



# Large-scale environmental niche variation between clonal and non-clonal plant species: Roles of clonal growth organs and ecoregions



Ji-Zhong Wan<sup>a,b,c</sup>, Chun-Jing Wang<sup>d</sup>, Fei-Hai Yu<sup>a,b,\*</sup>

<sup>a</sup> Institute of Wetland Ecology & Clone Ecology, Taizhou University, Taizhou 318000, China

<sup>b</sup> Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China

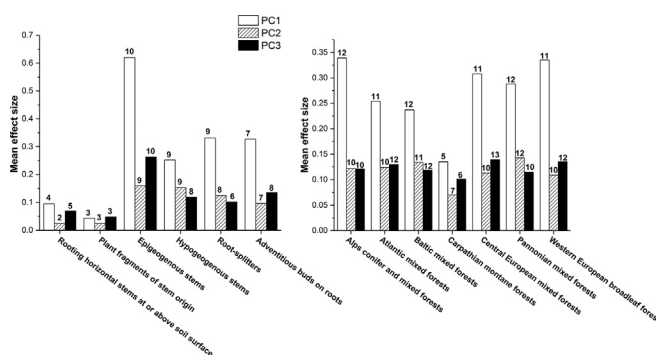
<sup>c</sup> State Key Laboratory of Plateau Ecology and Agriculture, Qinghai University, Xining 810016, China

<sup>d</sup> College of Agriculture and Animal Husbandry, Qinghai University, Xining 810016, China

## HIGHLIGHTS

- Potential evolutionary divergence between clonal and non-clonal plants is intriguing.
- We assessed environmental niches of 87 clonal and 50 non-clonal plant species.
- We found that clonal and non-clonal plant species differed in their environmental niches.
- Such niche differences varied depending on clonal growth organ types and ecoregions.
- Four clonal growth organs contributed to such niche differences.

## GRAPHICAL ABSTRACT



## ARTICLE INFO

### Article history:

Received 10 July 2018

Received in revised form 18 October 2018

Accepted 20 October 2018

Available online 22 October 2018

Editor: Elena PAOLETTI

### Keywords:

Clonality

Ecoregion

Europe

Growth form

Niche shift

Principal component analysis

## ABSTRACT

Clonal plant species can produce genetically identical and potentially independent offspring, and dominate a variety of habitats. The divergent evolutionary mechanisms between clonal and non-clonal plants are interesting areas of ecological research. A number of studies have shown that the environmental niche theory can support the mechanisms of evolution across plant species clades at large scales. However, few studies have explored large-scale environmental niche variation between clonal and non-clonal plant species. Here, we used principal component analysis to quantify the environmental niche of 137 plant species belonging to 13 genera, including 87 clonal species and 50 non-clonal species. We then used a standardized effect size to assess environmental niche variation between clonal and non-clonal plant species within each genus, based on types of clonal growth organs and ecoregions. Our study provided the first evidence that there were significant environmental niche differences between clonal and non-clonal plant species at large scales. Such differences varied depending on the types of clonal growth organs and ecoregions. Clonal plants with different growth organs (i.e., epigeogenous stems, hypogeogenous stems, root-splitters, and adventitious buds on roots) contributed greatly to differences in climatic niches between clonal and non-clonal plants. Differences in environmental niches between clonal and non-clonal plant species also depended on ecoregion types. Specifically, the ecoregions of temperate broadleaf and mixed forests can lead to environmental niche variation between clonal and non-clonal plant species. Our results provide new insights into the evolutionary divergence between clonal and non-clonal plant species.

© 2018 Elsevier B.V. All rights reserved.

\* Corresponding author at: Institute of Wetland Ecology & Clone Ecology, Taizhou University, Taizhou 318000, China.

E-mail address: [feihaiyu@126.com](mailto:feihaiyu@126.com) (F.-H. Yu).

## 1. Introduction

Clonal plants have the ability to produce genetically identical and potentially independent offspring (Price and Marshall, 1999; Cornelissen et al., 2014; Barrett, 2015; Herben et al., 2016). They are widely distributed and also the dominant plant species in a variety of habitats (Wijesinghe and Handel, 1994; Sosnova et al., 2010; Dong et al., 2014; Herben et al., 2015). Many clonal plants possess distinguished characteristics such as clonal spread, clonal integration and foraging response, which enable them to especially adapt to heterogeneous environments that are common in nature (Price and Marshall, 1999; Cornelissen et al., 2014; Wan et al., 2017). Due to such characteristics, clonal plants have a large potential to occupy new environmental niches (Ye et al., 2014; Herben et al., 2016), and may occupy a wider range of environmental niches than non-clonal plants (Sosnova et al., 2010; Klimešová and Doležal, 2011). Understanding variation of environmental niches at large spatial scales can provide new insights into evolutionary mechanisms of divergence between clonal and non-clonal plant species.

Environmental niche variation mediated by different plant traits can promote survival and growth of plant species, and enable them to adapt to various habitats at large geographical scales (Thuiller et al., 2004; Kraft et al., 2008; Kearney and Porter, 2009; Kearney et al., 2010; Violle et al., 2014; Díaz et al., 2016). Clonality, an important trait of many plant species, can play key roles in adaptation and persistence of clonal plants to changes of environmental conditions (e.g. temperature, precipitation, light and nutrients; Stuefer et al., 1994; Pakeman et al., 2009; Klimešová and Doležal, 2011; Dong et al., 2013; Ye et al., 2015). Invasive clonal plants express great root-foraging plasticity under homogeneous or heterogeneous nutrient conditions (Keser et al., 2014). A significant clonality-climate relationship was observed along a latitudinal gradient across China, indicating that clonality plays an important role in adaptation of plants to environment gradients (Ye et al., 2014). Hence, clonality may have potential contribution to environmental niche variation at large geographical scales. However, few studies have examined large-scale environmental niche variation of clonal plants and compared it with that of non-clonal plants. Here, we propose that there can be environmental niche variation between clonal and non-clonal plant species.

Clonal plants can be classified into several groups according to their clonal growth organs, including rooting horizontal stems at or above soil surface, plant fragments of stem origin, epigeogenous stems, hypogeogenous stems, root-splitters, and adventitious buds on roots (Sosnova et al., 2010; Klimešová and Herben, 2015; Klimešová et al., 2017). Clonal plants with different clonal growth organs may show differential responses to changing environmental conditions (Klimešová and Doležal, 2011; Song et al., 2013; Wang et al., 2013; Klimešová and Herben, 2015) and thus may occupy different environmental niches at large scales. For example, clonal plants with epigeogenous rhizomes have a strong ability to spread in bogs and wet heathland, and those with root-derived clonal growth organs are dominant in salt marshes (Brewer et al., 1998; Sosnova et al., 2010; Douhovnikoff and Dodd, 2015). Also, clonal plants with adventitious rooting are easy to live in environmental conditions of wet soil and low carbon availability (Herben et al., 2015). Therefore, types of clonal growth organs that clonal plants have may affect their ability to adapt to different environmental conditions, and thus may determine whether clonal and non-clonal plants differ in their environmental niches. So far, however, few studies have tested roles of clonal growth organ types in the difference in environmental niches between clonal and non-clonal plants at large scales.

Ecoregions accommodate geographically distinct assemblages of species and communities under specific environmental conditions (Olson et al., 2001). Environmental shifts in different ecoregions may result in evolutionary changes in physiological tolerance of plants to new or stressful environmental conditions (Gallagher et al., 2010; Schnitzler et al., 2012; Donoghue and Edwards, 2014). Such ecoregion shifts may lead to environmental niche variation of plant species and changes of

plant traits at large scales (Jacquemyn et al., 2006; Gallagher et al., 2010; Hardy et al., 2012; Donoghue and Edwards, 2014). Furthermore, environmental variation due to different ecoregions can provide a variety of habitats for clonal and non-clonal plants, and result in differential investment in sexual reproduction and clonal propagation. For example, the clonal plant *Paris quadrifolia* has a large potential to produce low levels of genetic variation and limited sexual reproduction in temperate forest ecoregions (Jacquemyn et al., 2006). Hence, ecoregions may shape environmental niche characteristics of clonal and non-clonal plants at large spatial scales. However, no study has investigated whether differences in environmental niches between clonal and non-clonal plants vary with types of ecoregions at large scales.

We conducted a data-synthesis on contribution of clonal growth organ types and ecoregions to potential divergence in environmental niches between clonal and non-clonal plants. We aimed at testing the hypothesis that there are environmental niche variations between clonal and non-clonal plant species at large scales.

## 2. Materials and methods

### 2.1. Study area and ecoregion data

Central Europe, including Austria, Croatia, Czech Republic, Germany, Hungary, Liechtenstein, Poland, Slovakia, Slovenia, and Switzerland, was selected as the study area (Fig. S1). Moreover, some parts of Western Europe were also included in our analysis. The climate of this region can be described as temperate. Western areas belong to temperate marine climate, and eastern areas belong to the temperate continent-humid climate (Mosbrugger et al., 2005). Here, seven ecoregions (downloaded from <https://www.worldwildlife.org>) were selected to conduct further analysis. These seven ecoregions include: 1) Alps conifer and mixed forests (biome: temperate coniferous forests), 2) Atlantic mixed forests (biome: temperate broadleaf and mixed forests), 3) Baltic mixed forests (biome: temperate broadleaf and mixed forests), 4) Carpathian montane conifer forests (biome: temperate coniferous forests), 5) Central European mixed forests (biome: temperate broadleaf and mixed forests), 6) Pannonian mixed forests (biome: temperate broadleaf and mixed forests), and 7) Western European broadleaf forests (biome: temperate broadleaf and mixed forests).

### 2.2. Clonal growth organ data

We selected 137 plant species that are widely distributed in Central Europe, including 87 clonal species and 50 non-clonal species belonging to 13 genera (<http://clopla.butbn.cas.cz>; Table S1). The selected species have been identified by CLO-PLA database (<http://clopla.butbn.cas.cz>) and The Plant List (release 1.0; [www.theplantlist.org](http://www.theplantlist.org)). CLO-PLA is a database of clonal and bud-bank traits of Central European flora (Klimešová et al., 2017). The 13 genera were *Cardamine*, *Centaurea*, *Crepis*, *Galium*, *Geranium*, *Lepidium*, *Myosotis*, *Orobanche*, *Senecio*, *Silene*, *Trifolium*, *Veronic*, and *Vicia*. Types of clonal growth organs were distinguished according to the CLO-PLA 3 database (<http://clopla.butbn.cas.cz/>). In this study, the 87 clonal plant species had six types of clonal growth organs, namely, 1) rooting horizontal stems at or above soil surface, 2) plant fragments of stem origin, 3) epigeogenous stems, 4) hypogeogenous stems, 5) root-splitters, and 6) adventitious buds on roots. Detailed information on clonal and non-clonal plant species is shown in Table S1, and further explanation can be found in the website (<http://clopla.butbn.cas.cz>). Species were considered as non-clonal if they did not have any clonal growth organs listed in CLO-PLA.

### 2.3. Environmental niche quantification

We quantified environmental niches based on climate and soil variables at a 5.0-arc-minute spatial resolution of grid cells (10 km at the equator; Kearney and Porter, 2004). Data on climate variables were

downloaded from the Worldclim database (Buckley et al., 2011; Fick and Hijmans, 2017; <http://worldclim.org/version2>). The eight selected climate variables, including temperature and precipitation, can affect the distribution and physiological performance of plant species (Buckley et al., 2011; Fick and Hijmans, 2017). Data on nine soil variables at a 0.5-arc-minute spatial resolution were downloaded from SoilGrids1km (<http://soilgrids.org>), and translated into the 5.0-arc-minute resolution using resample analyses in ArcGIS 10.2 (Geostatistical Analyst ESRI Corp. Redland, CA, USA). Detailed information on environmental variables is shown in Table S2.

We downloaded occurrence locality records of each study species from Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>; assessed in July, 2017). We removed the replicated occurrence locality records to decrease possible sampling bias (Kramer-Schadt et al., 2013). The final number of occurrence locality records of the study species ranged from 103 to 6808, with a mean value of 1174 (Table S1), which is sufficient to assess environmental niche quantification (Drake et al., 2006).

To quantify environmental niche, a principal component analysis (PCA) was performed on climate and soil variables based on all occurrence locality records, which were classified for each genus, each clonal growth organ and each ecoregion based on clonal and non-clonal plants (Lawson and Weir, 2014; Algar and Mahler, 2016). Here, we used the z-score normalization method to standardize each environmental variable by dividing it by its standard deviation (Abdi et al., 2013). Based on PCA, we obtained environmental niche spaces for clonal and non-clonal plants based on each genus, clonal growth organ, and ecoregion, respectively. We used scores of the first three principal components (PCs) as the indexes of environmental niches (Lawson and Weir, 2014; Algar and Mahler, 2016). PCA was performed in JMP 10.0 (SAS Institute, Cary, NC, USA).

#### 2.4. Data synthesis

First, we calculated mean environmental niches of clonal and non-clonal plant species, respectively, in each genus for each group based on the six clonal growth organs and for each of seven ecoregions (Alps conifer and mixed forests, Atlantic mixed forests, Baltic mixed forests, Carpathian montane forests, Central European mixed forests, Pannonian mixed forests, and Western European broadleaf forests). We then used independent-sample *t*-tests to examine the difference in mean environmental niches between clonal and non-clonal plant species within each genus for each type of the six clonal growth organs and for each of the seven ecoregions. The *t*-tests were performed in JMP 10.0 (SAS Institute, Cary, NC, USA).

Second, we evaluated differences in mean environmental niches between clonal and non-clonal plant species within each genus by calculating standardized effect size (SES; Gurevitch et al., 1992; Møller and Jennions, 2002):  $SES = (I_{clonal} - I_{non-clonal}) / SD_{non-clonal}$ , where  $I_{clonal}$  and  $I_{non-clonal}$  are the mean environmental niches of clonal and non-clonal plants within a genus, respectively, and  $SD_{non-clonal}$  is the standard deviation of environmental niches of non-clonal plants with that genus. SES was calculated for each type of the six clonal growth organs and for each of the seven ecoregions using absolute values.

Third, we calculated mean SES across the 13 genera (some genera with no data omitted) for each clonal growth organ type and for each ecoregion. For this calculation, we excluded non-significant values of SES based on the *t*-tests across each clonal growth organ and ecoregion of every genus to avoid the confounding effect of high values of SES with no significant difference on results.

### 3. Results

The first three PCs explained >60% of the total variance. PC1 was correlated most strongly with precipitation variables (i.e., annual precipitation, precipitation of the wettest month, and precipitation of the driest

month), PC2 was correlated most strongly with soil variables (e.g., soil texture fraction silt and clay), and PC3 was correlated most strongly with temperature variables (e.g., temperature seasonality and the minimum temperature of the coldest month; Tables S2 and S3). Thus, values of PC1, PC2 and PC3 represented for precipitation niches, soil niches and temperature niches, respectively.

Clonal and non-clonal plant species differed significantly ( $P < 0.05$ ) in precipitation niches in 11 of the 13 genera (except *Lepidium* and *Orobancha*), in soil niches in 10 of the 13 genera (except *Galium*, *Lepidium*, and *Orobancha*), and in temperature niches in 11 of the 13 genera (except *Silene*, and *Veronica*; Table 1). Clonality contributed to the largest variation of precipitation, soil, and temperature niches for species of *Centaurea* (Table 1). Regarding to roles of clonal growth organ types, epigeogenous stems, hypogeogenous stems, root-splitters, and adventitious buds on roots contributed greatly to significant variation in precipitation niches between clonal and non-clonal plant species ( $P < 0.05$ ; Fig. 1 and Table S4). Epigeogenous stems and hypogeogenous stems resulted in significant variation in soil niches between clonal and non-clonal plant species ( $P < 0.05$ ), but the effect sizes were smaller than those of precipitation niches ( $P < 0.05$ ; Fig. 1 and Table S4). There were the largest significant differences in temperature niches between clonal and non-clonal plant species owing to epigeogenous stems ( $P < 0.05$ ; effect size: 0.271; Fig. 1 and Table S4). Epigeogenous stems of *Myosotis* species led to the largest variation in environmental niches (i.e., precipitation, soil, and temperature) between clonal and non-clonal plant species ( $P < 0.05$ ; Table S4).

Regarding to effects of ecoregion types, the largest differences in precipitation niches between clonal and non-clonal plant species existed in Alps conifer and mixed forests and Western European broadleaf forests ( $P < 0.05$ ), that in soil niches existed in Baltic mixed forests and Pannonian mixed forests, and that in temperature niches occurred in Central European mixed forests ( $P < 0.05$ ; Fig. 2 and Table S5). Specifically, variation in precipitation niches was the largest for *Centaurea* species in Central European mixed forests and Western European broadleaf forests (effect size: 1.530), variation in soil niches was the largest for *Centaurea* species in Baltic mixed forests (effect size: 0.402), and variation in temperature niches was the largest for *Centaurea* species in Central European mixed forests and Western European broadleaf forests (effect size: 0.537; Table S5).

### 4. Discussion

Our study provides the first evidence of significant environmental niche differences between clonal and non-clonal plant species at large

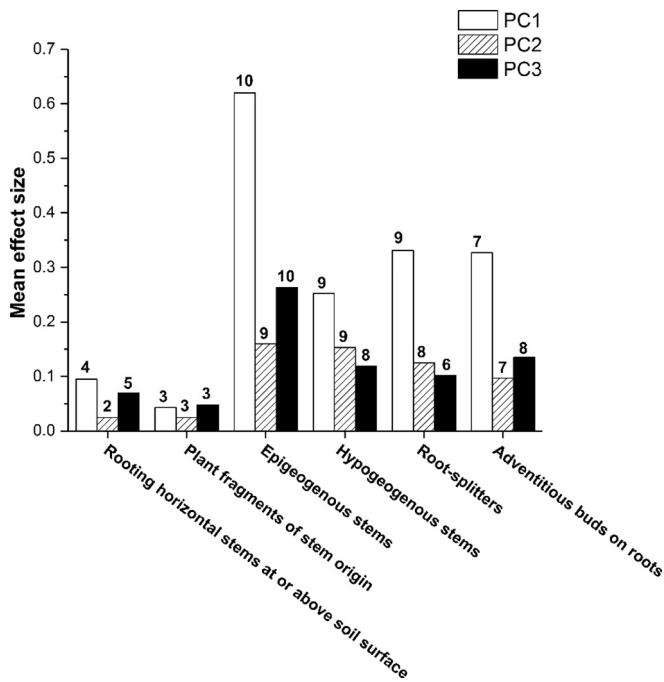
**Table 1**

Effect size values of environmental niches between clonal and non-clonal plant species for the 13 genera.

Genus	Effect size			Sampling size	
	PC1	PC2	PC3	Clonal	Non-clonal
<i>Cardamine</i>	<b>0.116</b>	<b>0.043</b>	<b>0.284</b>	12,118	10,659
<i>Centaurea</i>	<b>1.530</b>	<b>0.386</b>	<b>0.537</b>	678	6544
<i>Crepis</i>	<b>0.562</b>	<b>0.060</b>	<b>0.145</b>	6774	6247
<i>Galium</i>	<b>0.032</b>	0.011	<b>0.030</b>	45,811	8878
<i>Geranium</i>	<b>0.088</b>	<b>0.218</b>	<b>0.148</b>	14,996	21,984
<i>Lepidium</i>	0.044	0.014	<b>0.054</b>	3796	1646
<i>Myosotis</i>	<b>0.198</b>	<b>0.079</b>	<b>0.144</b>	8964	9439
<i>Orobancha</i>	0.026	0.067	<b>0.159</b>	2141	1319
<i>Senecio</i>	<b>0.167</b>	<b>0.172</b>	0.021	9108	15,366
<i>Silene</i>	<b>0.599</b>	<b>0.111</b>	<b>0.077</b>	11,385	1184
<i>Trifolium</i>	<b>0.219</b>	<b>0.051</b>	<b>0.071</b>	11,614	3206
<i>Veronica</i>	<b>0.377</b>	<b>0.082</b>	0.044	15,394	3186
<i>Vicia</i>	<b>0.516</b>	<b>0.218</b>	<b>0.055</b>	7651	2076

Numbers in bold represent significant differences in environmental niches between clonal and non-clonal plant species at the genus level (*t*-test:  $P < 0.05$ ). We excluded the pair of clonal and non-clonal plants without any significant variations in environmental niches to eliminate uncertainties in effect size quantification in environmental niches between clonal and non-clonal plant species.





**Fig. 1.** Effect size values of mean environmental niches between clonal and non-clonal plant species based on clonal growth organs. PC1 was most strongly correlated with precipitation variables (e.g., precipitation of the wettest month, precipitation of the driest month, and precipitation seasonality; Table S2). PC2 was most strongly correlated with soil variables (e.g., soil texture fraction silt and clay; Table S2), and PC3 was most strongly correlated with temperature variables (e.g., temperature seasonality and the minimum temperature of the coldest month; Table S2). The numbers on bars represent the number of genera that indicated significant differences in environmental niches between clonal and non-clonal plant species.

scales. We found that variation in precipitation, soil, and temperature niches all existed between clonal and non-clonal plant species, and that types of clonal growth organs and ecoregions played important roles in niche variation between clonal and non-clonal plants (Eriksson, 1985; Cody, 1991; Sosnova et al., 2010; Ye et al., 2014, 2016). However, the roles may differ depending on the genus (Van Groenendael et al., 1996; Klimešová and Doležal, 2011; Ye et al., 2016) because plant species may have different abilities to adapt to environmental variation owing to changes of clonal growth organs, and different suitable habitat ranges (i.e., ecoregion).

#### 4.1. Roles of clonal growth organs in environmental niche variation

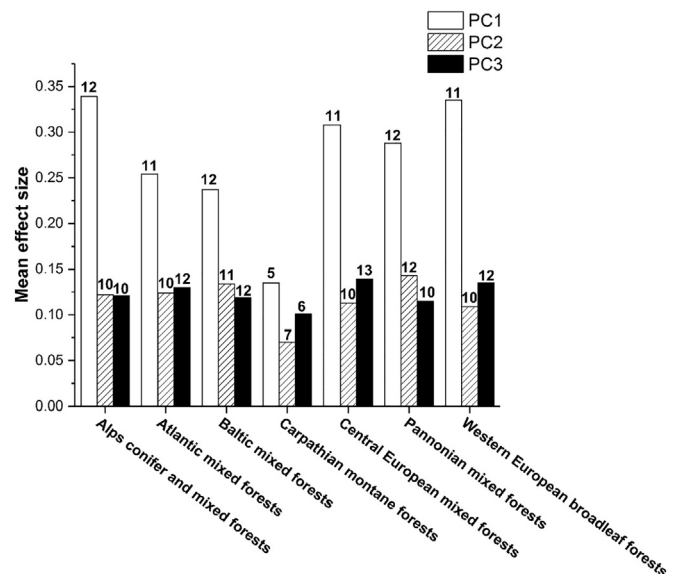
Our results showed that clonal plants with epigeogenous stems, hypogeogenous stems, root-splitters, and adventitious buds on roots contributed greatly to significant variation in climatic niches between clonal and non-clonal plants. Combining with our results, clonal growth organs such as stems, roots, and buds can contribute to climatic niche variation in terms of annual precipitation, precipitation of the wettest month, and precipitation of the driest month between clonal and non-clonal plant species (Larcher et al., 2010; Lawson and Weir, 2014; Moles et al., 2014). But some clonal plants with specific clonal growth organs could not have such a contribution to climatic niche variation. For example, *Orobanch* species with adventitious buds on roots did not contribute to differences in precipitation and soil niches between clonal and non-clonal plants.

We found that clonal plants with epigeogenous and hypogeogenous stems had a large contribution to significant variation in climatic niches between clonal and non-clonal plants. Horizontal spreading of clonal plant species with epigeogenous and hypogeogenous stems allow herbaceous plants to migrate over short distances, occupy areas experiencing different gradients of precipitation and temperature, and adapt to

the stressful or new climatic conditions (particularly, extreme precipitation), owing to rhizome- or root-mediated physiological integration and resource storage in organs such as tubers and bulbs (Eriksson, 1985; Suzuki and Stuefer, 1999; Jacquemyn et al., 2006; Luo and Zhao, 2015). Furthermore, stem growth can affect the photosynthetic pathway that is related to drought tolerance, and such stem growth is more strongly related to precipitation and temperature niches in clonal than in non-clonal plants (Eriksson, 1985; Jacquemyn et al., 2006; Chaves et al., 2009; Klimešová and Herben, 2015). Hence, variation in epigeogenous and hypogeogenous stems can lead to different clonal strategies and underlying traits of clonal plants to respond and adapt to climatic niche changes.

Environmental niches of clonal plants with root-derived clonal growth organs (i.e., root-splitters and adventitious buds on roots) differed significantly from those of non-clonal plants. For example, *Centaurea* species expressed the largest environmental niche variation in terms of precipitation, soil, and temperature. Most *Centaurea* species are robust weedy plants, and distributed around the world (Ditomaso, 2000). Regional climatic changes and nitrogen deposition can increase competitive abilities of clonal plants with some specific clonal growth organs such as root-splitters within the community (Gough et al., 2012; Zhu et al., 2016; Young et al., 2017; Broadbent et al., 2018). Moreover, *Lepidium* species may exist in particular habitats (i.e., wetlands and riparian areas), and their roots may be sensitive to precipitation changes (Fan et al., 2017; Xi et al., 2018). Therefore, *Lepidium* species with root-splitters contributed greatly to significant variation in precipitation niches between clonal and non-clonal plants.

Soil niches of clonal plants differed significantly from those of non-clonal plants. Shifts in the dominance of particular clonal growth organs have been predicted and observed along the gradients of productivity and soil fertility in various plant communities, and they lead to different levels of competition within communities (Eilts et al., 2011; Rusch et al., 2011; Herben et al., 2015). Short plant species with basal rosette organs are more common at low soil nutrient levels, whereas species with a tall and runner habit (e.g., hypogeogenous stems) tend to dominate higher productivity sites (Gough et al., 2012; Dickson et al., 2014; Herben et al.,



**Fig. 2.** Effect size values of mean environmental niches between clonal and non-clonal plant species based on ecoregion types. PC1 was most strongly correlated with precipitation variables (e.g., precipitation of the wettest month, precipitation of the driest month, and precipitation seasonality; Tables S2 and S3). PC2 was most strongly correlated with soil variables (e.g., soil texture fraction silt and clay; Tables S2 and S3), and PC3 was correlated most strongly with temperature variables (e.g., temperature seasonality and the minimum temperature of the coldest month; Tables S2 and S3). The numbers on bars represent the number of genera that indicate significant differences in environmental niches between clonal and non-clonal plant species.

2015; Ye et al., 2015). In our study, hypogeogenous stems may lead to greater soil niche changes in clonal than in non-clonal plant species due to the different levels of soil productivity (Blank, 2002).

Furthermore, responses of clonal growth organs to soil conditions can help clonal plants to survive in new and heterogeneous habitats (Stuefer et al., 1994; Luo et al., 2014). Hence, soil niche variation between clonal and non-clonal plant species may emerge from the competition of available resources within plant communities across different soil conditions and the contribution of clonal growth organs to environmental adaptability (Gurevitch et al., 1992; Dong et al., 2013, 2014). We found that clonal plants (particularly, *Myosotis* species) with epigeogenous and hypogeogenous stems contributed greatly to differences in soil niches between clonal and non-clonal plants, which were related to soil texture fraction clay and silt. Soil texture fraction clay and silt can affect the distribution and size of nutrient-rich patches (Bellemare et al., 2002). The distribution of clonal growth organs, the pattern of clonal branching, and the variation in rhizome or stolon internode length can affect the foraging responses of clonal plants to soil heterogeneity consisting of nutrient-rich and nutrient-poor patches (Cain, 1994; Keser et al., 2014). Hence, competition and foraging responses for soil fertility may be the sources of environmental niche variation between clonal and non-clonal plant species. Furthermore, we found that under-ground clonal growth organs (i.e., root-splitters) could affect environmental niche variation between clonal and non-clonal plant species, indicating that clonal growth organs play important roles in determining the adaptation, foraging, and competition ability of clonal plants to changes in water use efficiency, soil fertility, and available resources across above- and under-ground environmental conditions (Eriksson, 1985; Cain, 1994; Wang et al., 2013; Keser et al., 2014).

#### 4.2. Roles of ecoregions in environmental niche variation

We found that environmental niche variation between clonal and non-clonal plant species varied with ecoregion types. Plant species are likely to survive, grow, and expand in similar environmental conditions to those in previous habitats, leading to biomes with multiple plant species (Prinzing, 2001; Van Kleunen and Fischer, 2005; Wiens and Graham, 2005; Hardy et al., 2012). Ecoregions are classified by biomes, which are the major global plant communities determined by temperature and precipitation (Olson et al., 2001). There may be distinctive climate types for different plant associations (e.g., broadleaf and mixed forests versus conifer forests) (Olson et al., 2001). Ecoregions constrain the assembly and distribution of plant species at large scales (Olson et al., 2001). Hence, ecoregions (e.g. Pannonian mixed forests) have a large potential to result in the formation of distinct clades of clonal and non-clonal plant species owing to environmental niche variations at large geographical scales (Gallagher et al., 2010; Donoghue and Edwards, 2014; Wan et al., 2017).

We found that the largest shifts between clonal and non-clonal plant species occurred in terms of precipitation in Alps conifer and mixed forests and Western European broadleaf forests, that in soil niches existed in Baltic mixed forests and Pannonian mixed forests, and that in temperature niches occurred in Central European mixed forests, indicating that the habitats of temperate broadleaf and mixed forests affect environmental niche variation between clonal and non-clonal plant species. Such differences in soil niches may be related to adaption of clonal plants in stressful environments (i.e., low soil resource availability and harsh climate) (Price and Marshall, 1999; Klimešová and Doležal, 2011; Couteron et al., 2014; Dong et al., 2015; Ye et al., 2016), especially in extreme precipitation and soil conditions (Prinzing, 2001; Wiens and Graham, 2005; Hardy et al., 2012). However, the ability of clonal plants to adapt to stressful environmental conditions may decrease or not be different from non-clonal plant species in some conifer forest ecoregions. For example, there was small soil and temperature niche variation across all species in Carpathian montane conifer forests. The

climate of Carpathian montane conifer forests can be described as extremely low temperature with minimal precipitation and the soils contain low nutrients (Olson et al., 2001). Hence, the adaptive ability of clonal plants may be limited by the stress threshold of environmental niches. In some stressful conditions, the contribution of clonality to plant strategies and fitness to respond to extreme environmental changes may be weakened or there may be small differences between clonal and non-clonal plant species in terms of responses (Pennings and Callaway, 2000; Van Kleunen and Fischer, 2005; Ye et al., 2014, 2016).

## 5. Conclusions

Environmental niches of clonal plants differed significantly from those of non-clonal plants, but such differences depended on clonal growth organ types and ecoregions. Thus, our study provides the first evidence of the environmental niche variation between clonal and non-clonal plant species at large scales, and new insights into the ecological niche theory and plant evolution. Environmental niche theory has been widely used to predict distributions of plant species at large scales using ecological niche modelling. However, such predictions are based on environmental niche conservatism. Hence, further studies are needed to integrate clonality, growth organs, and ecoregions into ecological niche modelling to achieve better predictions about plant distributions.

## Acknowledgements

We thank for the valuable comments of editor and three reviewers on the improvement of the early manuscript. This research was supported by NSFC (31570413; 31761123001; 31800449; 31800464).

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.10.280>.

## References

- Abdi, H., Williams, L.J., Valentin, D., 2013. Multiple factor analysis: principal component analysis for multitable and multiblock data sets. *Wiley Interdiscip. Rev. Comput. Stat.* 5, 149–179.
- Algar, A.C., Mahler, D.L., 2016. Area, climate heterogeneity, and the response of climate niches to ecological opportunity in island radiations of *Anolis* lizards. *Glob. Ecol. Biogeogr.* 25, 781–791.
- Barrett, S.C., 2015. Influences of clonality on plant sexual reproduction. *Proc. Natl. Acad. Sci. U. S. A.* 112, 8859–8866.
- Bellemare, J., Motzkin, G., Foster, D.R., 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *J. Biogeogr.* 29, 1401–1420.
- Blank, R.R., 2002. Amidohydrolase activity, soil N status, and the invasive crucifer *Lepidium latifolium*. *Plant Soil* 239, 155–163.
- Brewer, J.S., Rand, T., Levine, J.M., Bertness, M.D., 1998. Biomass allocation, clonal dispersal, and competitive success in three salt marsh plants. *Oikos* 82, 347–353.
- Broadbent, A., Stevens, C.J., Peltzer, D.A., Ostle, N.J., Orwin, K.H., 2018. Belowground competition drives invasive plant impact on native species regardless of nitrogen availability. *Oecologia* 186, 577–587.
- Buckley, L.B., Waaser, S.A., MacLean, H.J., Fox, R., 2011. Does including physiology improve species distribution model predictions of responses to recent climate change? *Ecology* 92, 2214–2221.
- Cain, M.L., 1994. Consequences of foraging in clonal plant species. *Ecology* 75, 933–944.
- Chaves, M.M., Flexas, J., Pinheiro, C., 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Ann. Bot.* 103, 551–560.
- Cody, M.L., 1991. Niche theory and plant growth form. *Vegetatio* 97, 39–55.
- Cornelissen, J.H., Song, Y.B., Yu, F.H., Dong, M., 2014. Plant traits and ecosystem effects of clonality: a new research agenda. *Ann. Bot.* 114, 369–376.
- Couteron, P., Anthelme, F., Clerc, M., Escaff, D., Fernandez-Oto, C., Tlidi, M., 2014. Plant clonal morphologies and spatial patterns as self-organized responses to resource-limited environments. *Phil. Trans. R. Soc. A* 372, 20140102.
- Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., Garnier, E., Bonisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Wright, S.J., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D.,

- Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüter, N., Mahecha, M.D., Gorne, L.D., 2016. The global spectrum of plant form and function. *Nature* 529, 167.
- Dickson, T.L., Mittelbach, G.G., Reynolds, H.L., Gross, K.L., 2014. Height and clonality traits determine plant community responses to fertilization. *Ecology* 95, 2443–2452.
- Ditomaso, J.M., 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Sci.* 48, 255–265.
- Dong, B.C., Wang, J.Z., Liu, R.H., Zhang, M.X., Yu, F.H., 2013. Effects of heterogeneous competitor distribution and ramet aggregation on the growth and size structure of a clonal plant. *PLoS One* 8, e68557.
- Dong, M., Yu, F.H., Alpert, P., 2014. Ecological consequences of plant clonality. *Ann. Bot.* 114, 367.
- Dong, B.C., Alpert, P., Zhang, Q., Yu, F.H., 2015. Clonal integration in homogeneous environments increases performance of *Alternanthera philoxeroides*. *Oecologia* 179, 393–403.
- Donoghue, M.J., Edwards, E.J., 2014. Biome shifts and niche evolution in plants. *Annu. Rev. Ecol. Syst.* 45, 547–572.
- Douhovnikoff, V., Dodd, R.S., 2015. Epigenetics: a potential mechanism for clonal plant success. *Plant Ecol.* 216, 227–233.
- Drake, J.M., Randin, C., Guisan, A., 2006. Modelling ecological niches with support vector machines. *J. Appl. Ecol.* 43, 424–432.
- Eilts, J.A., Mittelbach, G.G., Reynolds, H.L., Gross, K.L., 2011. Resource heterogeneity, soil fertility, and species diversity: effects of clonal species on plant communities. *Am. Nat.* 177, 574–588.
- Eriksson, O., 1985. Reproduction and clonal growth in *Potentilla anserina* L. (Rosaceae): the relation between growth form and dry weight allocation. *Oecologia* 66, 378–380.
- Fan, Y., Miguez-Macho, G., Jobbágy, E.G., Jackson, R.B., Otero-Casal, C., 2017. Hydrologic regulation of plant rooting depth. *Proc. Natl. Acad. Sci. U. S. A.* 201712381.
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315.
- Gallagher, R.V., Beaumont, L.J., Hughes, L., Leishman, M.R., 2010. Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. *J. Ecol.* 98, 790–799.
- Gough, L., Gross, K.L., Cleland, E.E., Clark, C.M., Collins, S.L., Fargione, J.E., Pennings, S.C., Suding, K.N., 2012. Incorporating clonal growth form clarifies the role of plant height in response to nitrogen addition. *Oecologia* 169, 1053–1062.
- Gurevitch, J., Morrow, L.L., Wallace, A., Walsh, J.S., 1992. A meta-analysis of field experiments on competition. *Am. Nat.* 140, 539–572.
- Hardy, O.J., Couteron, P., Munoz, F., Ramesh, B.R., Péliissier, R., 2012. Phylogenetic turnover in tropical tree communities: impact of environmental filtering, biogeography and mesoclimatic niche conservatism. *Glob. Ecol. Biogeogr.* 21, 1007–1016.
- Herben, T., Šerá, B., Klimešová, J., 2015. Clonal growth and sexual reproduction: tradeoffs and environmental constraints. *Oikos* 124, 469–476.
- Herben, T., Tackenberg, O., Klimešová, J., 2016. Reproduction by seed and clonality in plants: correlated syndromes or independent strategies? *J. Ecol.* 104, 1696–1706.
- Jacquemyn, H., Brys, R., Honnay, O., Hermy, M., Roldan-Ruiz, I., 2006. Sexual reproduction, clonal diversity and genetic differentiation in patchily distributed populations of the temperate forest herb *Paris quadrifolia* (Trilliaceae). *Oecologia* 147, 434–444.
- Kearney, M., Porter, W.P., 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85, 3119–3131.
- Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350.
- Kearney, M., Simpson, S.J., Raubenheimer, D., Helmuth, B., 2010. Modelling the ecological niche from functional traits. *Philos. Trans. R. Soc. B* 365, 3469–3483.
- Keser, L.H., Dawson, W., Song, Y.B., Yu, F.H., Fischer, M., Dong, M., van Kleunen, M., 2014. Invasive clonal plant species have a greater root-foraging plasticity than non-invasive ones. *Oecologia* 174, 1055–1064.
- Klimešová, J., Doležal, J., 2011. Are clonal plants more frequent in cold environments than elsewhere? *Plant Ecol.* Divers. 4, 373–378.
- Klimešová, J., Herben, T., 2015. Clonal and bud bank traits: patterns across temperate plant communities. *J. Veg. Sci.* 26, 243–253.
- Klimešová, J., Danihelka, J., Chrtěk, J., Bello, F., Herben, T., 2017. CLO-PLA: a database of clonal and bud-bank traits of the central European flora. *Ecology* 98, 1179.
- Kraft, N.J., Valencia, R., Ackerly, D.D., 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322, 580–582.
- Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillefried, M., Heckmann, I., Scharf, A.K., Augeri, D.M., Cheyne, S.M., Hearn, A.J., Ross, J., Macdonald, D.W., Mathai, J., Eaton, J., Marshall, A.J., Semiadi, G., Rustam, R., Bernard, H., Alfred, R., Samejima, H., Duckworth, J.W., Breitenmoser-Wuersten, C., Belant, J.L., Hofer, H., Wilting, A., 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. *Divers. Distrib.* 19, 1366–1379.
- Larcher, W., Kainmüller, C., Wagner, J., 2010. Survival types of high mountain plants under extreme temperatures. *Flora* 205, 3–18.
- Lawson, A.M., Weir, J.T., 2014. Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. *Ecol. Lett.* 17, 1427–1436.
- Luo, F.-L., Chen, Y., Huang, L., Wang, A., Zhang, M.-X., Yu, F.-H., 2014. Shifting effects of physiological integration on performance of a clonal plant during submergence and de-submergence. *Ann. Bot.* 113, 1265–1274.
- Luo, W., Zhao, W., 2015. Burial depth and diameter of the rhizome fragments affect the regenerative capacity of a clonal shrub. *Ecol. Complex.* 23, 34–40.
- Moles, A.T., Perkins, S.E., Laffan, S.W., Flores-Moreno, H., Awasthy, M., Tindall, M.L., Sack, L., Pitman, A., Kattge, J., Arssen, L.W., Anand, M., Bahn, M., Blonder, B., Cavender-
- Bares, J., Cornelissen, J.H.C., Cornwell, W.K., Díaz, S., Dickie, J.B., Freschet, G.T., Griffiths, J.G., Gutierrez, A.G., Hemmings, F.A., Hickler, T., Hitchcock, T.D., Keighery, M., Kleyer, M., Kurokawa, H., Leishman, M.R., Liu, K., Niinemets, Ü., Onipchenko, V., Onoda, Y., Penuelas, J., Pillar, V.D., Reich, P.B., Shiodera, S., Siefert, A., Sosinski, E.E., Soudzilovskaia, N.A., Swaine, E.K., Swenson, N.G., van Bodegom, P.M., Warman, L., Weiher, E., Wright, I.J., Zhang, H., Zobel, M., Bonser, S.P., 2014. Which is a better predictor of plant traits: temperature or precipitation? *Ecol. Complex.* 25, 1167–1180.
- Møller, A., Jennions, M.D., 2002. How much variance can be explained by ecologists and evolutionary biologists? *Oecologia* 132, 492–500.
- Mosbrugger, V., Utescher, T., Dilcher, D.L., 2005. Cenozoic continental climatic evolution of Central Europe. *Proc. Natl. Acad. Sci. U. S. A.* 102, 14964–14969.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Loucks, C.J., 2001. Terrestrial ecoregions of the world: a new map of life on earth a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* 51, 933–938.
- Pakeman, R.J., Lepš, J., Kleyer, M., Lavorel, S., Garnier, E., Consortium, Vista, 2009. Relative climatic, edaphic and management controls of plant functional trait signatures. *J. Veg. Sci.* 20, 148–159.
- Pennings, S.C., Callaway, R.M., 2000. The advantages of clonal integration under different ecological conditions: a community-wide test. *Ecology* 81, 709–716.
- Price, E.A., Marshall, C., 1999. Clonal plants and environmental heterogeneity—an introduction to the proceedings. *Plant Ecol.* 141, 3–7.
- Prinzinger, A., 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proc. R. Soc. Lond. B Biol. Sci.* 268, 2383–2389.
- Rusch, G.M., Wilmann, B., Klimešová, J., Evju, M., 2011. Do clonal and bud bank traits vary in correspondence with soil properties and resource acquisition strategies? Patterns in alpine communities in the Scandian mountains. *Folia Geobot.* 46, 237–254.
- Schnitzler, J., Graham, C.H., Dormann, C.F., Schifffers, K., Peter Linder, H., 2012. Climatic niche evolution and species diversification in the cape flora, South Africa. *J. Biogeogr.* 39, 2201–2211.
- Song, Y.B., Yu, F.H., Keser, L.H., Dawson, W., Fischer, M., Dong, M., van Kleunen, M., 2013. United we stand, divided we fall: a meta-analysis of experiments on clonal integration and its relationship to invasiveness. *Oecologia* 17, 317–327.
- Sosnova, M., van Diggelen, R., Klimešová, J., 2010. Distribution of clonal growth forms in wetlands. *Aquat. Bot.* 92, 33–39.
- Stuefer, J.F., During, H.J., de Kroon, H., 1994. High benefits of clonal integration in two stoloniferous species, in response to heterogeneous light environments. *J. Ecol.* 511–518.
- Suzuki, J.J., Stuefer, J., 1999. On the ecological and evolutionary significance of storage in clonal plants. *Plant Species Biol.* 14, 11–17.
- Thuiller, W., Lavorel, S., Midgley, G.U.Y., Lavergne, S., Rebelo, T., 2004. Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* taxa. *Ecology* 85, 1688–1699.
- Van Groenendael, J.M., Klimes, L., Klimesova, J., Hendriks, R.J.J., 1996. Comparative ecology of clonal plants. *Philos. Trans. Biol. Sci.* 351, 1331–1339.
- Van Kleunen, M., Fischer, M., 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytol.* 166, 49–60.
- Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J., Kattge, J., 2014. The emergence and promise of functional biogeography. *Proc. Natl. Acad. Sci. U. S. A.* 111, 13690–13696.
- Wan, J.Z., Wang, C.J., Yu, F.H., 2017. Modeling impacts of human footprint and soil variability on the potential distribution of invasive plant species in different biomes. *Acta Oecol.* 85, 141–149.
- Wang, Z., Van Kleunen, M., During, H.J., Werger, M.J., 2013. Root foraging increases performance of the clonal plant *Potentilla reptans* in heterogeneous nutrient environments. *PLoS One* 8, e58602.
- Wiens, J.J., Graham, C.H., 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Syst.* 36, 519–539.
- Wijesinghe, D.K., Handel, S.N., 1994. Advantages of clonal growth in heterogeneous habitats: an experiment with *Potentilla simplex*. *J. Ecol.* 82, 495–502.
- Xi, B., Di, N., Liu, J., Zhang, R., Cao, Z., 2018. Hydrologic regulation of plant rooting depth: pay attention to the widespread scenario with intense seasonal groundwater table fluctuation. *Proc. Natl. Acad. Sci. U. S. A.* 201803987.
- Ye, D., Hu, Y., Song, M., Pan, X., Xie, X., Liu, G., Ye, X., Dong, M., 2014. Clonality-climate relationships along latitudinal gradient across China: adaptation of clonality to environments. *PLoS One* 9, e94009.
- Ye, D., Liu, G., Song, Y.B., Cornwell, W.K., Dong, M., Cornelissen, J.H., 2016. Strong but diverging clonality-climate relationships of different plant clades explain weak overall pattern across China. *Sci. Rep.* 6, 26850.
- Ye, X., Gao, S., Liu, Z., Zhang, Y., Huang, Z., Dong, M., 2015. Multiple adaptations to light and nutrient heterogeneity in the clonal plant *Leymus secalinus* with a combined growth form. *Flora* 213, 49–56.
- Young, D.J., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecol. Lett.* 20, 78–86.
- Zhu, Q., Iversen, C.M., Riley, W.J., Slette, I.J., Vander Stel, H.M., 2016. Root traits explain observed tundra vegetation nitrogen uptake patterns: implications for trait-based land models. *J. Geophys. Res. Biogeo.* 121, 3101–3112.