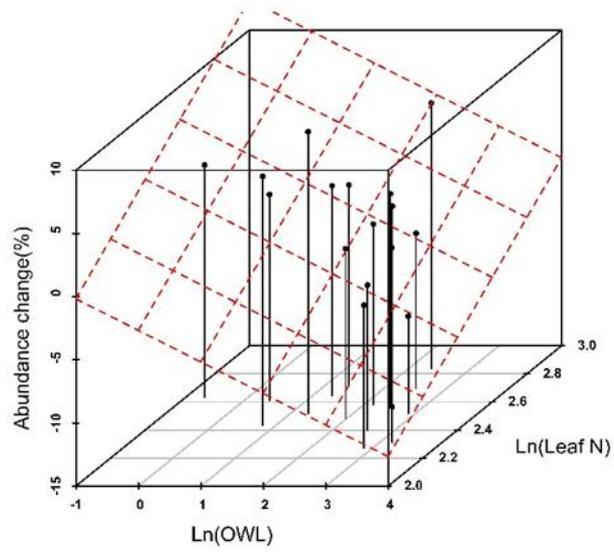
Fig. 5 The relationship between optimum water level, leaf N and species abundance changes (n=17 species).

Supplementary Material

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.