



Original Research Article

Persistence of remnant boreal plants in the Chiricahua Mountains, southern Arizona

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ABSTRACT

Boreal plants growing along the southern edge of their range on isolated mountains in a hot desert matrix live near the extreme of their physiological tolerance. Such plants are considered sensitive to small changes in climate. We coupled field observations (1974, 1993, 2019) about the abundance and vigor of small populations of ten remnant boreal plant species persisting in the uppermost elevations of spruce-fir forests of the Chiricahua Mountains, together with modeling of the species sensitivities to three stress factors associated with climatic change: warming, drought, and forest fire, in order to explore the persistence of frontier boreal plant species during climate change. We hypothesize that populations of these cryophilic plants have declined or become locally extinct during an adverse warming period since 1993, enforced by two large forest fires (1994, 2011). We used plant traits and principal component analysis to evaluate sensitivities of the studied plants to the combined actions of warming, drought, and forest fires. Our model predicted selective sensitivity to warming for two species: *Vaccinium myrtillus* and *Rubus parviflorus*. Other cryophilic species could be more sensitive to drought and fire. We surveyed the study area in 2019 and found eight of the ten previously investigated species still occur in the area. Five species occurred in wet canyons at lower elevations, but three species persisted in low vigor at the uppermost elevation, which was highly affected by fires. Neither warming-sensitive species showed signs of decline: populations of *R. parviflorus* increased in abundance and vigor, while *V. myrtillus* persists without significant changes since 1993. Despite the recorded increase in temperature in the study area $>1^\circ\text{C}$ between years 1975–1993 and 1994–2019, our study did not find direct evidence of warming effects on the observed species. We conclude that severe wildfires and the multi-decadal decrease in precipitation rather than warming are the main limiting factors of remarkable but limited persistence of the remnant boreal species in the Chiricahua Mountains. Our study demonstrates how field observations can be combined with modeling to evaluate species selective responses to different environmental stress factors to make better environmental management decisions, particularly in light of climate change.

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1. Introduction

During the last few decades, researchers and society have become increasingly worrying about climate warming impacts on species diversity and survival (Walther et al., 2002; Parmesan and Yohe, 2003; Shwom et al., 2015; Wiens, 2016). Some remnant boreal plants growing along the southern edge of their range and/or at their elevational limits are expected to be heralds of adverse climate change (Beniston, 2000; Freeman et al., 2018). Plants growing on isolated mountains in a hot desert matrix are often near the extreme of their physiological tolerance and may be sensitive to small gradual changes in temperature (Hoffmann and Sgro, 2011). Warming in mountain plant communities is accompanied not only by extreme heat waves, drought, and severe forest fires (Allen, 1994), but also by invasion pressure from lower-elevation plant communities (Lenoir et al., 2008). However, plant species growing under continuous climate fluctuations and persistent stresses have evolved strategies allowing them to survive such environmental changes. Such strategies include: (1) temporal persistence in refugia for rapid climate changes (Keppel et al., 2011); (2) shifting elevation or geographical range (migration) for slower changes (Kelly and Goulden, 2008; Lenoir et al., 2008; Morueta-Holme et al., 2015); and (3) physiological adaptations for slow climate changes if elevation or geographical range are limited (Siefert et al., 2015; Becklin et al., 2016). Surveys of remnant boreal plants growing near the extremes of their physiological tolerance could help to estimate the pressure of climate change on the biosphere and promote better understanding and protection of potential refuge areas for endangered species.

In European mountains, where plant survey traditions started more than 400 years ago (Stöckli et al., 2011), high-elevation plant communities are well studied. Various studies have investigated the impact of recent climate change on plant abundance and diversity (e.g., Pauli et al., 2012; Cannone and Pignatti, 2014). Some expected and unexpected results were found, such as: elevation upshifting or downshifting for different plant groups (Pauli et al., 2012; Cannone and Pignatti, 2014; Küchler et al., 2014; Rumpf et al., 2018); increase of local species richness (Pauli et al., 2012; Wipf et al., 2013; Steinbauer et al., 2018); and decrease of rare or endemic boreal plants (Dirnböck et al., 2011; Pauli et al., 2012). In the North American Southwest, boreal plants persist on the summits of isolated mountains – ‘sky islands’ – within a hot desert matrix that significantly limits their possibilities for adjusting to elevation and geographical range. Such desert islands are under-recognized natural laboratories for testing plant-climate interactions. As far back as in 1974, a set of remnant boreal plants was surveyed in the Chiricahua Mountains, Southeastern Arizona (Moir and Ludwig, 1979). The abundance and vigor of ten perennial boreal species persistent in the spruce-fir forests were recorded along five hiking trails around Chiricahua Peak. The second survey was done 19 years later (Moir, 1995), when most populations of the surveyed species were found at 1974 levels or had even increased in number. After a large forest fire in 1994, most populations were thought to be gone (see postscript in Moir, 1995).

In 2019, we performed the third field survey of the same boreal species in the Chiricahua Mountains of Southeastern Arizona. The aim of our study was to test a hypothesis that populations of cryophilic plants have declined or become locally extinct during an adverse warming period since 1993 and following extensive fire disturbances. We surveyed the abundance and vigor of the ten plant species along the same hiking trails around Chiricahua Peak. Fire severity was estimated from field observations, while multi-decadal changes in annual temperature and precipitation were calculated from local climatic data. We performed univariate and multivariate analyses to evaluate sensitivity of each species to three anticipated adverse stress factors associated with climatic change: warming, drought, and forest fire. The species were divided into functional groups according to their likelihood to be mainly sensitive to one of the stress factors (selective sensitivity). In this paper, we report changes in the remnant species abundance and vigor during the period between 1993 and 2019 and explain them by using a trait-based approach in the context of climate change. Our study reintroduces the historical surveys performed by Moir in 1974 and 1993 and paves the road for further systematic and regular surveys of species that are sensitive to climate change in the North American Southwest.

2. Materials and methods

2.1. Study area

The Chiricahua Mountains are located in southeastern Arizona (Fig. 1) and are the most extensive mountain range within the Madrean Sky Island Archipelago in the United States. The range is approximately 65 km long and 32 km wide, with maximum elevation of 2976 m a.s.l. (Bennett et al., 1996). The upper reaches of the range are dominated by a series of ridges and peaks in excess of 2700 m a.s.l. The local climate is characterized by bimodal precipitation with a wide range in daily and seasonal air temperature (Bennett et al., 1996). Approximately two-thirds of annual precipitation falls during summer thunderstorms; the remaining precipitation falls in winter as snow or rain (Bennett et al., 1996). Common trees at elevation above 2400 m a.s.l. are Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), southwestern white pine (*Pinus strobiformis*), quaking aspen (*Populus tremuloides*), white fir (*Abies concolor*), and Arizona pine (*Pinus ponderosa* var. *arizonica*).

The study area is located at elevations of 2400–2976 m, where the spruce-fir forests occur (Fig. 1). Note that the large-scale map of plant communities does not show little patches of spruce-fir forests dispersed along the trails. The area was severely affected by two of the largest recorded wildfires in the Chiricahua Mountains: the Rattlesnake Fire (11,129 ha forested area burned in June and July of 1994), and the Horseshoe 2 Fire (90,226 ha burned in 2011) (Youberg et al., 2013). These fires burned at various intensities across almost all upper elevation forests including all of the study area.

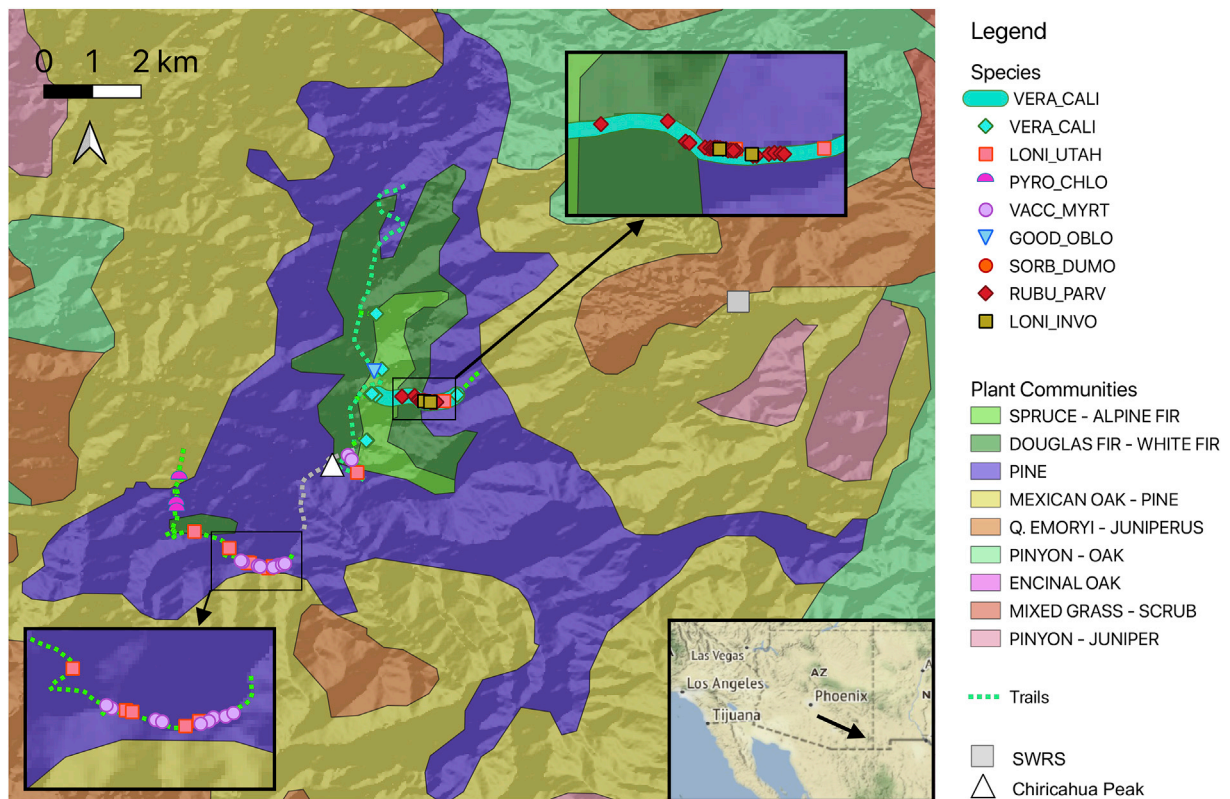


Fig. 1. Study area in the Chiricahua Mountains, southeastern Arizona: plant communities (AZGEO) and locations of the observed plant species in 2019. For species codes see Table 1. Surveyed trails shown by green dashed lines. SWRS – Southwestern Research Station, Portal, Arizona. The inset in lower right corner shows location of the Chiricahua Mountain range in Arizona, USA. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.2. Studied species and field survey

Ten boreal plant species were studied: *Chimaphila umbellata* (Ericaceae; prince's pine), *Erigeron scopulinus* (Asteraceae; rock fleabane), *Goodyera oblongifolia* (Orchidaceae; western rattlesnake plantain), *Lonicera involucrata* (Caprifoliaceae; black twinberry), *Lonicera utahensis* (Caprifoliaceae; red twinberry), *Pyrola chlorantha* (Ericaceae; greenflowered wintergreen), *Rubus parviflorus* (Rosaceae; thimbleberry), *Sorbus dumosa* (Rosaceae; Arizona mountain ash), *Vaccinium myrtillus* (Ericaceae; bilberry), *Veratrum californicum* (Melanthiaceae; California corn lily) (Table 1). These species occur in the uppermost elevations (>2400 m a.s.l.) of the Chiricahua Mountains and most of them are growing along the southernmost edge of their distributions. The exception is *Chimaphila umbellata*, for which the local subspecies *C. umbellata* subsp. *acuta* occurs in the American Southwest but which is distributed primarily in Mexico. This species was surveyed in our study to be consistent with previous surveys. Eight of the ten species are North American plants, while *Vaccinium myrtillus* and *Pyrola chlorantha* are circumboreal. Two species – *Erigeron scopulinus* and *Sorbus dumosa* – are endemic to the southwest of North America.

Plant species were inventoried along five hiking trails in September–October 2019. The surveyed trails were: Crest Trail, upper part of the Greenhouse Trail, Monte Vista Lookout Trail and adjacent trails where spruce-fir forests occurred (see Fig. 1, and Table S1 for description of trails). Plants were observed in a 10-m band on both sides of trails (5 m to each side). The total observation area was of 20.5 km length and 10 m width. A 10-m-long plot was assigned, when at least one of the surveyed species was encountered. That way the size of each plot was 10 × 10 m. In total, 98 plots were assessed. Observations of abundance (number of individuals or ramets) and vigor for each species in each plot were recorded. Vigor of each plant was assessed in three classes by evaluating shoot robustness, flowering/fruitlet capacity, and symptoms of disease/herbivory/insects/parasitism: low vigor (1), medium vigor (2), high vigor (3) (see for the vigor classes Table S2). The mean species vigor values from all plots, where individuals of a particular species occur, were calculated to evaluate overall species vigor. In addition, species habitat fire severity in the observation plots was estimated in five classes according Keeley (2009): unburned (1), scorched (2), light (3), moderate or severe surface burn (4), and deep burning or crown fire (5) (see for the fire severity classes Table S3). Mean fire severity value of all plots where individuals of a particular species occur was taken to evaluate an accumulated direct impact of forest fires (burn) on species habitats. In order to compare our data with historical data, the term 'location' was also introduced and adjacent plots with the same species were counted as one location.

Table 1

Abundance, vigor and habitat fire severity of ten boreal plant species in 2019. Plant abundance recorded for each species by counting the number of plots with a particular species, the number of locations, and the number of individuals/ramets. Values of species vigor and habitat fire severity per plot were averaged over all plots of each species. The data are reported as means with standard errors. For vigor and fire severity classes see Methods and Tables S2, S3.

Species	Species code	Number of			Vigor	Fire severity
		plots	locations	individuals		
<i>Chimaphila umbellata</i>	CHIM_UMBE	0	0	0	—	—
<i>Erigeron scopulinus</i>	ERIG_SCOP	0	0	0	—	—
<i>Goodyera oblongifolia</i>	GOOD_OBLO	1	1	7	1.5 ± 0.20	3.2
<i>Lonicera involucrata</i>	LONI_INVO	2	2	6	2.8 ± 0.29	3 ± 0.30
<i>Lonicera utahensis</i>	LONI_UTAH	9	7	18	1.6 ± 0.26	3.4 ± 0.29
<i>Pyrola chlorantha</i>	PYRO_CHLO	3	3	9	1.8 ± 0.17	2.8 ± 0.17
<i>Rubus parviflorus</i>	RUBU_PARV	22	6	259	2.5 ± 0.12	2.9 ± 0.10
<i>Sorbus dumosa</i>	SORB_DUMO	1	1	1	1	3
<i>Vaccinium myrtillus</i>	VACC_MYRT	11	5	90	1 ± 0.02	4 ± 0.30
<i>Veratrum californicum</i>	VERA_CALI	54	5	389	2.9 ± 0.03	2.5 ± 0.10

Therefore, species abundance data were expressed in three levels: as a number of plots with a particular species, as a number of individuals/ramets, as well as a number of locations (only for comparison with the historical data). Locations of plots were recorded by taking geo-referenced photos with a smartphone (accuracy < 30 m). Specimens of the seven studied species were also collected for the SWRS (Southwestern Research Station) Herbarium (see for the herbarium data Supplement S4).

2.3. Data processing and analysis

Daily temperature and precipitation data for the years 1956–2019 (measured at the SWRS weather station PORTAL 4 SW, Portal, Arizona, at elevation 1644 m a.s.l., <6 km northeast from the study area, see Fig. 1) were obtained from the GHCN (Global Historical Climatology Network) server (Menne et al., 2012). The weather data were averaged each year as a time series in Wolfram Language; then multidecadal mean values of three time segments: 1956–1974, 1975–1993, and 1994–2019, corresponding to time periods between the field surveys, were compared. Field data were tested for ecological relevance by calculating Pearson correlation coefficients (r values) between observed species abundance and both vigor and habitat fire severity. Elevations of the observed plants were obtained in QGIS by matching plant locations points with an elevation map (Aster Global Digital Elevation Map, vertical accuracy < 25 m). Elevation uncertainty of studied plots conservatively estimated from location accuracy and maximum surface inclination was <30 m.

Plant traits were used to estimate possible impact of the three following stress factors of climate change on the surveyed plants: increasing temperature (warming), decreasing precipitation (drought), and extreme climatic events (forest fire). Species tolerances to fire and to drought were obtained from trait databases, while species tolerance to warming was derived from niche traits directly related to the species response to temperature extremes. We used a set of four traits related to the lower (Minimum hardness zone, Minimum temperature) and the upper (Maximum hardness zone, Minimum elevation in Arizona) limits of the species temperature ranges to estimate the species tolerance to warming. We also used two additional traits (Plant moisture-use type, Minimum precipitation) to improve accuracy of the species tolerance to drought. All traits were obtained from the global plant trait database TRY (Kattge et al., 2011), except elevation data that were obtained from SEINet data portal (SEINet Portal Network, 2020), and hardness zones stemming from the PFAF database (Plants For A Future, 2020). Traits of *Sorbus scopulina* were used where those of *Sorbus dumosa* were undefined. When multiple traits were used, the means of scaled numerical values were taken to estimate tolerances. We used principal component analysis (PCA, `dudi.pca` in `ade4` package, R language) to model species sensitivities (negative tolerances) to the combined actions of warming, drought, and fire.

3. Results

3.1. Local climate change estimate

Mean temperature in the study area increased by 1.2 °C between years 1975–1993 and 1994–2019 (Fig. 2a) that is consistent with 0.27 °C increase per decade (Intergovernmental Panel on Climate Change, 2007). Hereinafter, we consider that an absolute difference of mean values, which exceeds the sum of their standard errors of the means (SEM) is quantitatively significant. The weather data shows first an increase (in 1975–1993) and then a significant decrease (in 1994–2019) in precipitation during the observed period (Fig. 2b). This decrease falls into the long-term oscillating drought pattern of the Southwest (Sheppard et al., 2002). We did not find a significant shift in local snowfall (Fig. 2c). There was, however, a significant downward shift in mean snow depth in 1994–2019 (Fig. 2d) that coincides with a period of human-caused large wildfires, which occurred in the area and thus may reflect fire impacts. The changes in mean annual snow depth correlate positively with the changes in mean annual precipitation ($r = 0.44$). The changes in mean annual precipitation are unlikely a consequence of the temperature changes as it follows from the small Pearson correlation $r = 0.15$.

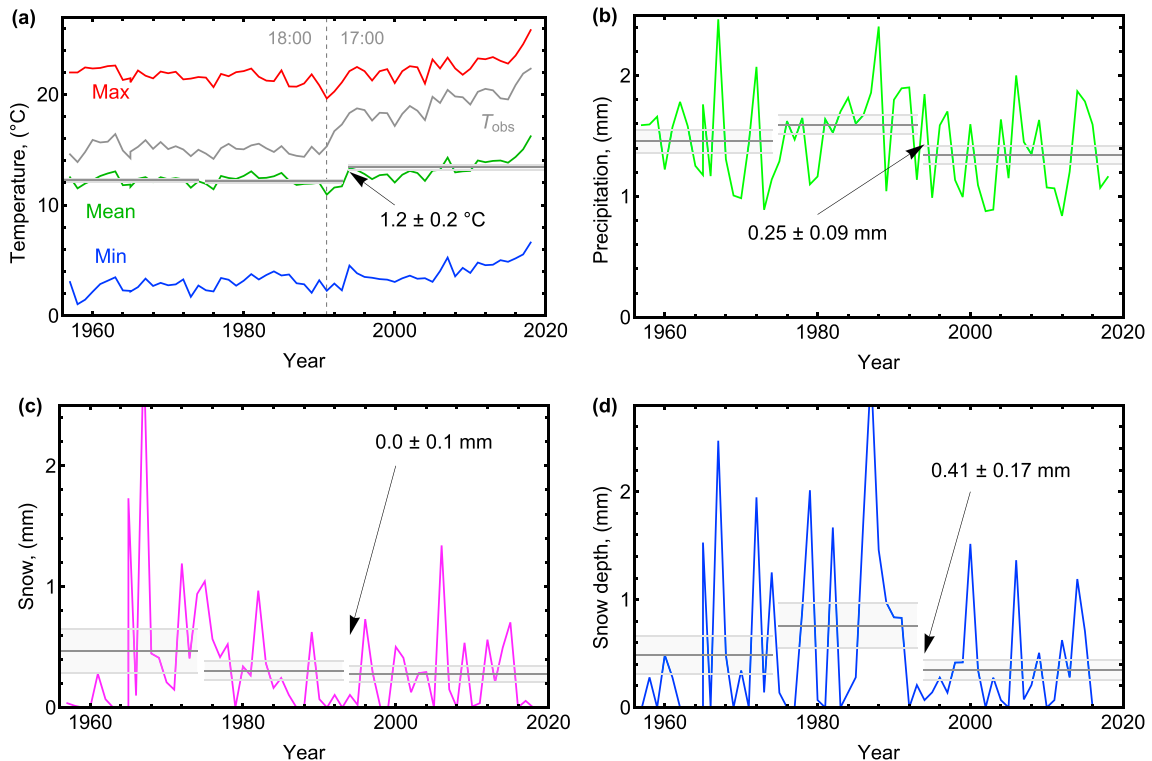


Fig. 2. Weather data of the PORTAL 4 SW weather station, averaged per year. Multi-decadal means (for years 1956–1974, 1975–1993, 1994–2019) are shown by gray horizontal lines with standard-error-of-the-mean intervals (lighter lines). Numbers are values of multi-decadal shifts shown with standard errors of the means. (a) Average annual temperatures. T_{obs} is the temperature at the time of observation. The vertical dashed line shows the year when the time of the observation was changed. (b) Average annual precipitation. (c) Average annual snowfall. (d) Average annual snow depth. See annual mean values in Table S5.

3.2. Field observations

In 2019, we located eight of the ten focal species (Table 1). In five plots, more than one of the surveyed species were found. The most abundant and the most vigorous were populations of *Veratrum californicum* (found in 54 plots, average vigor 2.9) and *Rubus parviflorus* (22 plots, average vigor 2.5). *Vaccinium myrtillus* were relatively abundant, but their shoots were weak and sparse, and some of them had only a few leaves (about 4–6 per shoot). We did not observe any *Chimaphila umbellata* or *Erigeron scopulinus*, and we found only one individual of *Sorbus dumosa*, which was in poor condition (vigor 1). Species habitat fire severity varied from: scorched (2); to deep burning/crown fire (5). None of the plots were unaffected by fire. Populations of *Vaccinium myrtillus* were observed most frequently in areas where fire damage was severe (average fire severity is 4) and populations of *Veratrum californicum* occurred in places with the least fire impact (average habitat fire severity is 2.5). Abundance of the observed species correlated positively with species vigor ($r = 0.58$) and negatively with habitat fire severity ($r = -0.44$; Fig. 3a). The correlation between surveyed species vigor and habitat fire severity was $r = -0.68$. *Goodyera oblongifolia* and *Vaccinium myrtillus* occupied the uppermost elevations (higher than 2800 m a.s.l.; Fig. 3b); *Pyrola chlorantha* grew at the lowest elevations and at one location even below 2200 m a.s.l., i.e., at the lowest edge where spruce–fir forests occur (see Fig. 1). Individuals of *Lonicera utahensis* observed at the lower edge of its elevation range had low vigor (1.1 ± 0.2). For detailed descriptions, locations, and photos of species see Supplement S4.

3.3. Trait-based model of species sensitivities to climate change

The plants show different sensitivities to warming, drought, and fire (see Fig. 4a), and multivariate analysis is helpful to make clear their sensitivities to combined effects of all the three environmental factors. Fig. 4b shows ordination (PCA) of the species sensitivities with two principal axes explaining ~80% of variability. Three axes with eigenvalues 1.3, 1.1, and 0.6 were used in calculations (See Table S7 for factor loadings). Based on the PCA the plants are divided into four functional groups marked by different colors on the plot. The first group (colored in green) includes *Erigeron scopulinus*, *Pyrola chlorantha*, and *Chimaphila umbellata* that are less sensitive to any of the studied environmental factors. However, the division for *Erigeron scopulinus* might be rough since trait data for this species were limited. The second group (colored in red) includes *Sorbus dumosa* and *Goodyera oblongifolia* that are sensitive primarily to forest fires. The third group (brown) includes both *Lonicera*

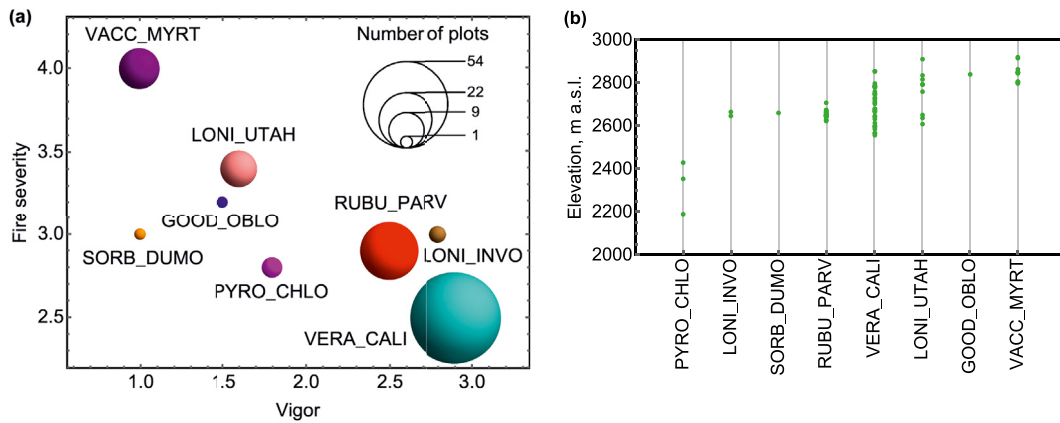


Fig. 3. (a) Species abundance (number of plots with a particular species) versus habitat fire severity (averaged per species) and species vigor (averaged per species). (b) Elevation of the observed species in meters above sea level. For species codes see Table 1.

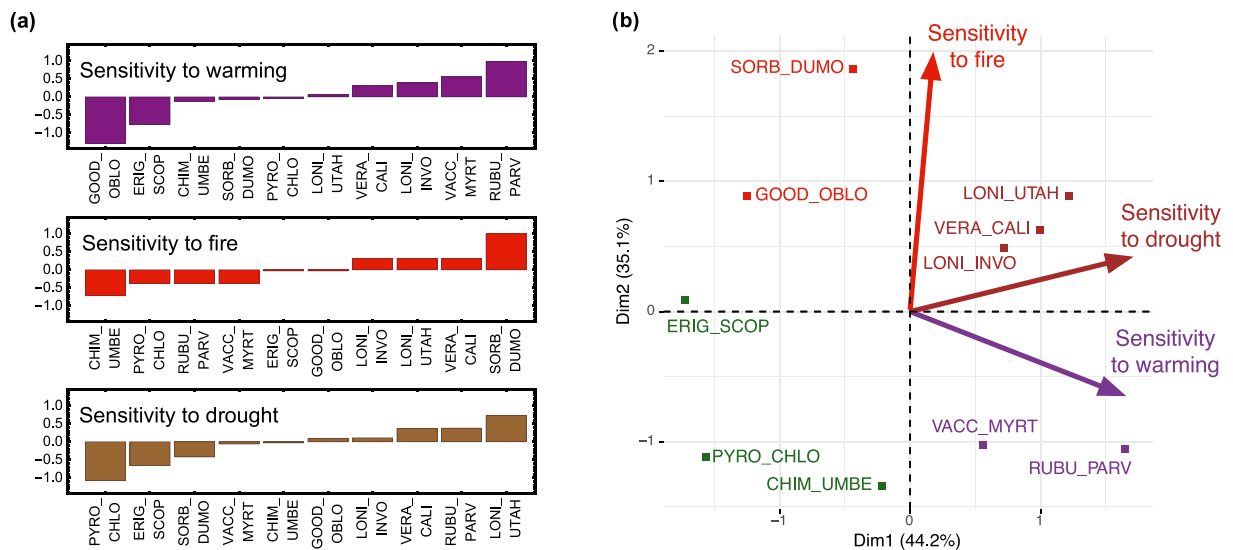


Fig. 4. (a) Estimated species sensitivities to the three environmental factors of climate change: warming, forest fire, and drought. The dimensionless sensitivities (negative tolerances) are shown scaled. See exact values in Table S6. (b) Predictive model (PCA ordination) for species sensitivities to simultaneous and equal action of the warming, forest fire, and drought. Species colors show functional groups with similar sensitivities to the considered set of factors. For species codes see Table 1.

species and *Veratrum californicum* that are more sensitive to precipitation decrease (and fire) than to warming. Finally, the fourth group (purple) includes *Vaccinium myrtillus* and *Rubus parviflorus* that are of special interest in this study since these species are more sensitive to warming but less sensitive to forest fires and drought.

3.4. Comparison to the historical data

Comparison of current species observations with historical observations of 1974 and 1993 (Moir and Ludwig, 1979; Moir, 1995) is shown in Table 2. Species sensitive to warming (according to our trait-based model: *Vaccinium myrtillus*, *Rubus parviflorus*, see Fig. 4b) have not become extinct. Contrary to expectations, the abundance and the vigor of populations of *Rubus parviflorus* have increased (compared to observations in 1993). Note that in previous surveys different metrics of abundance were used for some plants. Thus, *Vaccinium myrtillus* was previously reported as ‘occasional small populations’ (Moir, 1995), without counting locations and/or ramets. Conservatively interpreting the historical data, we assumed the changes in abundance of *Vaccinium* were small; however, we point out the low vigor of population of this species. Fire-sensitive species (according to the model: *Sorbus dumosa* and *Goodyera oblongifolia*) decreased since 1993 both in abundance and vigor, as did most of drought-sensitive species, except *Veratrum californicum*, which was still common, robust, and

Table 2

Number of species locations and number of individuals in 1974, 1993, 1994 (after Rattlesnake Fire), and in 2019. Population vigor (averaged per species) in 1993 and 2019. Changes in species abundance and vigor 1993–2019 are marked as red arrows (decreasing), green arrows (increasing), or white circles (no change). The data is reported as means with standard errors. Abbreviations: occ. – occasionally, com. – common; part.surv. – partly survived.

Species code	Number of locations/individuals				Changes 1993–2019	Vigor		Changes 1993–2019
	1974	1993	1994	2019		1993	2019	
CHIM_UMBE	1/20	10/220	gone?	0/0	▼	2	–	–
ERIG_SCOP	1/3	1/3	gone	0/0	?	2	–	–
GOOD_OBLO	2/11	3/15	part.surv.	1/7	▼	2	1.5 ± 0.20	▼
LONI_INVO	4/4	7/7	no data	2/6	▼	–	2.8 ± 0.29	–
LONI_UTAH	24/24	21/21	part.surv.	7/18	▼	2	1.6 ± 0.26	▼
PYRO_CHLO	1/3	1/4	gone	3/9	▲	–	1.8 ± 0.17	–
RUBU_PARV	occ.	4/38	gone?	6/259	▲	2	2.5 ± 0.12	▲
SORB_DUMO	1/1	4/4	gone	1/1	▼	2	1	▼
VACC_MYRT	occ.	occ.	part.surv.	5/90	○	1	1 ± 0.02	○
VERA_CALI	com.	com.	survived	5/389	○	3	2.9 ± 0.03	○

dominating wet sites along springs to the exclusion of other species. *Chimaphila umbellata* was reported in 1993 as quite common, nevertheless we did not observe any individuals of these plants. The only abundant populations of similar *Chimaphila maculata* were along the Morse Canyon and Crest trails. We did not estimate the abundance of *Erigeron scopulinus* since plants reported in 1993 (at rock outcrops near Raspberry Peak; Moir, 1995) were outside the surveyed area.

4. Discussion

The comparison of the species abundance and vigor with historical data of 1974 and 1993 shows varied responses of the species to climate change in the Chiricahua Mountains. Such differences are also indicated by our plant trait-based predictive model (see Fig. 4b) showing that the chosen remnant boreal plant species have various life histories. All plant species sensitive to fire first increased in abundance (in 1974–1993) and afterwards evidently decreased in both abundance and vigor (in 1974–2019), as did most of drought-sensitive species. This is explained by the local climate data: the period of 1974–1993 was characteristic with increased amount of precipitation (see Fig. 2b) and with no large forest fires. Since 1993, the study area endured severe large forest fires and pressure from gradual climate change. However, we did not find evident signs of pressure from warming effects. One of the species most sensitive to warming – *Rubus parviflorus*, increased in abundance and vigor that may be because *Rubus parviflorus* is commonly appearing as an early part of the ecological succession in forest fire areas. The second most warming-sensitive species – *Vaccinium myrtillus*, has remained more or less unchanged in terms of abundance and low vigor. We explain the low vigor of *Vaccinium* with the fact that this dwarf shrub needs deep snow cover during winters (Boonstra et al., 2016; Saarinén et al., 2015), but the local snow depth decreased since 1993 (see Fig. 2d) that could be both due to decrease in precipitation ($r = 0.44$, see Results) and due to increased exposure to sun and wind caused by two large forest fires. Lower vigor of *Vaccinium* may be occurring not because of any short climate trend, but possibly driven by a more general warming since the end of the Little Ice Age about 150 years ago (Moir, 1995). Globally, increasing temperatures tend to increase evaporation, which leads to more precipitation. However, the regional precipitation pattern could be different from the global trend (Trenberth, 2011) and requires careful consideration of all involved factors for an accurate interpretation. Large forest fires are recognized as having synergistic consequences of both the decrease in precipitation and the exclusion of fire as a forest management tool (Allen, 1994).

We did not find two of the three plant species, which were predicted to be most resistant to all analyzed environmental factors according to our trait-based model. In fact, neither of these two species are appropriate for testing our hypothesis and were included in our study to be consistent only with previous surveys. One species – *Chimaphila umbellata* subsp. *acuta* grows along the northern edge of its range (Liu et al., 2019) and, consequently, is not suitable for testing our hypothesis about the southern-edge-species persistence. Another missing plant – *Erigeron scopulinus* – is extremely rare (there are only two

known locations in the Chiricahua Mountains (Nesom and Roth, 1981)) and we did not encounter these plants because our survey area was limited to only 10 m band along trails, which was not appropriate for counting rare plants. Also, this species does not necessarily need a cryic soil temperature (Moir, 1995). We explain the good condition of *Veratrum californicum* by the fact that this species is not on its southern geographic range limit in the Chiricahua Mountains, rather its distribution range extends well into northern Mexico. Species persistence is enhanced by proximity of permanent water sources as evidenced by our findings of *Veratrum californicum*, as well as *Rubus parviflorus* and the only individuals of *Sorbus dumosa* and *Lonicera involucrata*, which were encountered only in wet canyons. Such water sources mitigate the adverse impacts of drought and forest fire and thus serve as a refugia (Keppel et al., 2011). However, the wet canyons do not prevent invasion pressure from lower-elevation plant communities, whose movement is enhanced by climate warming.

While tolerance (sensitivity) to warming is actively studied and discussed worldwide (see Bita and Gerats, 2013; Foden et al., 2013; Allen et al., 2016; de los Ríos et al., 2018), such studies are practically limited by lack of consistent knowledge about plant traits. Particularly, data on tolerance to warming are missing in existing plant trait databases, and data on tolerances to fire and drought are available only for about 1.7% and 0.95% of all accepted taxonomic names of vascular plant species, respectively (Kattge et al., 2011; Cornwell et al., 2019). In this paper, we estimated the sensitivity to warming by using niche traits directly associated with temperature extremes for a given species in its natural range. Note that sensitivity to warming is not strongly related to species maximum temperature tolerance, but it is also affected by indirect factors such as competition from thermophilic species. It is especially true for cryophilic species that rely on stress-tolerant strategy and are weak competitors. A more challenging but powerful approach would be to estimate warming tolerance from multiple soft traits such as plant parts characteristics, or from 'harder' traits related to life-history strategies. For wider discussion of the warming tolerance assessment see, for example, a review Pacifici et al. (2015). In all cases, warming tolerance needs to be considered together with other environmental factors, when modeling warming impacts to a plant taxon. Of particular importance is to identify indicator species that are sensitive to temperature change but resistant to other environmental stress factors. Alternatively, to identify and study localities/regions, where climate warming is a dominant stress factor, for example, localities around a stable water supply. We note that species sensitivity to warming in this study are a practical measure of the species vulnerability (as in Potter et al., 2017), since we study remnant boreal plants with presumably high exposure to warming and that have limited adaptation capacity due to small populations isolated on this sky island, which translates to low genetic diversity (Frankham et al., 2017).

When analyzing historical and weather data, we encountered some challenges typical for the studied time period. During the last decades of the 20th century, technologies, scientific methods and metrics were drastically changed, leading to disparities in observations. Particularly, the daily temperature data from the local weather station indicate a shift of local observation time made in 1991 from 18:00 to 17:00 (see Fig. 2a). The time of observation can affect averaged daily temperatures due to solar forcing (Karl et al., 1986). The shift in the time of observation could be responsible for the sudden change of the temperature trend in 1991, since the positive drift is maximal when observations are taken in the late afternoon and gradually becomes zero when observations shifted toward midnight (Karl et al., 1986). Thus, we concluded that reliable estimates of local temperature changes are unlikely during the studied time period. The time of observation bias would be also propagated in climate interpolation models that extend and downscale the observations from weather stations. New weather stations have made weather monitoring nearly continuous and potentially bias-free, but such data are available for the Chiricahua Mountains only since 2016. For further studies, it is reasonable to quantify local climate history by using core samples from local trees – as the most accessible, trustful and developed method (Sheppard et al., 2002). Using core samples, it should be noted that trees growing near a permanent water source could be less sensitive to drought, but trees in open spaces could be more exposed to temperature extremes. By analyzing core samples from trees exposed differently to environmental stresses, one could exclude combined actions of some of these stresses.

5. Conclusion

We compared the historical and current abundance/vigor of ten remnant boreal plant species at high elevation in the Chiricahua Mountains referring to a 45-yrs time period (1974, 1993–1994 and 2019). We found that all previously studied species except two still persist in the study area, however five of them are in low vigor. We used traits of the surveyed plant species to model their sensitivities to the three environmental stresses: warming, drought, and forest fire. Our model predicted that only *Rubus parviflorus* and *Vaccinium myrtillus* are selectively sensitive to warming, but other plant species are rather sensitive to fire, as well as to decrease in precipitation. Our comparison with previous field surveys shows evident adverse impacts of both: large forest fires and decreased precipitation in the study area since 1994. However, we did not find evident signs of climate warming impacts on abundance and vigor of the surveyed species. Populations of the warming-sensitive species have not declined. *Rubus parviflorus* increased in number and is in good vigor, but populations of *Vaccinium myrtillus* persist in the same abundance and vigor as previously studied. In our work, we demonstrate how a combination of two basic ecological methods – field surveys and modeling, can be used for better understanding and prediction of the ecological consequences of different environmental factors to support environmental management decisions, particularly decisions related to climate change. Further combined studies are necessary to model climate-species interactions, to collect comprehensive spatio-temporal data on species abundance and vigor, and finally, to predict and prevent species and ecosystems losses due to climate change.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01131>.

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