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Higher risk for six endemic and endangered *Lagochilus* species in Central Asia under drying climate

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ABSTRACT

The high-mountain ecosystems of Central Asia are a biodiversity hotspot with unique plant communities and many endemic species. Intense human pressure and global warming have caused habitat destruction in these areas and a parallel increase in the number of endangered species. *Lagochilus* species are key medicinal herbaceous plants native to Central Asia, many of which have been recently added to the endangered of species in Uzbekistan.

To assess the climate sensitivity of *Lagochilus* species, we (1) located populations of six species in their native sites across Uzbekistan, and assessed their health by partitioning to ontogenetic stages along five consecutive years; (2) collected plant materials from these species, as well as from old herbarium samples (1918–1964); and (3) analyzed the carbon-13 composition in those samples, as an indicator for drought stress.

Over the course of five years (2014–2018) of continuous monitoring, fluctuations in annual precipitation in the region indicated a decrease by ~20 %, and the fraction of young plants in each population decreased from 20–50% to 0–5 %, depending on the species. Comparing the carbon-13 composition in current and historical leaf samples showed an increase of 1.5–3.5‰ associated with a decrease in precipitation of 2–30 %, depending on the site and species.

Our results show the high sensitivity of *Lagochilus* populations' regeneration to drying, among six species and in sites across Uzbekistan. On a multi-decadal temporal scale, the dramatic changes in carbon-13 indicate that the response to precipitation reduction is related with drought stress. Considering the expectation for drier and hotter climate in Uzbekistan in the coming decades, conservation of *Lagochilus* populations should become a priority in Central Asia.

1. Introduction

Uncontrolled use of plant resources for human well-being drives the loss of plant biodiversity worldwide (World Conservation and Monitoring Centre: (Groombridge and Jenkins, 1992), IPCC, 2001). Global warming is likely to intensify this loss by triggering changes in vegetation cover (Ehleringer et al., 1997). In terms of biodiversity, the mountain ecosystems of Central Asia belong to the most valuable areas in the world, called hotspots. These ecosystems embrace unique plant communities and many endemic species (Mittermeier et al., 2004). A high level of endemism in the mountains is linked to environmental conditions such as geological structure, high mountain ranges and

climatic conditions. Threats to the biodiversity of Central Asia have been recognized since the middle of the 20th century (Zakirov, 1971). Indeed, these ecosystems are exposed to intense anthropogenic pressure, which has caused habitat destruction (Rahmonov et al., 2013). Currently, global climate change is reducing the vegetation cover of many sub-regions, e.g. the Tian Shan mountains (Dimeyeva et al., 2015). Consequently, there has been an increase in the number of endangered species (Tojibaev et al., 2014).

Climatic scenarios are expected to become more extreme, with changes in precipitation characterized by heavier rainfall and longer dry periods (Connor and Hawkes, 2018). Global warming is likely to drive a biodiversity loss by triggering changes in vegetation cover, and

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specifically, in desert C3 plants (Ehleringer, 1989; Ehleringer et al., 1997). The ecosystem response capacity is already under pressure. The extra stresses forced by climate change in the near future will require very unusual adaptation. The ^{13}C composition of plant matter is a useful index to study induced changes in water availability, for example in trees growing along a river which has dried up (Bachar et al., 2020). In another example, *Thuja occidentalis* leaf $\delta^{13}\text{C}$ measurements extending from present-day to pre-industrial historical records, using both newly collected and herbarium material, were used to study the climate sensitivity of the species (Stein et al., 2019). Studies show a monotonic increase in plant $\delta^{13}\text{C}$ with decreasing mean annual precipitation (MAP) that differs from past models. These relationships are sufficiently robust to make deductions about paleoclimate and paleoecology (Kohn, 2010). Carbon isotope fractionation by plants during CO_2 uptake and fixation (Δleaf) changes with environmental conditions, but quantitative models of Δleaf across environmental gradients at the global scale are missing (Diefendorf et al., 2010). In arid environments, plant growth and photosynthesis are limited by apparent seasonal droughts and low atmospheric humidity. It is generally accepted that major episodic heatwaves in temperate regions lead to large decreases in ecosystem productivity (Ciais et al., 2005). Arid lands are forecasted to become drier due to increasing global temperature and drought (Dantas et al., 2020). Climate change will vary global precipitation patterns, making it more important to understand how ecosystems will be impacted by more frequent and extreme droughts (Lemoine et al., 2018). On a long temporal scale, Asia became increasingly dry and cold during the late Quaternary (An et al., 2013). In addition, desert ecosystems in the region have responded to climate changes in the past (Qian et al., 2016; Yang et al., 2019). Desert species are typically sensitive to infrequent, intense pulses of precipitation. Small changes in precipitation are expected to have large influence on vegetation cover and biodiversity (Salguero-Gomez et al. 2012). In combination with the effects of climate, these factors have changed the flora of Uzbekistan, with an increase in endangered species in the last 30 years, from 163 in 1984 to 324 in 2009 (Red Book of Uzbekistan, 2009).

Biodiversity and species interaction networks are highly and unexpectedly changed by climate change (Harley, 2011). The Millennium Ecosystem Assessment estimates a global reduction of vascular plant biodiversity of between 13 and 19 %, between 1970 and 2050, and a reduction of between 7 and 9%, from 2000 to 2050 has also been predicted (Alkemade et al., 2009). Species can react to climate change challenges in time (phenology), space (e.g. range) and via self-acclimation (e.g. physiology) (Bellard et al., 2012). Conservation biology in the face of climate change is one of the global issues in the 21st century (Dawson et al., 2011). The loss of species and populations has been directly linked to anthropogenic factors (Mooney et al., 2009). According to the IUCN Red List update in 2008, over 900 species have gone extinct since 1500 (<http://www.iucnredlist.org/static/stats>) including many vertebrates, invertebrates and plants. Among endangered, red listed, species are 23 species in the Lamiaceae family.

Lamiaceae, a family with a cosmopolitan distribution, comprises 236 genera with 6900–7200 species, including economically and medicinally important herbs, horticultural shrubs, and trees (Harley et al., 2004). The Lamiaceae flora of Uzbekistan includes 201 species in 41 genera (Vvedensky, 1961). The genus *Lagochilus* is the most economically important of the Lamiaceae family. This genus comprises 46 species worldwide (www.theplantlist.org). In the flora of Uzbekistan, the genus *Lagochilus* is represented by 18 species, four of which (*Lagochilus vvedenskyi*, *L. olgae*, *L. proskorjakovii* and *L. inebrians*) are in the Red Book of the Republic of Uzbekistan (2009). Uzbekistan Red Book is a state document established for documenting rare and endangered species of animals, plants and fungi, that exist within the territory of Uzbekistan. The book has been adopted by Uzbekistan to enact a common agreement on rare and endangered species protection. These species are classified as either disappearing (category I, “species with quantity close to the critical level of extinction from the area”) or “rare species” (category II,

“that are not under direct threat of disappearance, but existing in such small numbers or in such limited and specific places of habitation, that they can quickly disappear; they need to be carefully monitored”). Species of this genus are of great economic importance and are extensively used as medicinal raw material (Sokolov and Zamotaev, 1988, Malikova and Rakhimov, 1997; Prato et al., 2006). The leaves contain alcohols, lagochilin (0.6–2 %), essential oils (0.03 %) and vitamin K, and most of the genus’ members contain narcotic, haemostatic, and other substances. For example, *Lagochilus leiocanthus* is a folk medicine used for treatment of inflammation and ulcer in Xinjiang, China. In Japan, this species has been studied for two new flavanones (Furukawa et al., 2011). Locally, most species of this genus are used for treating skin illnesses, controlling bloodletting and nervous disorders (Malikova and Rakhimov, 1997).

Populations of *Lagochilus* species are under pressure from anthropogenic factors, such as overgrazing, harvesting for fodder, fuel, medicinal raw material and trampling, which have resulted in a decrease in the natural habitats of these plants, as previously observed (Beshko, 1997; Shomurodov et al., 2014). Inadequate supply of water and extreme drought have already caused mortality of *Lagochilus* species (Meng and Zhang, 2013, Akhmedov, 2017). Formation of *Lagochilus* populations in certain environmental conditions, and their further growth and development make an exceptionally complex system, but, in turn, an interesting process to study. Understanding these processes requires a comprehensive and detailed study of the species of *Lagochilus* under different environmental conditions using state-of-the-art methodology. To be able to develop science-based and practical measures for the preservation and rehabilitation of these focal species, a detailed and in-depth ecological study of these plants is needed.

Predicting the response of biodiversity to climate change has become an extremely active field of research. Predictions play an important role in alerting scientists and decision makers to potential future risks, provide a means to bolster attribution of biological changes to climate change and support the development of proactive strategies to reduce climate change impacts on biodiversity (Reyer et al., 2013). Among global change environmental factors, desert plant populations are particularly at risk with respect to precipitation (Salguero-Gomez et al., 2012). Here we integrated a geo-botanical approach with a climatic and stable carbon isotope analysis, to study the long-term effects of climate change on *Lagochilus* spp in Uzbekistan. Populations of six *Lagochilus* species across the country were studied along five consecutive years. Leaf samples from these populations were measured for $\delta^{13}\text{C}$ values and were compared to historical samples from herbarium collections, some of which >100 years-old. We hypothesized that *Lagochilus* populations are under increasing drought stress, expressed as (1) a decrease in regeneration; and (2) a decrease in ^{13}C discrimination, i.e., less negative $\delta^{13}\text{C}$.

2. Materials and methods

2.1. Study species

The study focuses on six *Lagochilus* species: *Lagochilus acutilobus* (species name code in figures, LA), *L. gypsaceus* (LG), *L. inebrians* (LI), *L. olgae* (LO), *L. proskorjakovii* (LP) and *L. vvedenskyi* (LV), the latter four being increasingly rare. Species characteristics are detailed in Table 1. In general, the six species are semi- or dwarf-shrubs of 20–60 cm height, with divided leaves and white or pink flowers in summer, between May and August. Four of the species are categorized as Red List species, either as rare (II) or disappearing (I). All six species are harvested for human use, mostly for medicinal purposes, but also as fodder for grazing livestock. *L. olgae* belonged to caudex, polycarpic dwarf-shrubs, whose perennial axes form a short multiaxial caudex. Renewal buds are at a height of 1–2 cm above the substrate.

Table 1

Characteristics of the six studied *Lagochilus* species. Information is based on earlier studies in the region (Vvedensky et al. 1961, Akhmedov et al., 2017, 2019).

Parameter	LA	LG	LI	LO	LP	LV
Full name	<i>Lagochilus acutilobus</i>	<i>Lagochilus gypsaceus</i>	<i>Lagochilus inebrians</i>	<i>Lagochilus olgae</i>	<i>Lagochilus proskorjakovii</i>	<i>Lagochilus vvedenskyi</i>
Endemic region	Ustyurt	Tajikistan, Uzbekistan	Pamir Alay	Nuratau	Nuratau	Kyzyl-Kum
Life form	Semi- shrub	Semi- shrub	Semi- shrub	Dwarf- shrub	Semi- shrub	Semi- shrub
Height (cm)	20–30	20–30	20–60	30–40	20–35	20–35
flower colour	White	White	White-pink	White	Pink	Pink
Form of leaves	Divided, covered with prickles	Divided	Divided	Divided	Lobed	Divided
Flowering	June- July	May-August	June-August	May- June	June- July	May- June
Fruiting	August-September	August-September	July-September	August	August	July- August
Uses	Medicinal	Medicinal	Blood stopping	Fodder	Blood stopping	Medicinal
Red List category	–	–	II- rare	II- rare	I- disappearing	II- rare

2.2. Study sites and climate

Field surveys were conducted during the growing seasons of 2012–2018. Selected study areas are located on three elevational zones, namely, desert, foothill, and mountain, as classified earlier by Zakirov (1971). Within each elevational zone we selected different study areas which differ in terms of soil and climatic conditions (Fig. 1). Site

characteristics and climate are reported in Table 2. Describing the sites from West to East, the Ustyurt Plateau is a large flat plain located in the north-west part of Uzbekistan. In the north, it is bordered by the Caspian lowlands, in the east - with Aral Sea, in the south- delta of Amudarya and Sarikamish lake, and in the west - depression on the Caspian Sea. The plateau is bordered with cliffs almost all around. The soils of Ustyurt are saline and grey-brown. The climate of Ustyurt is characterized by strong

Lagochilus acutilobus, Ustyurt *Lagochilus vvedenskyi*, Kuljiktai *Lagochilus gypsaceus*, Kokchatau

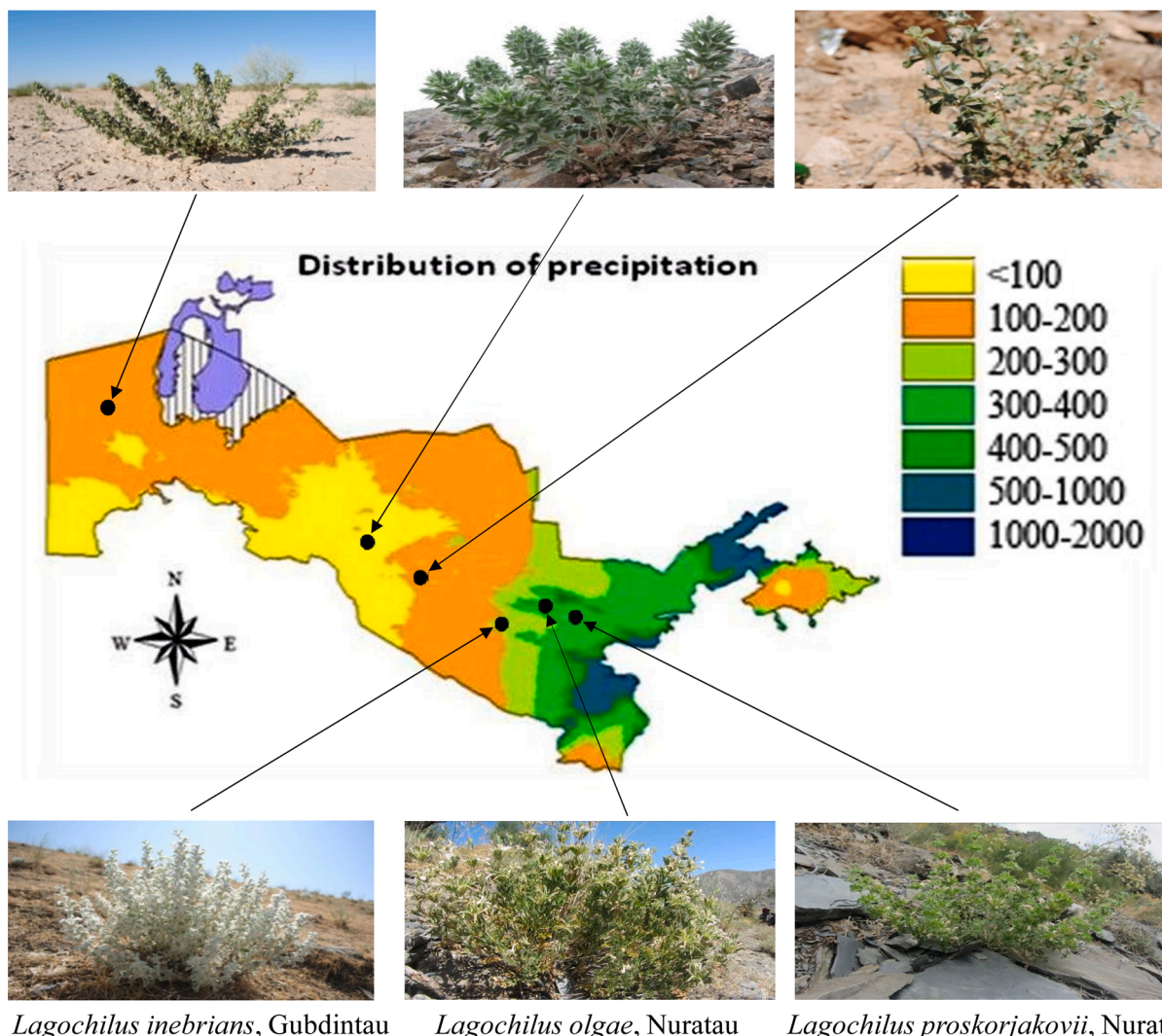


Fig. 1. The studied *Lagochilus* species and their sampling sites across Uzbekistan. Colors on map specify the mean annual precipitation (mm yr⁻¹).

Table 2Site characteristics of *Lagochilus* spp. MAP, mean annual precipitation; MAT, mean annual temperature.

Region	MAP (mm yr ⁻¹)	MAT (°C)	Soil	Landscape	Latitude/ N	Longitude/ E	Elevation (masl)
Ustyurt	150	10.1	Takyr	Plateau	44°49'20.2"	57°07'29.3"	157
Kokchatau	125	15.7	Grey-brown	Desert	40°32'50.7"	65°01'37.0"	341
Nuratau	206	13.3	Grey-brown, Sandy and brown	Mountain	40°30'644"	66°43'344"	1850
Gubdintau	201	14.6	Grey-brown	Foothill	40°51'192"	66°18'112"	705
Kuldjukttau	60	15.3	Grey-brown	Desert	40°76'41.8"	63°77'723.5"	436

inter-annual variations in temperature between years, seasons (with hot and dry summers and cold winters) and even days. Kuldjukttau is represented by a low elevation mountain range and is located in the South-West part of Kyzyl-Kum desert. The average elevation is 520–560 m a.s.l, and the highest point reaches 850 m. The climate of the area is characterized by low annual rainfall and high air temperature (maximum temperature 46 °C). The small mountain island Kokchatau is a low mountain located in the Central part of Kyzyl-Kum desert, to the west part of the Nuratau mountain range. The climate of this area is characterized by sharp fluctuations in daily and annual temperatures: The absolute minimum reaches –31 °C (December and January); and the absolute maximum is 48 °C (July). The Nuratau ridge includes several mountains (Nuratau, Koytash, Gubdintau, Karachatau, Aktau and Karatau) and is located at the north-western edge of the Pamir-Alai mountain range. The highest point in Nuratau reaches 2169 m above sea level. Long-term meteorological data are not available in Uzbekistan. Thus, mean monthly precipitation and temperature data were obtained from the Climatic Research Unit (CRU) TS3.10 dataset (Harris et al., 2014) for each site.

Climate projections for Uzbekistan include 5–10 % decrease in mean annual precipitation and 3.5 °C increase in mean temperature by the end of this century (IPCC, 2007, Mitchell et al., 2017). Among 21 models, only 3–7 models projected increases in precipitation, while 14–18 models projected similar or lower levels than today. These changes are not consistent along the year, as winter drying and warming are expected to be mild. However, summer rains should decrease by 10–20 %, and summer temperatures should increase by 4.0 °C. This is particularly alarming, since summer months in the region are already very dry and hot. Warming will increase the atmospheric vapor demand, further exacerbating the drying, potentially creating hyper-arid conditions for plant communities currently growing in arid and semi-arid climates. The impact of such drought scenarios has already been calculated for the agriculture sector in Uzbekistan, showing major reductions in crop productivity (Mitchell et al., 2017).

2.3. Population structure measurements

At each of the sites we set out three transects, starting from a common random point. From this point, one transect was established to the north, one to the south and one to the east. Each transect was 1 m wide and 10 m long and was subdivided into ten squares of 1 m². In each of the squares, the number of individuals in each ontogenetic stage was counted (s - seedlings, j - juvenile, im - immature, v - virginile, g1 - young generative, g2 - mature generative, g3 - old generative, ss - subsenile, s - senile; Rabotnov, 1950; Uranov, 1975; Coenopopulations, 1976). The ontogenetic spectrum of the population was then determined according to the standard method by Uranov (1975) and Uranov and Smirnova (1969). Four types of ontogenetic spectra can be distinguished (Zaugolnova, 1994; Table 3), depending on the proportion of individuals in the pre-generative states (s, j, im, v), generative states (g1, g2, g3) and post-generative states (ss, s). The four population structure scenarios are: 1. Left-sided spectrum. This consists of prevalent individuals in the pre-generative state or in one of the generative states. This type of spectrum is very dynamic and members of the groups in specific populations are quite diverse. 2. Centred spectrum. Individuals of the

Table 3

Types of ontogenetic spectra.

Ontogenetic spectrum	Ontogenetic stages	Dominated by
Left sided	j, im, v and g1	Regenerative and generative stages
Bimodal	j, im with g2 or g3	Regenerative, generative or post-generative
Centered	g2	Generative
Right sided	g3, ss and s	Generative and post-generative

average age generative ontogenetic state prevail. 3. Bimodal spectrum. For this type of spectrum, two maximums are characteristic, one in the regenerative part and one in older (less often mature) generative plants. 4. Right-sided spectrum. In this spectrum, old individuals are dominant and there is lack of the young ontogenetic stages.

2.4. Historical (herbarium specimens) and current (field specimens) samples

We collected samples of green and healthy leaves of historical and current specimens of five *Lagochilus* species and prepared them for ¹³C isotope analyses. Specimens were collected between 1918 and 1964 (Table 4). Specimens were obtained from two herbarium sources: 1. The National Herbarium of Uzbekistan (Code-TASH), located in Tashkent; an important source for compilation of the database of the flora of Uzbekistan. It is the largest herbarium collection of Middle-Asian species worldwide, with more than 1.5 million; 2. The herbarium collection of Samarkand State University, established in 1927 and has about 20,000 herbarium specimens (Khaydarov et al., 2013). The absence of a consistent digital source of information on the plant diversity of Uzbekistan is a serious shortcoming for the practical activities of the nature conservation agencies and protected areas, as well as for monitoring, education and scientific research. Present samples (green and healthy

Table 4Historical herbarium samples of *Lagochilus* species, available at Samarkand State University and Institute of Botany of Uzbek Academy of sciences.

Species name	Oldest specimen	Youngest specimen	Sampling location	Environmental zone
<i>Lagochilus acutilobus</i> (Ldb.) Fisch. et Mey.	1945	2015	Ustyurt, Churuk	Desert
<i>Lagochilus gypsaceus</i> Vved.	1940	2015	Kukchatau	Foothill
<i>Lagochilus olgae</i> R. Kam.	1937	2015	Nuratau	Mountain
<i>Lagochilus proskorjakovii</i> Ikram.	1964	2015	Nuratau	Mountain
<i>Lagochilus vvedenskyi</i> R. Kamelin & Tzukerv.	1918	2015	Kyzyl-Kum	Desert

leaves) of mature individuals of six *Lagochilus* species were collected during field investigation and collections from natural populations in June–July 2015.

2.5. Isotopic analysis of ^{13}C in historical and current leaf samples

Isotopic analyses for carbon-13 were conducted at the Department of Plant & Environmental Sciences, Weizmann Institute of Science, using a Cavity Ring Down Spectroscopy (CRDS) method. An amount of 1 mg (0.9–1.2) was mounted onto a combustion module equipped with an auto-sampler (ECS 4010, Costech Analytical, Valencia, CA, USA). The resultant CO_2 gas product was analyzed with the ^{13}C analyzer (Picarro G2131i, Picarro, Santa Clara, CA, USA), which was directly interfaced to the combustion module. Results were expressed as parts per thousand (‰) deviations from the international carbon isotope standard (Vienna Pee Dee Belemnite, VPDB) according to:

$$\text{corrected } \delta^{13}\text{C}_i = \delta^{13}\text{C}_a + a + (b - a) \times \left(\frac{C_i}{C_a}\right) \quad (1)$$

Where $\delta^{13}\text{C}_i$ is the leaf isotopic carbon composition, $\delta^{13}\text{C}_a$ is the atmospheric $\delta^{13}\text{C}$, a is the maximum ^{13}C fractionation from diffusion of CO_2 into the leaf (-4.4‰), b is the maximum ^{13}C fractionation from carboxylation reactions (-27‰), and C_i and C_a are CO_2 concentrations in the leaf intercellular cavity and atmosphere respectively. Three samples were measured and averaged. An international standard (IAEA-CH-3, Cellulose, International Atomic Energy Agency, Vienna, Austria) was used and internal standards (homogeneous *Spirulina* powder with a ^{13}C of -29.2‰) and Glucose (Sigma, St. Louis, MI, USA) were used every 9 samples. To account for the depletion of $\delta^{13}\text{C}$ in atmospheric CO_2 resulting from anthropogenic emissions, we subtracted the change in $\delta^{13}\text{C}$ in atmospheric CO_2 that occurred between the years covered in our analysis (e.g., -1.55‰ from 1918 to 2015). Global $\delta^{13}\text{C}$ values were taken from Graven et al. (2017). The correction was done as follows:

$$\text{corrected } \delta^{13}\text{C}_{i,x} = \delta^{13}\text{C}_{i,x} - (\delta^{13}\text{C}_{a,x} - \delta^{13}\text{C}_{a,1918}) \quad (2)$$

Where $\delta^{13}\text{C}_{i,x}$ is the leaf isotopic carbon composition of year x , $\delta^{13}\text{C}_{a,x}$ is the atmospheric $\delta^{13}\text{C}$ of year x and $\delta^{13}\text{C}_{a,1918}$ is the atmospheric $\delta^{13}\text{C}$ of 1918 (-6.87‰).

2.6. Description of the vascular plant communities and environmental conditions

Plant community description of each of the six *Lagochilus* species was made according to conventional geobotanical methods and then inventoried all plant species occurring in one randomly selected 10×1 m plot. Unidentified plant species were collected for identification. Total vegetation cover was estimated in each plot using the method developed by Braun-Blanquet (1965), where each species cover was assessed based on cover classes (0–5 %, 5–25 %, 25–50 %, 50–75 %, and 95–100 %). The life form of plants was described as trees, shrubs, semi-shrubs, dwarf-shrubs and herbs (perennial, biennial and annual) according to the 9th volume of Plant Identifier of Central Asia (Abdulayeva, 1987). Plant taxonomy was according to Czerepanov (1995) and www.plantlist.org. For each site, we estimated the following environmental variables: aspect, slope, distance to water, annual precipitation and anthropogenic factors. Aspect was measured using GPS (Garmin 62, Garmin Ltd., Olathe, KA, USA) and slope was visually estimated.

2.7. Statistical analysis

Statistical analysis was done using JMP (Cary, NC, USA). We used Two-way ANOVA to test for differences among years (5 years of measurements) in each of the developmental stages of the population. In addition, a t -test was applied to test $\delta^{13}\text{C}$ differences between historical and current samples, and P -values were calculated for the correlation

coefficients between the percent of young plants in each population in a specific year and the precipitation amount in that year.

3. Results

3.1. Climatic trends over the study sites in the past 100 years

Climatic trends in the past 100 years showed similar patterns across the six Uzbek sites (Fig. 2). There were large inter-annual fluctuations in precipitation, but no change in the site-specific mean, and smaller fluctuations in temperature, but an overall warming of 2–4 °C. Across the sites, the 100 years minimum and maximum annual precipitation amounts were 62 mm yr^{-1} (in Ustyurt in 1975), and 615 mm yr^{-1} (in Nuratau 1 in 1969), respectively. The inter-annual standard deviation in precipitation was different among sites, but overall 20–26 % of the mean, rendering Ustyurt, Kuljiktai, and Kokchatau with arid climate, and Gubdintai and the Nuratau sites with semi-arid climate. The 100 years minimum and maximum annual mean temperatures were 7.2 °C (in Ustyurt in 1928), and 16.4 °C (in Kokchatau in 2016), respectively. The inter-annual standard deviation in temperature was $0.9\text{--}1.0 \text{ °C}$ in all the sites, i.e. 11 % in Ustyurt, and 6–7 % in the other, warmer sites. At the shorter temporal scale of 2014–2018, changes in temperatures were minor, whereas precipitation increased slightly in 2015, and then decreased steadily from 2016 to 2018 (Fig. 2 insets).

3.2. Changes in population structure of six *Lagochilus* species

Plant population dynamics, detected by developmental stage distribution along five years (2014–2018), revealed ontogenetic differences over the years. In general, spectra were single-peak and there was a decrease in the number of regenerating individuals with time, in all the six species (Fig. 3). Aside from four juveniles of *L. acutilobus*, there was zero regeneration across the different populations in 2017 and 2018. We detail the patterns observed for each species: *L. acutilobus* – a centred spectrum with a left-side tail in 2012 and 2015 evidenced abundant fruiting and rapid development of young individuals. *L. gypsaceus* – this population switched from left-sided spectra in 2014–2015 to right-sided

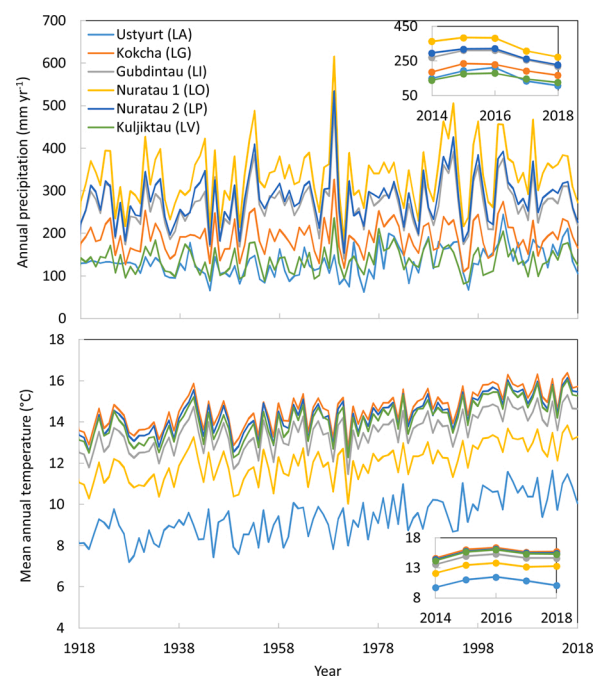


Fig. 2. Climate conditions in *Lagochilus* sites in Uzbekistan over the past 100 years, with zoom in on 2014–2018 (insets). For species name codes see text. Data retrieved from the Climatic Research Unit TS3.10 dataset.

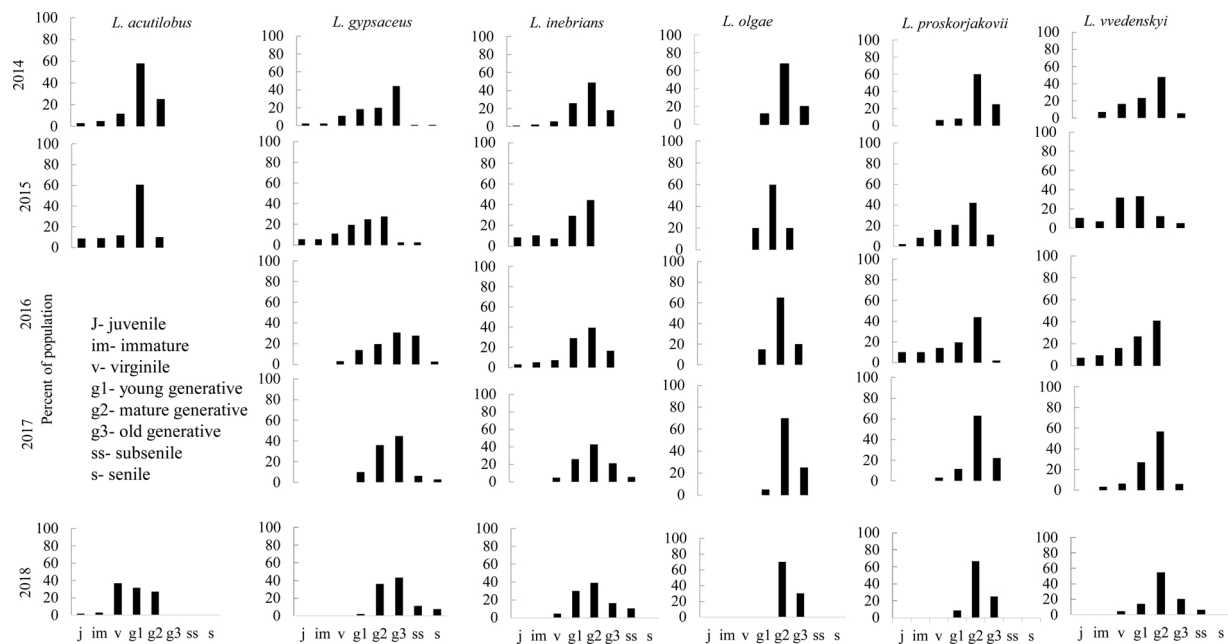


Fig. 3. Dynamics of population partitioning to developmental stages of six *Lagochilus* species in Uzbekistan in 2014-2018 (2012 instead of 2014 in *L. acutilobus*).

spectra, with an absolute maximum on individuals of the old generative state (44 %), in 2016–2018. *L. inebrians* – the population was centred, with the peak found in the middle generative plants (39 % of all plants). The loss of a young fraction in this population in 2016–2017 was due to the irregularity of seed renewal. In turn, this was caused, on the one hand, by dry climate and high temperature, and on the other, by a constant wind blowing plant seeds beyond the boundaries of the population. *L. olgae* - The percentage of mature and old generative stages was 60 %, and increased to 100 % in 2018, i.e. without any young plants. Such sharply centred spectra typically corresponds with difficult germination of seeds, harvest by shepherds for fodder immediately after flowering, and minimal elimination of individuals of mature individuals. *L. proskorjakovii* – this species showed a dramatic change from right-sided spectra in 2014 to centred spectra in 2015–2016, followed by the loss of young generative individuals in 2017–2018, when it was represented only by generative individuals. This species has low seed germination rate, rapid transition to flowering and slow development of individuals in the mature generative state. *L. vvedenskyi* – left-sided

spectra measured in 2014 and 2016 changed to centred spectra in the following years, which meant losing all juvenile and immature plants in the population. In general, all *Lagochilus* species decreased in the number or regenerating individuals over the years. The effect of year on the number of individuals was significant for sub-senile plants of *L. gypsaceus* ($P = 0.0090$) and *L. inebrians* ($P = 0.0434$); for g2 plants in *L. inebrians* ($P = 0.0072$); and for g3 plants in *L. olgae* ($P = 0.0467$). In addition to the changes in population structure, the number of individuals of each of the six species also decreased from 2015 to 2018, by 8–30 %, depending on the species (Fig. S1).

3.3. $\delta^{13}C$ analysis of historical and current leaf samples of *Lagochilus* species

$\delta^{13}C$ values of plant leaves collected in the past and present revealed physiological differences of the plants among the years. *Lagochilus* leaf $\delta^{13}C$ values of present and historical samples were significantly different (paired t -test, p -value = 0.004), showing a 1.4–3.5‰ more depleted

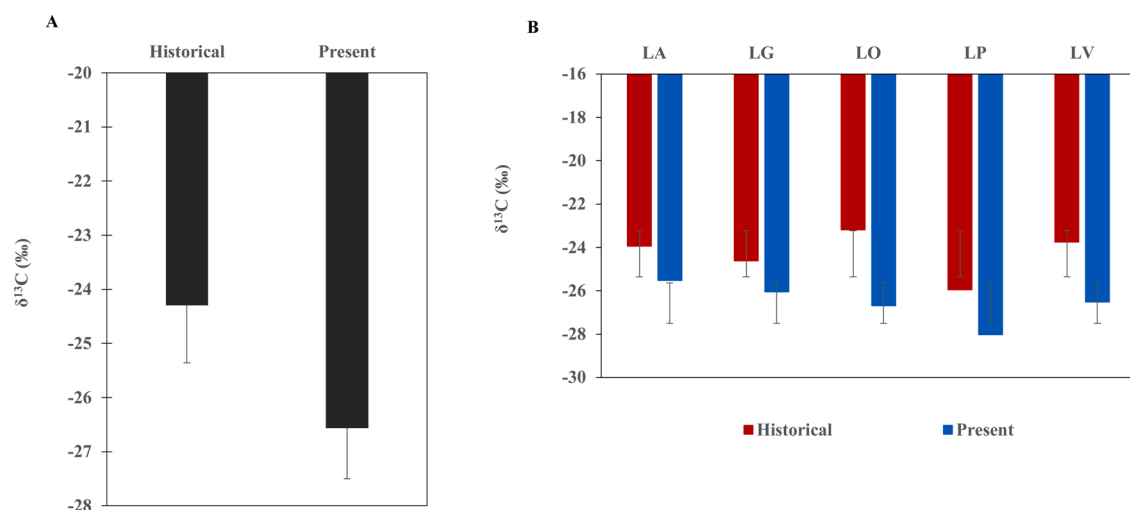


Fig. 4. $\delta^{13}C$ of leaf samples of *Lagochilus* species from field sites across Uzbekistan. A. Means for historical and present samples of the five species; B. Species-specific values. For species name codes see text.

values for present than historical samples (Fig. 4). On average, historical $\delta^{13}\text{C}$ was $-24.3 \pm 1.1\text{‰}$, and present $\delta^{13}\text{C}$ was $-26.6 \pm 0.9\text{‰}$, and the linear correlation between historical and present samples showed this decreasing pattern, with r^2 of 0.40 (data not shown). However, this type of comparison is inadequate, because historical samples represent a wide range of sampling years, between 1918 and 1964 (Table 4). Moreover, considering the lack of an inter-annual trend in annual precipitation over the past 100 years (Fig. 2), and the fact that $\delta^{13}\text{C}$ typically increases with drying (see Introduction), the decreasing trend was unexpected. Nevertheless, precipitation in 2015 was 16–29 % higher than in each of the historical sampling years, with the whole period 2011–2016 having higher-than-average precipitation (except for *L. proskorjakovii* in one of the wetter sites, in Nuratau).

3.4. Relationships between leaf $\delta^{13}\text{C}$ and annual precipitation

To test the relationships between leaf $\delta^{13}\text{C}$ and precipitation, we plotted leaf $\delta^{13}\text{C}$ as a function of the precipitation at the year of sampling. For four out of five *Lagochilus* species, this analysis revealed the expected $\delta^{13}\text{C}$ increase with drying (Fig. 5). *L. proskorjakovii* was an outlier, since it presented the $\delta^{13}\text{C}$ change without any parallel change in precipitation in Nuratau. The largest precipitation change was for *L. olgae*, again in Nuratau, from 271 to 384 mm, with a parallel 3.5% decrease in $\delta^{13}\text{C}$. To account for climatic effects at a longer term than the year of sampling, we repeated the analysis, this time averaging the precipitation over the past five years. This yielded very similar patterns as before, yet without any exception (Fig. 5).

3.5. Relationships between population structure and annual precipitation

To test for potential effects of climate on population structure, we took advantage of the climatic variations during the five years between 2014 and 2018, when population dynamics were measured. These climatic variations included mild fluctuations in mean annual temperature, and a drying trend in annual precipitation (Fig. 2). Among different parameters of population health, we used the sum of fractions of the three young stages (juvenile, immature, and virginile) as an indicator for

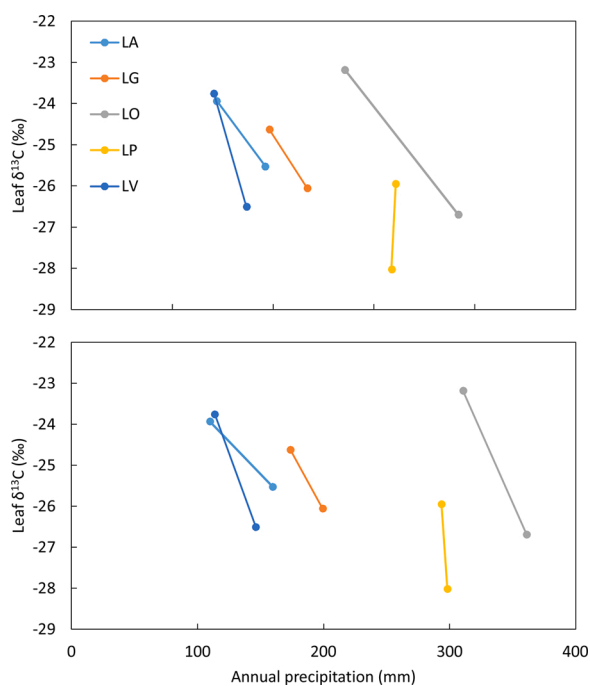


Fig. 5. Relationships between leaf $\delta^{13}\text{C}$ of five *Lagochilus* species and annual precipitation at their field sites in the same year (top) and mean annual precipitation of the past five years (bottom). For species code names see text.

regeneration. Plotting the rate of young plants in *Lagochilus* populations against the site-specific precipitation of the respective years yielded strong linear regressions for four out of six species (Fig. 6; $0.61 < r^2 < 0.77$). The exceptions were *L. acutilobus*, which only had three data-points, and *L. olgae*, which had no young plants in its populations along the five years. The remaining four species presented different sensitivities to changes in precipitation, with the dry-adapted *L. vvedenskyi* responding stronger than the desert *L. gypsaceus*, in turn responding stronger than the semi-arid *L. inebrians* and *L. proskorjakovii*. Overall, young plants accounted for up to 50 %, typically around 35 % of populations in wet years, and decreased to 0–10 % during dry years.

4. Discussion

This study investigated the climate sensitivity and population dynamics of *Lagochilus* species in Uzbekistan. The results presented here confirmed our hypotheses that these *Lagochilus* populations are under increasing risk, expressed as (1) a decrease in regeneration with lower precipitation amounts in recent years; and (2) high physiological sensitivity to drought, reflected by a decrease in ^{13}C discrimination, i.e., less negative $\delta^{13}\text{C}$, in dry, compared to wet, years. To the best of our knowledge, this is among the first studies to show the climatic risks threatening key plant species in Central Asia. The sensitivity to drought of the unique arid ecosystems of Central Asia has just recently been explored (Zang et al., 2020).

4.1. Differences between species in terms of climate sensitivity

The six studied species diverged in their site conditions, ranging from arid desert to semi-arid mountain ranges. Of the six species, the desert *L. vvedenskyi* showed the highest sensitivity in terms of loss of young plants in its populations along the drying sequence of 2014–2018 (Fig. 6). *L. inebrians*, from the wetter Gubdintau region (yet not the least dry here) showed the least sensitivity. In accordance, sensitivity of the isotopic geochemical values of *L. vvedenskyi* was also higher than that of most other species (Fig. 5). These observations are in line with the perception that desert plants are living closer to their physiological capacities to withstand drought. Semi-arid landscapes suffer highly inadequate water and are characteristically more responsive to changes in precipitation amount and occasion size (Post and Knapp, 2019). Consequently, mortality of plants can relate to lack of precipitation (Salguero-Gómez et al., 2012). However, the other desert plant in our study, *L. acutilobus*, showed milder responses to drought in both population structure and $\delta^{13}\text{C}$. Still, there was a gradient of population climate sensitivities, with species from wetter sites responding in a milder fashion than species from drier sites (Fig. 6). In *L. acutilobus* in

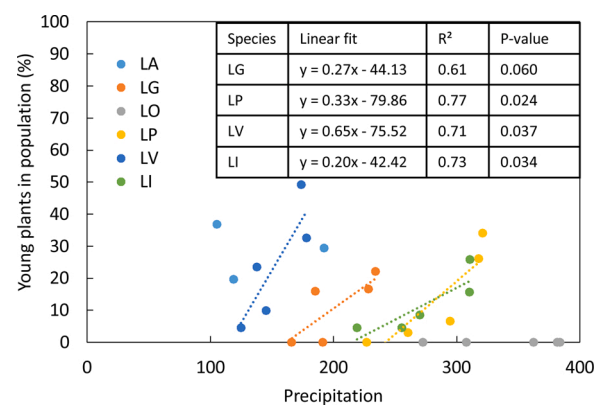


Fig. 6. Relationships between the percentage of young individuals in populations of six *Lagochilus* species and annual precipitation (mm) at their field sites in 2014–2018. Linear fits are excluded for LA (3 years only) and LO (zero percent throughout the period). For species code names see text.

2018, the population lost almost all of its juvenile and immature plants, at least partly due to a freezing event. It is possible that anthropogenic disturbance contributed to loss of the duration of the middle generative state, the transition of individuals to the old generative state and their quick death of *L. gypsaceus*. Interspecific differences in $\delta^{13}\text{C}$ were harder to interpret, with the strongest response recorded for *L. olgae*, a species located at the wettest site, in Nuratau mountains (Fig. 5). Notably, this species also showed the most consistent and severe lack of population regeneration (Fig. 3). It is hence possible that this species suffered a unique combination of site stressors, putting it at greater danger under an ongoing climate change.

4.2. Shrub populations under a changing climate

Past studies have shown that plant species richness is changed by climatic extremes within the growing season (Padilla et al., 2019). Extreme drought decreases plant cover, rendering only the species with a higher resistance to drought stress (Zhong et al., 2019). Low precipitation and mean temperature decreased species richness (Zhang et al., 2018). In particular, studies on desert and mountain shrub communities seem to correspond to our observations in *Lagochilus*. For example, increasing temperature negatively affected growth and flowering of *Arnica montana* and decreased the size of eight populations of *A. montana* (Vikane et al., 2019). Salguero-Gómez et al. (2012) found a positive relationship between population growth rate and higher precipitation over *Cryptantha flava* and *Carrichtera annua* shrub populations in the Mediterranean basin and the Great Basin Desert, respectively. In the Sonoran Desert, there was a steep population decrease due to negative effects of climate change. However, the demography of this population shows that the survival of mature individuals is the only process that maintains the population, as no new individuals are being listed. Thus, the population will be healthy as long as mature individuals survive (Larios et al., 2020). In our case, the *Lagochilus* genus is relatively tolerant to drought (Meng and Zhang, 2013). Mature and old individuals of *Lagochilus* species have a prolific root system that penetrates deep into the soil, about 1.5–2 m. This might explain why mature and old individuals were more resistant (Fig. 3). Whether *Lagochilus* populations are able to recover from climate instability in the long term is beyond the scope of this five-year study. Future climate scenarios are not limited to changes in the mean annual precipitation, but rather include changes in the variability among years, each with different effects (Reyer et al., 2013). Moreover, even changes in the timing and distribution of precipitation events can exert large effects on plant populations (Raz-Yaseef et al., 2012). Specifically, end-of-century projections for Uzbekistan include mild changes in winter, and severe drying and warming in summer (IPCC, 2007). Last, extreme drought could potentially increase biomass allocation to reproductive organs, as has been shown in a dune ecosystem in western China (Zang et al., 2020).

4.3. Study limitations

Detailed population surveys along five years and access to old plant material in botanical collections facilitated this study. However, the lack of sampling between historical and current samples rendered the analysis as two-point trends alone, which are hard to rely on (Fig. 5). This fact was further expressed when, probably by chance, all historical samples came from dry years, which was against the current predictions of drying climate for the region. Nevertheless, the overall trend across the species helped demonstrate the general physiological response of increasing $\delta^{13}\text{C}$ in response to drying. Another important limitation was the lack of meteorological data from each of the sites. Instead, we used upscaled data coming from a global database, which, although useful, is generally less accurate than on-site measurements. While this upscaling probably reduced the accuracy of our analyses, it seemed to capture well the differences between the sites and their long-term climatic trends

(Fig. 2), even at relatively high proximity, such as the two Nuratau sites (Fig. 1). Finally, our analysis lacked the societal dimension, which is clearly a threat to *Lagochilus* populations across Uzbekistan, through activities such as harvest for fodder and medicinal use. Here, we selected sites that were rather remote, with minimum human interference, in order to isolate the climatic effect. A future study should also test and quantify the societal impacts on these populations, also weighing the climatic effects described here.

4.4. Implications for conservation

Natural environment loss due to increased anthropogenic pressure is one of the principal reasons for global biodiversity loss (Cardinale et al., 2012). Natural environment loss and fragmentation result in significant landscape changes that eventually influence plant diversity and add suspense to how natural zones will respond to future global change (Zambrano et al., 2019). Global warming and increased anthropogenic pressure on natural ecosystems adversely affect the state of populations of endemic and rare components of biodiversity. Today, the protection of natural populations of rare and endangered species is one of the priority areas for biodiversity conservation. In this context, assessing the status of populations of rare and endangered species and developing measures to prevent threats to them is of great scientific and practical importance. The high climatic sensitivity of the six *Lagochilus* species studied here is a red alert for the survival of these species in their native habitats. To conserve the remaining populations, we hence propose the following steps: (1) to develop a long-term, national, monitoring program for *Lagochilus* species in Uzbekistan; (2) to promote conservation of natural populations by removal of societal threats, e.g. through outreach activities, and by providing alternatives through cultivation of the most useful species for human use; (3) to test the viability of an assisted migration program, that would plant new *Lagochilus* populations in more mesic sites, to replace current sites once they become climatically inhospitable for the *Lagochilus* species; and (4) to create a *Lagochilus* gene bank and a living collection of *Lagochilus* populations from an array of sites and ecosystems, e.g. in a rescue botanical garden.

Author contributions

AA collected all samples and surveyed the plant populations in the field, under the supervision of HS and MN. IR performed the isotopic analysis. AB performed the climatic analysis. TK designed the analysis and the paper, and wrote it jointly with AA.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ppees.2020.125586>.

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