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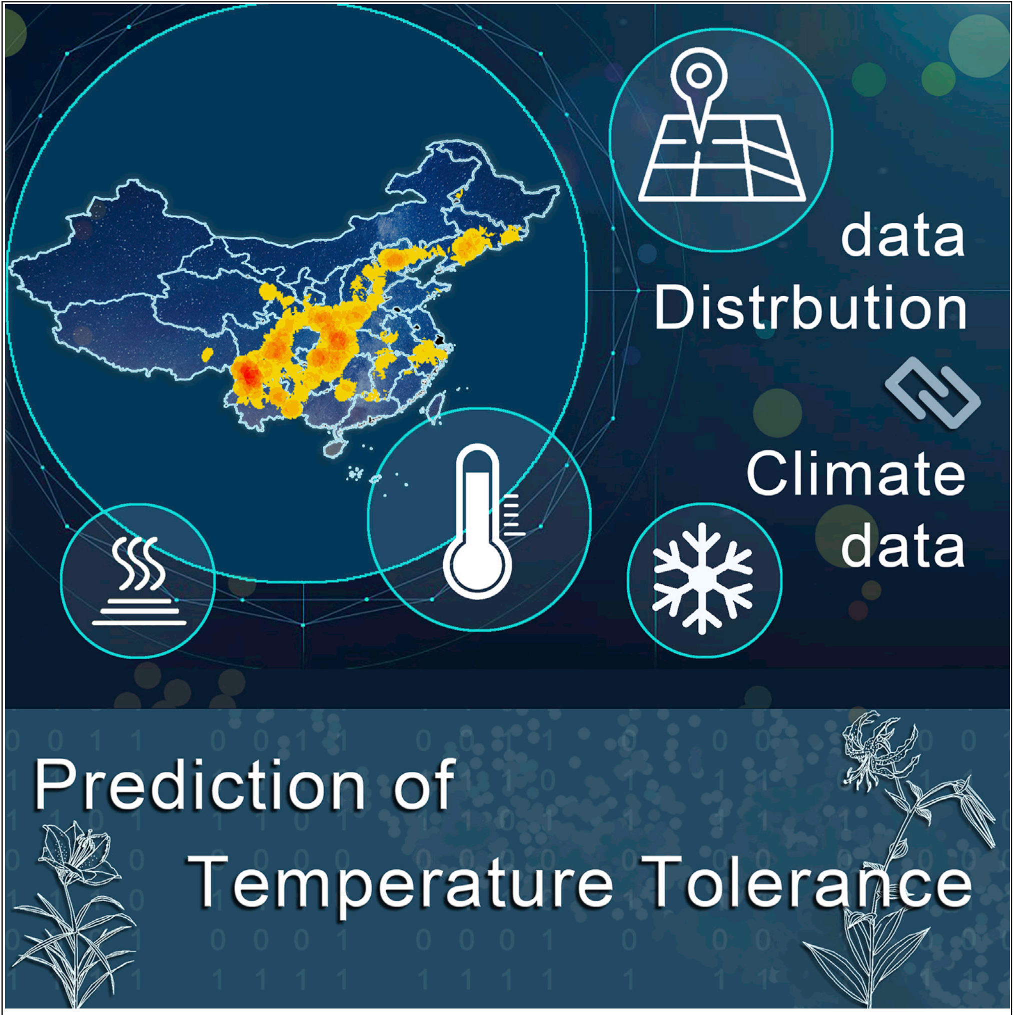

Jie Xu, Nan Chai,
Ting Zhang, ...,
Shunzhao Sui,
Mingyang Li,
Daofeng Liu

liu19830222@163.com

Highlights

A concise method predicts the temperature tolerance of wild *Lilium* in China

This method relies on a combination of online botanical and environmental data sets

Thirteen taxa with potential temperature tolerance were predicted of 42 taxa

Our findings can be used to rapidly screen the potential tolerant taxa

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Prediction of temperature tolerance in *Lilium* based on distribution and climate data

Jie Xu,[1,3] Nan Chai,[1,3] Ting Zhang,[1] Ting Zhu,[1] Yulin Cheng,[2] Shunzhao Sui,[1] Mingyang Li,[1] and Daofeng Liu[1,4,*]

SUMMARY

There are plenty publications providing guidance for resistant taxa selection by experimental researches while the number of experimental taxa is often restricted. In this study, we presented a concise method to predict the temperature tolerance of wild *Lilium* in China based on open access botanical and associated environmental datasets. We divided all taxa into five groups to present an overview of *Lilium*'s adaptability to temperature stress. Furthermore, according to the environmental conditions, the prediction of heat and cold tolerance in *Lilium* was made based on the combined multi-sources data at taxon level. Thirteen taxa with potential temperature tolerance were predicted of 42 taxa. The results showed that not only is tolerance prediction created by large-scale data analysis possible, but that it may supplement traditional laboratory researches with a comprehensive list of taxa.

INTRODUCTION

Temperature stress cause multifarious, and often adverse, alterations in physiological, biochemical, and molecular processes in plants (Hasanuzzaman et al., 2013; Lipiec et al., 2013; Theocharis et al., 2012). Confronted with temperature stress, a number of wild taxa have evolved various eco-physiological strategies to survive and reproduce, which make them valuable for breeding and agricultural production (Cairns et al., 2013; Tian et al., 2016; Dyderski et al., 2018). There are plenty publications providing guidance for resistant taxa selection by studying either morphological or physiological traits in experimental researches (Ji et al., 2020; Ma and Fan, 2014). However, the number of experimental taxa is often restricted by the time-consuming fieldwork, compounded by the possibility that practitioners would be interested in just a small proportion of the resources (Albani Rocchetti et al., 2021; Watkins et al., 2020). With ever-improving digital technologies enhancing our ability to access information, using digitized collections data to predict the abiotic stress tolerance of plants is an alternative strategy to complement the experimental resource lists (James et al., 2018). Climate is known as the main determinant of plant distribution at a global scale (Woodward and Williams, 1987; Bonetti and Wiens, 2014). The assumption that the range of climate conditions encompassed by the geographic distribution of a taxon accurately reflects its tolerances, has been applied in a wide range of fields, including biodiversity conservation (Lloret and Kitzberger, 2018; Margalef-Marrase et al., 2020), environmental science (Gong et al., 2020; Nascimbene et al., 2020), ecology and evolutionary biology (Descombes et al., 2016; Napier et al., 2019), etc. Appling this assumption to plant science allows us to develop a taxa evaluation method based on open access botanical and associated environmental datasets.

The Global Biodiversity Information Facility (GBIF, www.gbif.org) is the largest global data portal of occurrence records, including ~850 million records for all groups of organisms. Moreover, the National Plant Specimen Resource Center (NPSRC, www.cvh.ac.cn) holds digitized records of over 9.4 million of plant specimens from 140 herbaria of China. A combination of GBIF and NPSRC enables an abundant taxa list, especially considering that the digitization efforts drastically improve access to collections (Hufft et al., 2018; James et al., 2018). Extracting the GPS information from the specimen records can be used for visualization of plant distribution and connection with environmental datasets such as WorldClim version 2.1(www.worldclim.org), a global dataset of spatially interpolated monthly climate data which can be used for mapping and spatial modeling (Fick and Hijmans, 2017). Taken together, the multi-source data could be consolidated into taxa distribution models to predict the potential temperature tolerance of wild taxa.

The genus *Lilium* in the family Liliaceae includes about 110–115 taxa, primarily distributes throughout cold and temperate regions of the northern hemisphere (Du et al., 2013). It's one of the most important

[1] Chongqing Engineering Research Center for Floriculture, Key Laboratory of Horticulture Science for Southern Mountainous Regions of Ministry of Education, College of Horticulture and Landscape Architecture, Southwest University, Chongqing 400715, People's Republic of China

[2] School of Life Science, Chongqing University, Chongqing 401331, China

[3] These authors contributed equally

[4] Lead contact

*Correspondence: liu19830222@163.com

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flowering crops as cut flower, garden plant and pot plant (Suh et al., 2013). Temperature stress induce changes in *Lilium* at physiological and molecular levels, thus affect its growth and development (Jia et al., 2012). The optimum temperature for *Lilium* growth is around 18–22°C (Yin et al., 2007; Xin et al., 2010). High temperature (>28°C) has negative effects on the growth of *Lilium* such as short stems, reduced number of flower buds, shortened flower bud length (Steininger and Pasian, 2003; Ding et al., 2021). Besides, previous studies showed that cold stress inhibit the growth of lily bulbs: for non-hardy taxa, –6°C can lead to bulb lethality in most cases; at –8°C, virtually all bulbs were dead and did not regrow (Du and Anderson, 2009; Tian et al., 2020). China is known as an significant distribution zone of *Lilium*, with 55 taxa having been reported in this country thus far (Du et al., 2013). Covering a vast territory, China spans several different climatic zones, including tropical, subtropical, warm temperate and cold temperate climatic zones (Zhang et al., 2019). The complicated climate provides multifarious conditions from cool plateau to hot basin for populations of variety lilies (Li and Geng, 2013), which makes China an ideal region to study the relationship between the temperature tolerance and distribution of *Lilium*.

In this study, the distribution data from herbarium specimens and literatures was connected with climate information, which enabled us to derive data on temperature conditions for each specimen location. Besides, the GPS data was linked to other environmental data to develop a comprehensive understanding of the realized niche of *Lilium*. We divided the wild *Lilium* of China into five groups according to their temperature conditions and made prediction of their heat and cold tolerance based on the combined multi-sources data at taxon level. The comprehensive list created by large-scale data analysis allowed us to identify exhaustive valuable taxa rather than particular ones which were commonly concerned.

RESULTS

Database construction

Firstly, we created an original data set of 7,362 specimens based on 7,048 specimens and 314 locations obtaining from NPSRC, GBIF and literatures (see STAR Methods). Then the 7,362 specimens were resampled within a 0.5° grid, 2,201 specimens were retained and partitioned into 38 species and 16 varieties. These species accounted for 100% of the original species in China, while variants accounted for 94% of the described Chinese lily varieties. The species and varieties were regarded as the same level of separate taxa in subsequent analysis. The number of specimens varied from 1 to 365 per taxon and only the taxa with more than 5 specimens per taxon were selected. Furthermore, a comparative assessment of the taxonomy, GPS locations in our database with the distribution range described in Iplant (www.iplant.cn) have been carried out. The result showed that there were 42 taxa (2,066 specimens) fitting more than 70% of the distribution information in Iplant (Table 1). Finally, by combining the GPS data with climate information, we built a database of 42 taxa, totaling 2,066 specimens, including the information of original distribution, the mean temperature of coldest quarter (TOC), and temperature of flowering period (TOF) etc. for subsequent data analysis (Tables S1 and S2).

Lilium and environmental conditions

We inputted the climatic zone map (Zhang and Yan, 2013) into ArcGIS 10.2 together with the GPS data of 2,066 specimens, thereby drawing the distribution map of wild *Lilium* in China (Figure 1). The distribution map showed that wild *Lilium* were mainly distributed in the temperate and subtropical climate zones, which was in line with the result of specimens' distribution in the temperature conditions. A vast majority of specimens were distributed at the mean TOF range of 25–30°C and the TOC range between 0 and 10°C, while most taxa were likely to grow in the mean TOF range of 20–25°C and the TOC range between - 5 and 10°C (Figures 2A and 2B). According to the result of hierarchical cluster analysis (Figure S1), we divided the taxa into five groups representing by different colors: purple, red, yellow, green, and blue group (Table 2). The purple group exhibited highly tolerant to heat stress, and its corresponding TOC was about 5°C. The red group was located in the areas with the mean TOF ranging between 18 and 23°C. Taxa of the red group preferred a warmer winter with TOC ranging from 5 to 10°C compared to the purple group. These two groups distributed in the higher TOF and TOC compared to the others, while the lowest value of TOF and TOC appeared in the yellow and green group, respectively. Lilies in the yellow group required the lowest temperature during flowering period compared with other groups, indicating that they may belong to the least heat-resistant group. The green and blue groups were able to withstand extreme low temperature during winter, representing the hardiest *Lilium* taxa (Figure 2B).

Table 1. Database construction of *Lilium* specimens, see also Tables S1 and S2.

	Number of specimens			Flowering period		
Latin name	Before resample	After resample	Fitting rate (%)	June	July	August
L. distichum	65	47	70.21		❀	❀
L. papilliferum	19	17	70.59		❀	
L. rosthornii	51	38	71.05		❀	❀
L. bakerianum var. rubrum	29	27	74.07		❀	
L. regale	9	9	77.78	❀	❀	
L. taliense	37	27	77.78		❀	❀
L. davidii var. willmottiae	19	19	78.95	❀		
L. henryi	41	34	82.35		❀	
L. bakerianum var.yunnanense	8	6	83.33		❀	
L. leichtlinii var. maximowiczii	19	18	83.33		❀	❀
L. speciosum var. gloriosoides	36	32	87.50		❀	❀
L. fargesii	26	26	84.62		❀	❀
L. bakerianum	89	49	93.88		❀	
L. leucanthum	67	61	85.25	❀	❀	
L. primulinum var. ochraceum	43	29	86.21		❀	❀
L. amoenum	12	11	90.91	❀		
L. wardii	23	11	90.91	❀	❀	❀
L. cernuum	20	16	93.75		❀	
L. duchartrei	143	73	94.52		❀	
L. davidii	136	95	94.74		❀	❀
L. dauricum	67	48	95.83	❀	❀	❀
L. concolor var. pulchellum	63	57	96.49	❀	❀	
L. sargentiae	80	58	96.55		❀	❀
L. concolor	167	116	98.28	❀	❀	
L. brownii	619	353	98.58	❀	❀	❀
L. pumilum	456	316	99.68		❀	❀
L. apertum	31	13	100.00	❀	❀	
L. bakerianum var. aureum	20	17	100.00		❀	
L. bakerianum var. delavayi	27	25	100.00		❀	
L. callosum	41	37	100.00		❀	❀
L. henrici	6	6	100.00		❀	
L. lancifolium	236	187	100.00		❀	❀
L. martagon var. pilosiusculum	6	5	100.00	❀		
L. lankongense Franchet	23	12	100.00	❀	❀	
L. nanum	54	19	100.00	❀		
L. nepalense	32	11	100.00	❀	❀	
L. nepalense var. burmanicum	17	15	100.00	❀	❀	
L. saluenense	18	7	100.00	❀	❀	❀
L. sempervivoideum	11	7	100.00	❀		
L. souliei	41	18	100.00	❀	❀	
L. sulphureum	50	40	100.00	❀	❀	
L. lophophorum	156	54	100.00	❀	❀	

The “❀” in each taxon represented the flowering period lasting 1–3 months.

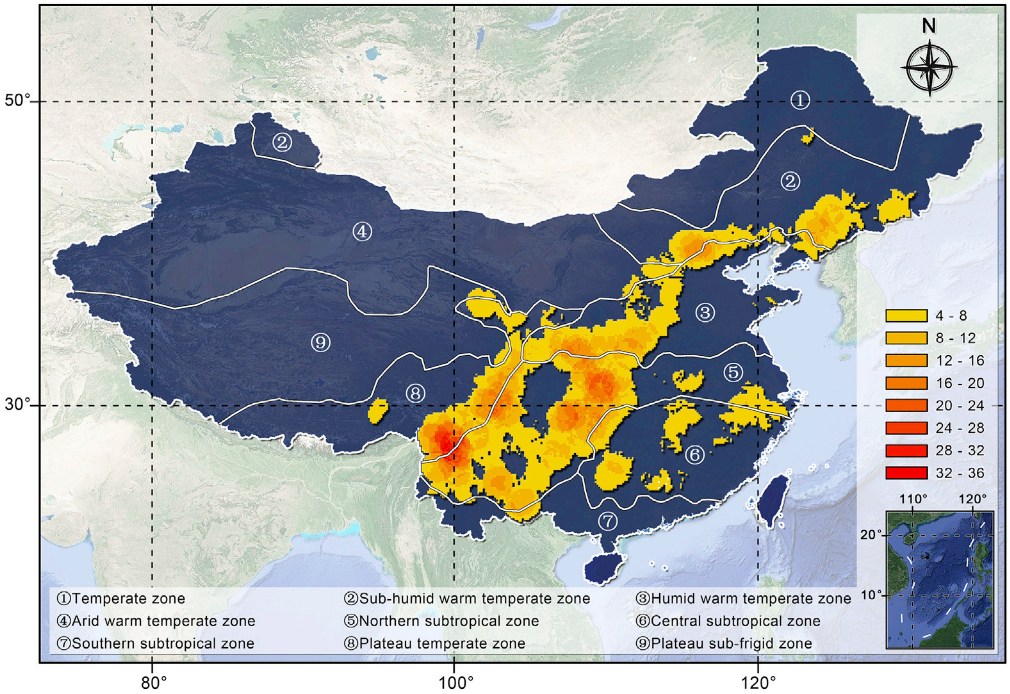

Figure 1. Specimens' distribution in the climatic zones

Heatmap (Point Density) showed the distribution of 2,066 *Lilium* specimens present in our database. The wild *Lilium* were mainly distributed in the plateau, sub-humid and humid warm temperate zones and northern, central subtropical zones.

After linking *Lilium* location to other environmental data, we were able to develop a comprehensive understanding of the realized niche of *Lilium*. The results (Figures S2–S4) showed that wild lilies distributed in the suitable soil conditions within the pH (median value) and salinity (Elco) range of 6.8–7.2 and 0–0.5 dS/m, respectively. According to the Harmonized World Soil Database (HSWD), pH values ranging from 5.5 to 7.2 are indicative of acid to neutral soils, which are the best conditions for nutrient availability and suitable for most crops (Jones and Thornton, 2015). And in most cases, an ECe value <2 indicates a very low degree of salt stress (Saslis-Lagoudakis et al., 2015). The Standardized Precipitation and Evapotranspiration Index (SPEI) values of *Lilium* ranged from –0.1 to 0.1, representing suitable water conditions without drought stress (Li et al., 2019).

Tolerance potential of Lilium taxa to heat

Our data reported the actual environment conditions experienced by lilies in their natural ranges, showing that there are significant inter-specific differences in the TOF (Table S1). The mean and maximum TOF experienced by wild-growing *Lilium* taxa illustrated these differences (Figure 3), showing that most *Lilium* populations are likely to grow in mild climate where the mean temperature range is about 20–25°C. Using the median values of mean TOF >25°C and maximum TOF >30°C as thresholds, 6 *Lilium* taxa were identified as potentially tolerant to heat stress, which are characterized by a higher temperature during flowering. In the predicted tolerant taxa (*L. lancifolium, L. callosum, L. brownii, L. rosthornii, L. henryi, L. speciosum var. gloriosoides*), 474 and 207 specimens were distributed in heat (the mean TOF >25°C) and non-heat (the mean TOF ≤25°C) environment, respectively. And in the predicted non-tolerant taxa, 269 and 1,116 specimens were distributed in heat and non-heat environment, respectively (Table 3). The Chi-square test showed that the distribution of specimens in heat stress and non-heat environment was significant different between predicted tolerant and non-tolerant taxa (X^2 was 499.18, df = 1 and p value <0.05). Among the predicted tolerant taxa, *L. speciosum var. gloriosoides* showed the strongest resistance to heat stress and occupied a restricted range of conditions, while *L. lancifolium* and *L. brownii* with a niche width larger than the median showed a wide range of adaptability in the TOF. *L. henryi* with a smaller niche width showed stenotypic behaviors (Figure 4A).

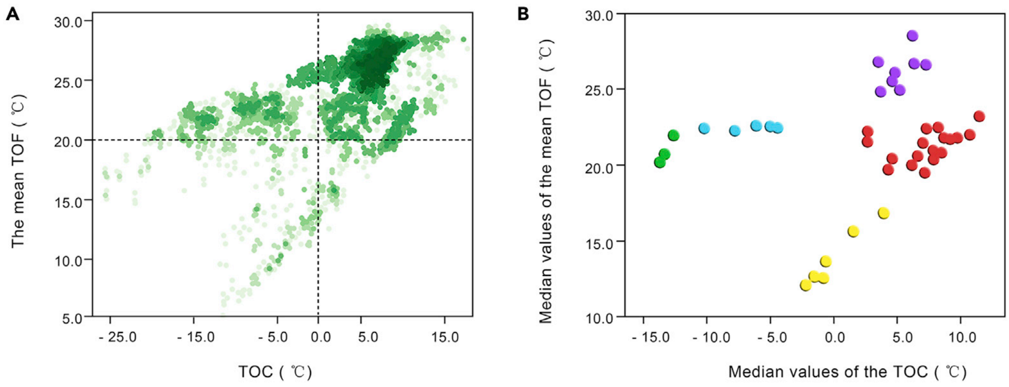

Figure 2. *Lilium* and climate conditions

(A) The distribution of *Lilium* specimens in their corresponding temperature conditions.

(B) The distribution of *Lilium* taxa in their corresponding temperature conditions, see also Figure S1.

Tolerance potential of Lilium taxa to cold

The TOC experienced by the *Lilium* in their distribution ranged from –25.5°C to 17.7°C (Table S2). There are significant inter-specific differences in the mean temperature of coldest quarter (Figure 5). Most *Lilium* populations were likely to grow in mild climate (TOC range of –5 to ~10°C). Using the median values of TOC $\leq$ –5°C as a threshold, 7 *Lilium* taxa were identified as potentially tolerant to cold stress, which were characterized by a lower temperature during coldest quarter. In the predicted tolerant taxa (*L. dauricum, L. martagon var. pilosiusculum, L. distichum, L. cernuum, L. concolor var. pulchellum, L. concolor, L. pumilum*), 375 and 230 specimens were distributed in cold and non-cold environment, respectively. And in the predicted non-tolerant taxa, 93 and 1,368 specimens were distributed in cold and non-cold environment, respectively (Table 3). The chi-square test showed that the distribution of specimens in cold stress and non-cold environment was significant different between predicted tolerant and non-tolerant taxa (X^2 was 755.34, df = 1 and p value < 0.05). *L. dauricum* showed the strongest resistance to cold stress and occupied a wide range of conditions. *L. pumilum*, *L. concolor,* and *Lilium concolor var. pulchellum* also showed eurytopic tolerances; however, they had a weaker cold tolerance than others. In addition, *L. cernuum*, *L. distichum,* and *L. martagon var. pilosiusculum* showed stereotypic behaviors but had a strong tolerance to low temperature (Figure 4B).

DISCUSSION

Lilium taxa have been known and cultivated in China for thousands of years, with significant ecological and commercial values (Fang et al., 2021). However, the majority of *Lilium* cannot grow well in heat (temperature >28°C) or cold (temperature < –6°C) conditions (Higgins and Stimart, 1990; Kim et al., 2007a, 2007b). Combining that with the threat posed by climate change has led to the impelling demand of climate-resilient lilies. The wild taxa have been challenged in diverse environmental stresses for centuries and maintain a high level of genetic diversity, making them significant to the resistance breeding (Zhang et al., 2017). China is considered as a center of origin for *Lilium*, yet a small number of studies have been carried out on the researches of wild *Lilium*' evaluation and utilization, especially abiotic tolerances. Previous studies about Chinese *Lilium* have focused on morphological characterization (Niu et al., 2010; Xiang et al., 2005), taxonomic (Liu et al., 2017), phylogenetic (Kim et al., 2019; Zhou et al., 2020), genetic variability, and diversity (Wang et al., 2016). Thus, we want to develop a comprehensive understanding of the realized niche of *Lilium* in this study, which can provide a new insight into the tolerance evaluation of *Lilium*.

While a great deal of experimental research has been carried out in the area of wild plants' response to abiotic stresses, it is often difficult and time-consuming to achieve a comprehensive list of wild taxa (Watkins et al., 2020). Considering the practical difficulties in the collection of wild resources, preliminary data analysis is an applicable way to make predictions. Among a wide variety of factors that affect the geographical distribution of plants at different spatial and temporal scales, climate is at the core and plays a key role especially at larger spatial scales (Guisan and Thuiller, 2005; Maiorano et al., 2013). Ecologists are modeling species distribution models based upon this understanding (Zurell et al., 2020), whereas the question for botanists is whether the reverse can be modeled, i.e., whether we can speculate that traits vary in

Table 2. The cold-heat relations of *Lilium* taxa

		Temperature conditions (°C)	
Group name	*Lilium* taxa	The mean TOF	The TOC
Purple group	*L. lancifolium, L. callosum, L. brownii, L. rosthornii, L. henryi, L. speciosum var. gloriosoides, L. papilliferum, L. leucanthum, L. fargesii*	24 - 29	3 - 8
Red group	*L. nepalense var. burmanicum, L. nepalense, L. sempervivoideum, L. bakerianum var. yunnanense, L. amoenum, L. bakerianum var. delavayi, Lilium sulphureum, L. sargentiae, L. taliense, L. primulinum var. ochraceum, L. henrici, L. souliei, L. bakerianum, L. bakerianum var. aureum, L. davidii var. willmottiae, L. davidii*	18 - 23	2 - 12
Yellow group	*L. lankongense Franchet, L. wardii, L. bakerianum var. rubrum, L. saluenense, L. lophophorum, L. nanum, L. apertum*	11 - 17	- 3 - 5
Blue group	*L. cernuum, L. concolor, L. concolor var. pulchellum, L. pumilum, L. leichtlinii var. maximowiczii*	22 - 23	- 10 - - 4
Green group	*L. dauricum, L. martagon var. pilosiusculum, L. distichum*	20 - 22	−15 - - 13

The 42 taxa were divided into five groups according to their cold-heat relations.

accordance to ecological niche: this process is well established in the selection of trees in urban forestry and the predictions on salinity tolerance of horticultural plants (Wang et al., 2018a; Watkins et al., 2020; Sjoman and Watkins, 2020), but is not as developed in the temperature tolerance of plants. In this study, we tried to provide a preliminary data analysis to supplement the laboratory experiments. Online herbaria, accessible via the GBIF and NPSRC, conserve hundreds of millions of specimens collected by botanists and satisfy the demands of information acquisition by the scientists with a digital platform for knowledge sharing (Hallgren et al., 2016; La Salle et al., 2016). When the NPSRC data were supplemented with the GBIF data, the completeness of datasets increased, which enabled us to avoid negative impacts on results and conclusions derived from incomplete taxa lists as much as possible (Qian et al., 2018).

In our final extracted database of 2,066 specimens, the majority (76.4%) of reported Chinese *Lilium* taxa were present. After linking *Lilium* location to physiographic and climate characteristics, we were able to analysis the natural conditions for lilies. The results suggested that there were no significant differences in the drought, saline and alkali niches of *Lilium* in China (Figures S2–S4). Excluding the impact of the non-temperature factors helps us draw more informed predictions because the non-temperature factors regularly prevent a taxon from occupying locations that are otherwise climatically suitable (Bush et al., 2019).

The wild lilies go through different stages in the growing season and experience the coldest and hottest temperatures during winter and flowering stage, respectively (Han and Jia, 2008; Tsuchiya et al., 2006). In addition, longer periods of environment information can help us better understand *Lilium*'s tolerance to temperature stress, compared to heat waves or extreme cold events. Thus, our analysis focused primarily on environmental data excavated from the TOF and TOC. Our results showed that the majority of *Lilium* taxa were located in the mean TOF ranging from 20 to 23°C and the TOC ranging from 5 to 10°C, while the distribution of specimens could be explained by the uneven sampling (Tables S2 and S3). Before tolerance predictions, all the taxa were divided into five groups to deepen our understanding of *Lilium* adaptability to temperature. The cold-tolerant (green and blue) groups were able to tolerate a cold environment below - 5°C but preferred a stress-free condition during flowering period. While, the heat-resistant (purple) group was consistent with the cold-tolerant group: although the members could adapt to the mean TOF above 25°C, their optimum temperature in the coldest season was roughly the same as the temperate (red)

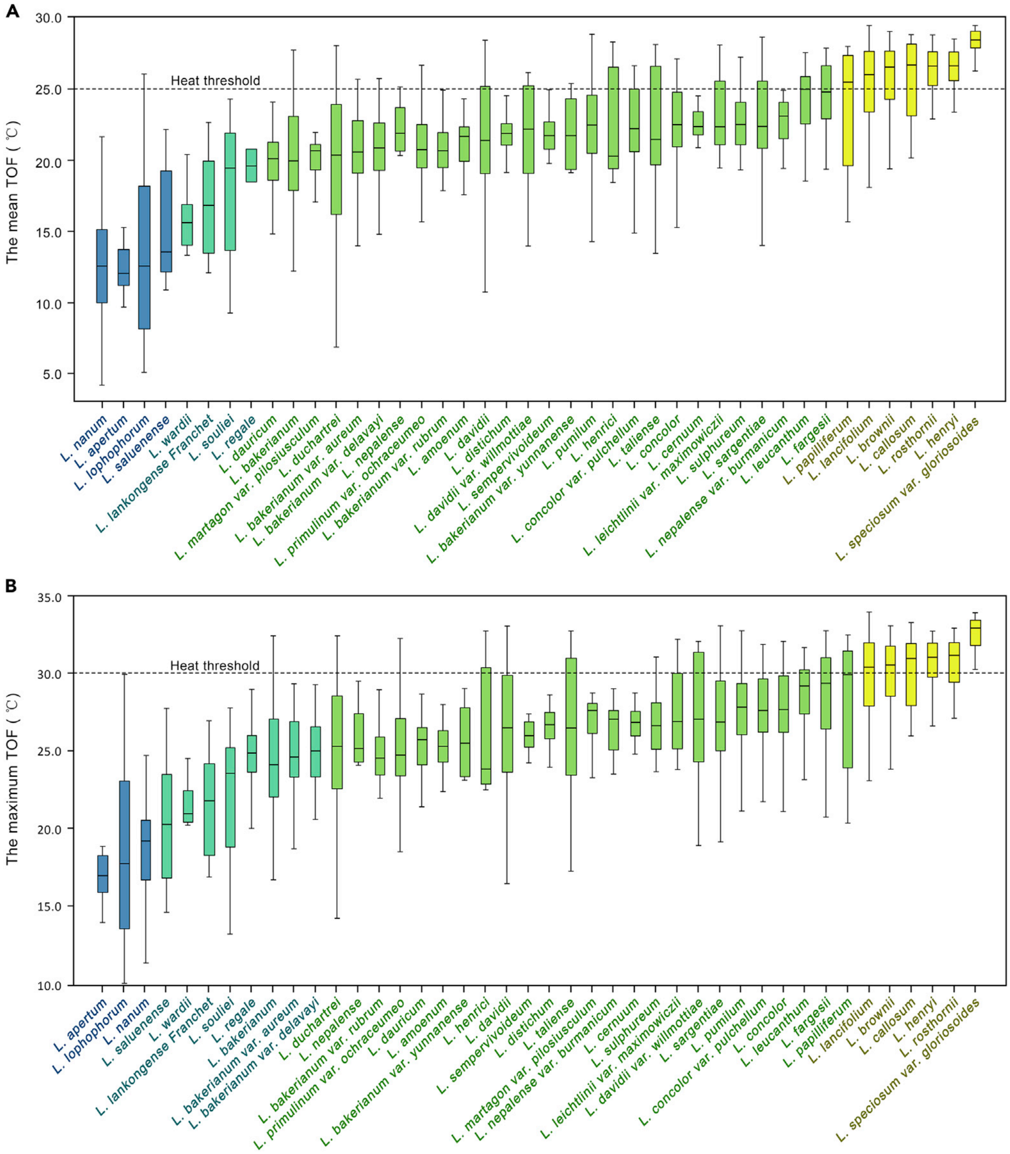

Figure 3. Tolerance potential of *Lilium* taxa to heat

The mean TOF (A) and the maximum TOF (B) experienced by wild-growing *Lilium* species, as reported in our database. The change in color represented diverse tolerance to heat stress. The boxes and taxa name were colored every 5°C to make the figures more intuitively.

See also Table S1.

group. The red group has the highest percentage of all groups (42.8%), representing the general temperature preference of *Lilium*: the mean TOF <25°C and the TOC > –5°C (Tsuchiya et al., 2006; Zieslin and Tsujita, 1988). Among all the groups, only the yellow group corresponded to a value lower than 20°C for the mean TOF, suggesting its potential for extensive application in the areas with low annual cumulative temperatures (Dai et al., 2019; Dorado-Linan et al., 2020). Further phylogenetic analysis and molecular biology research will be useful to explore more interconnections between groups.

Using data analysis, we tried to predict the potential tolerant taxa with the median values of the mean TOF >25°C, maximum TOF >30°C and TOC < –5°C as thresholds. Eventually, we compiled a list of 13 potentially tolerant taxa. For some taxa mentioned in our prediction, support was found in horticultural and physiological studies for their temperature tolerance. Yao et al. (2019) classified *L. henryi* as heat tolerant taxa.

Table 3. *Lilium*'s distribution in different temperature ranges

		Number of specimens	
Category	temperature range (°C)	Tolerant taxa	Non-tolerant taxa
Heat	The mean TOF ≤25	207 (30.4%)	1,116 (80.6%)
	The mean TOF >25	474 (69.6%)	269 (19.4%)
Cold	The TOC ≤ - 5	375 (62.0%)	93 (6.4%)
	The TOC > - 5	230 (38.0%)	1368 (93.6%)

The 2,066 specimens were divided into tolerant and non-tolerant taxa (42 in total) according to their temperature of flowering period (TOF) and the mean temperature of coldest quarter (TOC) ranges.

L. callosum was mentioned as a promising gene resource for breeding heat tolerant lilies (Liping and Rui, 2012). *L. lancifolium* was the most extensively studied taxa among the heat tolerant resources. *L. lancifolium* and *L. brownii* were identified by Zhang et al. (2010) as heat tolerant taxa based on growth and physiological index, followed by *L. regale*. The results of niche width in Figure 4 supported the proposal by Liang et al. (2018) that *L. lancifolium* performed high ecological adaptability compared to the other tested taxa from Midwestern China, as well as *L. brownii*. Furthermore, Wang et al. (2014) conjectured the heat stress signal transduction pathway in *L. lancifolium*, identified the expected key ingredients regulating the stress tolerance. More notably, *L. lancifolium* was also considered as a cold tolerant taxa as reported by Yong et al. (2018), indicating its potential in the researches of multiple stresses. Wang et al. (2018b) classified *L. pumilum* as a northern cold-hardy wild taxon and studied its dormancy mechanism at the molecular level. In addition, some predicted temperature tolerant taxa can also be supported from investigational studies. *L. dauricum*, *L. distichum,* and *L. pumilum* were distributed in the severely cold regions of Northeast China, including the Changbai Mountains and the Xiaoxingan mountains in Liaoning, Jilin, and Heilongjiang provinces (Du et al., 2013). Low temperature in winter of these areas can reach 40°C below zero (Zhang and Yan, 2013). Study on phylogeny of *Lilium* showed that *L. henryi* and *L. rosthornii* should be classified into the same subsect (Du et al., 2014), which is in agreement with the result of temperature niche in our study (Figures 2 and 3).

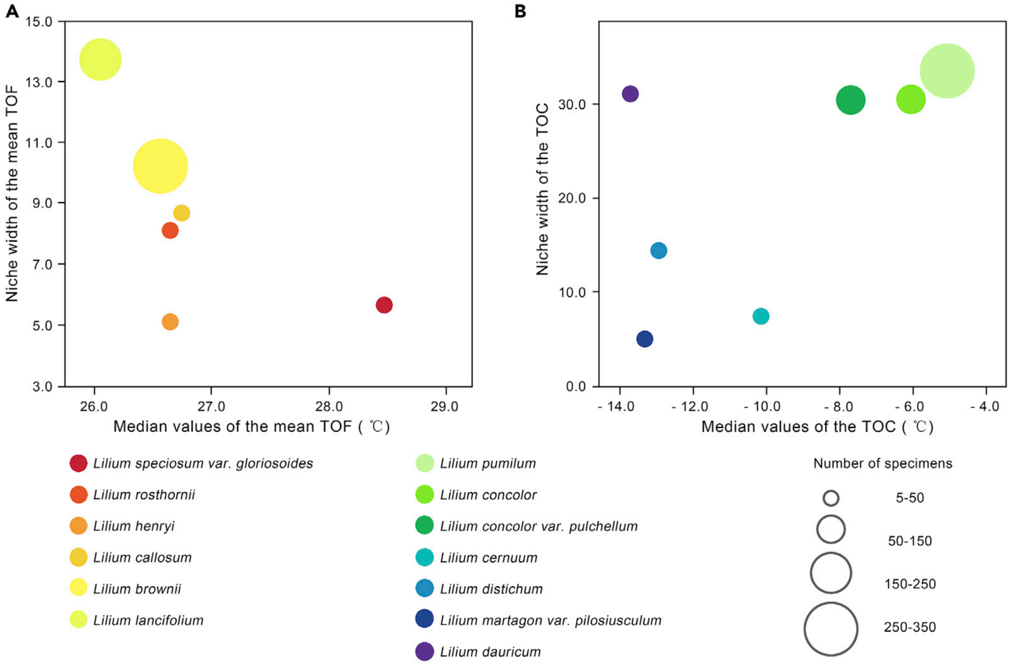

Figure 4. Niche width of the potential tolerant taxa

The niche width of heat (A) and cold (B) tolerant taxa, as reported in our prediction.

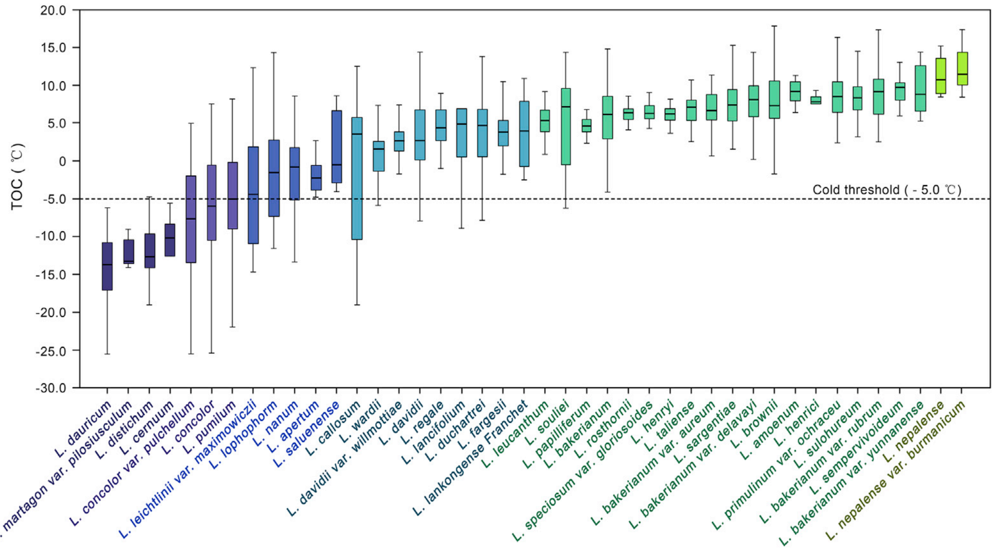

Figure 5. Tolerance potential of *Lilium* taxa to cold

The TOC experienced by wild-growing *Lilium* taxa, as reported in our database. The change in color represented diverse tolerance to cold stress. The boxes and taxa name were colored every 5°C to make the figures more intuitively.
See also Table S2.

As a supplement to the taxa list with temperature tolerance which was already reported, our work has identified several potentially taxa. *L. speciosum var. gloriosoides* showed great patience with the heat stress. *L. concolor* and *L. concolor var. pulchellum* showed eurytopic tolerances to cold which making them ideal material for hardy breeding. More studies on the evaluation of lilies' temperature tolerance were required and our prediction expands the new space for the resistant breeding of wild *Lilium*.

CONCLUSION

In this study we developed a method for temperature tolerance prediction that could be drawled upon well-established biogeographical theory and herbarium data. Online herbarium data allowed an effective study of the whole wild *Lilium* resources in China with large amounts of plant samples, increase our ability to inform research and avoid missing overlooked taxa. Our results showed that the information combing geo-coded specimen information and climate database might be used to identify potentially valuable genetic resources in *Lilium* at group and taxon level. Our findings could be used to rapidly screen the potential tolerant taxa and communicate evidence to botanical researches. While further testing in other genera is required, this approach holds considerable promise for an in-depth evaluation of potential resources for temperature tolerance and using genetic material in breeding or studies of abiotic stress.

Limitations of the study

Our method is developed based on the current distribution (i.e., the realized niche) of *Lilium*. Considering the effect of interspecific interactions, dispersal capacity and other factors, there is an inherent risk when using the realized niche that the environmental tolerances will be underestimated. However, this uncertainty does not prevent us from finding important patterns: the positively correlation between the temperature tolerance and climate conditions proposed by Bush et al. (2018) and Lancaster and Humphreys (2020) provides a compelling explanation for our method. Thus, we emphasize the use of data analysis for taxa evaluation before the laboratory experiments, which can help us rapidly screen the potential tolerant taxa with a comprehensive list of taxa.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2021.102794.

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AUTHOR CONTRIBUTIONS

Conceptualization and methodology, J.X., N.C., and D.L.; software, J.X., T. Zhang, and T. Zhu; validation and formal analysis, N.C. and Y.C.; resources, S.S., D.L., and M.L.; writing – original draft, J.X., N.C., and D.L.; visualization, J.X.; supervision, M.L. and D.L.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

Albani Rocchetti, G., Armstrong, C.G., Abeli, T., Orsenigo, S., Jasper, C., Joly, S., Bruneau, A., Zytaruk, M., and Vamosi, J.C. (2021). Reversing extinction trends: new uses of (old) herbarium specimens to accelerate conservation action on threatened species. New Phytol. *230*, 433–450.

Bonetti, M.F., and Wiens, J.J. (2014). Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. Proc. Biol. Sci. *281*, 20133229.

Bush, A., Catullo, R., Mokany, K., Harwood, T., Hoskins, A.J., Ferrier, S., and Algar, A. (2019). Incorporating existing thermal tolerance into projections of compositional turnover under climate change. Glob. Ecol. Biogeogr. *28*, 851–861.

Bush, A., Catullo, R.A., Mokany, K., Thornhill, A.H., Miller, J.T., and Ferrier, S. (2018). Truncation of thermal tolerance niches among Australian plants. Glob. Ecol. Biogeogr. *27*, 22–31.

Cairns, J.E., Crossa, J., Zaidi, P.H., Grudloyma, P., Sanchez, C., Araus, J.L., Thaitad, S., Makumbi, D., Magorokosho, C., Bänziger, M., et al. (2013). Identification of drought, heat, and combined drought and heat tolerant donors in maize. Crop Sci. *53*, 1335–1346.

Dai, Y., Yuan, L., Zhang, S., Wang, J., Xie, S., Zhao, M., Chen, G., Sun, R., and Wang, C. (2019). Comprehensive evaluation for cold tolerance in wucai (Brassica campestris L.) by the performance index on an absorption basis (PIabs). Agronomy-Basel *9*, 61.

Descombes, P., Pradervand, J.-N., Golay, J., Guisan, A., and Pellissier, L. (2016). Simulated shifts in trophic niche breadth modulate range loss of alpine butterflies under climate change. Ecography *39*, 796–804.

Ding, L., Wu, Z., Teng, R., Xu, S., Cao, X., Yuan, G., Zhang, D., and Teng, N. (2021). LlWRKY39 is involved in thermotolerance by activating LlMBF1c and interacting with LlCaM3 in lily (Lilium longiflorum). Hortic. Res. *8*, 36.

Dorado-Linan, I., Valbuena-Carabana, M., Canellas, I., Gil, L., and Gea-Izquierdo, G. (2020). Climate change synchronizes growth and iWUE across species in a temperate-submediterranean mixed oak forest. Front. Plant Sci. *11*, 706.

Du, F., and Anderson, N. (2009). Bulb tissue cold-tolerance sensitivity differences in non-hardy and winter hardy Lilium. Hortscience *44*, 1013.

Du, Y.-P., He, H.-B., Wang, Z.-X., Li, S., Wei, C., Yuan, X.-N., Cui, Q., and Jia, G.-X. (2014). Molecular phylogeny and genetic variation in the genus Lilium native to China based on the internal transcribed spacer sequences of nuclear ribosomal DNA. J. Plant Res. *127*, 249–263.

Du, Y.-P., He, H.-B., Wang, Z.-X., Wei, C., Li, S., and Jia, G.-X. (2013). Investigation and evaluation of the genus Lilium resources native to China. Genet. Resour. Crop Evol. *61*, 395–412.

Du, Y., Mao, L., Queenborough, S.A., Freckleton, R.P., Chen, B., and Ma, K. (2015). Phylogenetic constraints and trait correlates of flowering phenology in the angiosperm flora of China. Glob. Ecol. Biogeogr. *24*, 928–938.

Dyderski, M.K., Paz, S., Frelich, L.E., and Jagodzinski, A.M. (2018). How much does climate change threaten European forest tree species distributions? Glob. Chang Biol. *24*, 1150–1163.

Fang, D., Chen, J., Yi, C., Li, Z., Guo, L., Wang, T., Deng, Q., Xu, J.P., and Gao, C. (2021). First report of Fusarium fujikuroi causing bulb rot on Lilium lancifolium in China. Plant Dis. https://doi.org/10.1094/PDIS-06-20-1197-PDN.

Fick, S.E., and Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. *37*, 4302–4315.

Gong, X., Chen, Y., Wang, T., Jiang, X., Hu, X., and Feng, J. (2020). Double-edged effects of climate change on plant invasions: ecological niche modeling global distributions of two invasive alien plants. Sci. Total Environ. *740*, 139933.

Guisan, A., and Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. Ecol. Lett. *8*, 993–1009.

Hallgren, W., Beaumont, L., Bowness, A., Chambers, L., Graham, E., Holewa, H., Laffan, S., Mackey, B., Nix, H., Price, J., et al. (2016). The biodiversity and climate change virtual laboratory: where ecology meets big data. Environ. Model. Softw. *76*, 182–186.

Han, X.-L., and Jia, G.-X. (2008). Studies on optimal germination conditions of different cultivars and heat-resistance techniques for seeds of Lilium x formolongi. For. Res. *21*, 729–733.

Hasanuzzaman, M., Nahar, K., Alam, M.M., Roychowdhury, R., and Fujita, M. (2013). Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. Int. J. Mol. Sci. *14*, 9643–9684.

Higgins, W.S., and Stimart, D.P. (1990). Influence of invitro generation temperature and post-invitro cold-storage duration on growth-response of lilium-longiflorum bulblets. J. Am. Soc. Hortic. Sci. *115*, 930–933.

Hufft, R.A., Deprenger-Levin, M.E., Levy, R.A., and Islam, M.B. (2018). Using herbarium specimens to select indicator species for climate change monitoring. Biodiversity and Conservation *27*, 1487–1501.

James, S.A., Soltis, P.S., Belbin, L., Chapman, A.D., Nelson, G., Paul, D.L., and Collins, M. (2018). Herbarium data: global biodiversity and societal botanical needs for novel research. Appl. Plant Sci. *6*, e1024.

Ji, L., Li, P., Su, Z., Li, M., and Guo, S. (2020). Cold-tolerant introgression line construction and low-temperature stress response analysis for bell pepper. Plant Signal. Behav. *15*, 1773097.

Jia, W.-J., Ma, L.-L., Ding, K., Cui, G.-F., Wu, L.-F., Wang, X.-N., and Wang, J.-H. (2012). Characters of sap flow of Lilium and its relations with environment factors. Xibei Zhiwu Xuebao *32*, 2498–2505.

Jones, P.G., and Thornton, P.K. (2015). Representative soil profiles for the Harmonized World Soil Database at different spatial resolutions for agricultural modelling applications. Agric. Syst. *139*, 93–99.

Kim, H.T., Lim, K.B., and Kim, J.S. (2019). New insights on Lilium phylogeny based on a comparative phylogenomic study using complete plastome sequences. Plants (Basel) *8*, 547.

Kim, S.H., Niedziela, C.E., Jr., Nelson, P.V., De Hertogh, A.A., Swallow, W.H., and Mingis, N.C. (2007a). Growth and development of Lilium longiflorum ‘Nellie White’ during bulb production under controlled environments - I. Effects of constant, variable and greenhouse day/night temperature regimes on scale and stem bulblets. Scientia Horticulturae *112*, 89–94.

Kim, S.H., Niedziela, C.E., Jr., Nelson, P.V., De Hertogh, A.A., Swallow, W.H., and Mingis, N.C. (2007b). Growth and development of Lilium longiflorum ‘Nellie White’ during bulb production under controlled environments - II. Effects of shifting day/night temperature regimes on scale bulblets. Scientia Horticulturae *112*, 95–98.

La Salle, J., Williams, K.J., and Moritz, C. (2016). Biodiversity analysis in the digital era. Philos. Trans. R. Soc. Lond. B Biol. Sci. *371*, 20150337.

Lancaster, L.T., and Humphreys, A.M. (2020). Global variation in the thermal tolerances of plants. Proc. Natl. Acad. Sci. *117*, 13580–13587.

Li, R.-L., and Geng, S. (2013). Impacts of climate change on agriculture and adaptive strategies in China. J. Integr. Agric. *12*, 1402–1408.

Li, X., Li, Y., Chen, A., Gao, M., Slette, I.J., and Piao, S. (2019). The impact of the 2009/2010 drought on vegetation growth and terrestrial carbon balance in Southwest China. Agric. For. Meteorol. *269-270*, 239–248.

Liang, Z.-X., Niu, L.-X., Farooq, A., Li, L.-H., and Zhang, Y.-L. (2018). Investigation of the wild Lilium resources native to midwestern China. Pakistan J. Bot. *50*, 589–598.

Lipiec, J., Doussan, C., Nosalewicz, A., and Kondracka, K. (2013). Effect of drought and heat stresses on plant growth and yield: a review. Int. Agrophysics *27*, 463–477.

Liping, Y., and Rui, L. (2012). Heat stress response of lily hybrid seedlings and its inbred parents. J. Northeast For. Univ. *12*, 63–66.

Liu, G., Zhang, X., Lan, Y., Xin, H., Hu, F., Wu, Z., Shi, J., and Xi, M. (2017). Karyotype and fluorescence in situ hybridization analysis of 15 Lilium species from China. J. Am. Soc. Hortic. Sci. *142*, 298–305.

Liu, J., Chen, X., Yang, W., Zhang, S., Wang, F., and Tang, Z. (2010). Chemical fingerprinting of wild germplasm resource of ophiopogon japonicus from sichuan basin, China by RP-HPLC coupled with hierarchical cluster Analysis. Anal. Lett. *43*, 2411–2423.

Lloret, F., and Kitzberger, T. (2018). Historical and event-based bioclimatic suitability predicts regional forest vulnerability to compound effects of severe drought and bark beetle infestation. Glob. Change Biol. *24*, 1952–1964.

Ma, W., and Fan, W. (2014). Determination and comprehensive evaluation on cold-tolerance of wild citrus from guizhou. Acta Botanica Boreali-Occidentalia Sinica *34*, 2063–2069.

Maiorano, L., Cheddadi, R., Zimmermann, N.E., Pellissier, L., Petitpierre, B., Pottier, J., Laborde, H., Hurdu, B.I., Pearman, P.B., Psomas, A., et al. (2013). Building the niche through time: using 13,000 years of data to predict the effects of climate change on three tree species in Europe. Glob. Ecol. Biogeogr. *22*, 302–317.

Margalef-Marrase, J., Angeles Perez-Navarro, M., and Lloret, F. (2020). Relationship between heatwave-induced forest die-off and climatic suitability in multiple tree species. Glob. Change Biol. *26*, 3134–3146.

Nachtergaele, F.O., Velthuizen, Verelst L., Batjes, N.H., Dijkshoorn, J.A., Engelen, V., Fischer, G., Jones, A., and Montanarella, L. (2012). Harmonized World Soil Database (Version 1.2).

Napier, J.D., De Lafontaine, G., Heath, K.D., and Hu, F.S. (2019). Rethinking long-term vegetation dynamics: multiple glacial refugia and local expansion of a species complex. Ecography *42*, 1056–1067.

Nascimbene, J., Benesperi, R., Casazza, G., Chiarucci, A., and Giordani, P. (2020). Range shifts of native and invasive trees exacerbate the impact of climate change on epiphyte distribution: the case of lung lichen and black locust in Italy. Sci. Total Environ. *735*, 139537.

Niu, L., Zhang, Y., Zhang, Q.-X., Jiang, C.-Z., and Reid, M.S. (2010). Morphological characterization of wild Lilium species collected from the vicinity of the qin-Ba mountains, China. Hortscience *45*, S160.

Qian, H., Deng, T., Beck, J., Sun, H., Xiao, C., Jin, Y., and Ma, K. (2018). Incomplete species lists derived from global and regional specimen-record databases affect macroecological analyses: a case study on the vascular plants of China. J. Biogeogr. *45*, 2718–2729.

Rolland, J., and Salamin, N. (2016). Niche width impacts vertebrate diversification. Glob. Ecol. Biogeogr. *25*, 1252–1263.

Saslis-Lagoudakis, C.H., Hua, X., Bui, E., Moray, C., and Bromham, L. (2015). Predicting species’ tolerance to salinity and alkalinity using distribution data and geochemical modelling: a case study using Australian grasses. Ann. Bot. *115*, 343–351.

Sjoman, H., and Watkins, J.H.R. (2020). What do we know about the origin of our urban trees? - a north European perspective. Urban For. Urban Green. *56*, 126879.

Steininger, J., and Pasian, C.C. (2003). Prediction of development of asiatic lilies based on air temperature and thermal units. Hortscience *38*, 1100–1103.

Suh, J.K., Wu, X.W., Lee, A.K., and Roh, M.S. (2013). Growth and flowering physiology, and developing new technologies to increase the flower numbers in the Genus Lilium. Hortic. Environ. Biotechnol. *54*, 373–387.

Theocharis, A., Clement, C., and Barka, E.A. (2012). Physiological and molecular changes in plants grown at low temperatures. Planta *235*, 1091–1105.

Tian, X., Xie, J., and Yu, J. (2020). Physiological and transcriptomic responses of Lanzhou Lily (Lilium davidii, var. unicolor) to cold stress. PLoS One *15*, e0227921.

Tian, Z., Yang, Y., and Wang, F. (2016). A comprehensive evaluation of heat tolerance in nine cultivars of marigold. Hortic. Environ. Biotechnol. *56*, 749–755.

Tsuchiya, H., Okubo, H., Hiramatsu, M., and Kim, J.H. (2006). Control of flowering in Lilium brownii var. colchesteri. Sci. Bull. Fac. Agric. Kyushu Univ. *61*, 165–170.

Vicente-Serrano, S.M., Beguería, S., and López-Moreno, J.I. (2010a). A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Clim. *23*, 1696–1718.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., Angulo, M., and El Kenawy, A. (2010b). A new global 0.5° gridded dataset (1901–2006) of a multiscalar drought index: comparison with current drought index datasets based on the palmer drought severity index. J. Hydrometeorol. *11*, 1033–1043.

Wang, J., Wang, Q., Yang, Y., Liu, X., Gu, J., Li, W., Ma, S., and Lu, Y. (2014). De novo assembly and characterization of stress transcriptome and regulatory networks under temperature, salt and hormone stresses in Lilium lancifolium. Mol. Biol. Rep. *41*, 8231–8245.

Wang, J.M., Ma, S.L., Li, W.Q., Wang, Q., Cao, H.Y., Gu, J.H., and Lu, Y.M. (2016). Genetic variability and diversity of the main resources of lily assessed via phenotypic characters, pollen morphology, and ISSR markers. Genet. Mol. Res. *15*. https://doi.org/10.4238/gmr.15027638.

Wang, S., Leus, L., Van Labeke, M.C., and Van Huylenbroeck, J. (2018a). Prediction of lime tolerance in Rhododendron based on herbarium specimen and geochemical data. Front. Plant Sci. *9*, 1538.

Wang, W., Su, X., Tian, Z., Liu, Y., Zhou, Y., and He, M. (2018b). Transcriptome profiling provides insights into dormancy release during cold storage of Lilium pumilum. BMC Genomics *19*, 196.

Watkins, J.H.R., Cameron, R.W.F., Sjöman, H., and Hitchmough, J.D. (2020). Using big data to improve ecotype matching for Magnolias in urban forestry. Urban For. Urban Green. *48*, 126580.

Woodward, F.I., and Williams, B.G. (1987). Climate and plant distribution at global and local scales. VEGETATIO *69*, 189–197.

Xiang, D.-Y., Zhang, Y.-L., and Niu, L.-X. (2005). Study on morphological diversity of wild lily from Qinba Mountain and its adjacent area. Wuhan Zhiwuxue Yanjiu *23*, 385–388.

Xin, H., Zhang, H., Chen, L., Li, X., Lian, Q., Yuan, X., Hu, X., Cao, L., He, X., and Yi, M. (2010). Cloning and characterization of HsfA2 from lily (Lilium longiflorum). Plant Cell Rep. *29*, 875–885.

Yao, J., Wen-Bo, C., Jiang-Zhong, H., and Qi-Bing, C. (2019). Effects of high temperature stress on physiological indexes of wild Lilium henryi. J. Northwest For. Univ. *34*, 62–68.

Yin, H., Chen, Q., and Yi, M. (2007). Effects of short-term heat stress on oxidative damage and responses of antioxidant system in Lilium longiflorum. Plant Growth Regul. *54*, 45–54.

Yong, Y.B., Li, W.Q., Wang, J.M., Zhang, Y., and Lu, Y.M. (2018). Identification of gene co-expression networks involved in cold resistance of Lilium lancifolium. Biologia Plantarum *62*, 287–298.

Zhang, X., He, X., Gao, J., and Wang, L. (2019). Latitudinal and climate effects on key plant traits in Chinese forest ecosystems. Glob. Ecol. Conservation *17*, e00527.

Zhang, H., Mittal, N., Leamy, L.J., Barazani, O., and Song, B.-H. (2017). Back into the wild-Apply untapped genetic diversity of wild relatives for crop improvement. Evol. Appl. *10*, 5–24.

Zhang, X., and Yan, X. (2013). Temporal change of climate zones in China in the context of climate warming. Theor. Appl. Climatol. *115*, 167–175.

Zhang, Y., Niu, L., Zhang, Q.-X., and Jiang, C.-Z. (2010). Survey of wild Lilium species in the vicinity of the qin-Ba mountains, China. Hortscience *45*, S159.

Zhou, Y.-P., Wang, Z.-X., Du, Y.-P., Li, J.-W., He, H.-B., and Jia, G.-X. (2020). Fluorescence in situ hybridization of 35S rDNA sites and karyotype of wild Lilium (Liliaceae) species from China: taxonomic and phylogenetic implications. Genet. Resour. Crop Evol. *67*, 1601–1617.

Zieslin, N., and Tsujita, M.J. (1988). Regulation of stem elongation of lilies by temperature and the effect of gibberellin. Scientia Horticulturae *37*, 165–169.

Zurell, D., Franklin, J., König, C., Bouchet, P.J., Dormann, C.F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., et al. (2020). A standard protocol for reporting species distribution models. Ecography, 1261–1277.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
ArcGIS 10.2	Environmental Systems Research Institute	https://developers.arcgis.com/
Microsoft Excel 2016	Microsoft	https://www.microsoft.com/zh-cn/
IBM SPSS Version 20.0	International Business Machines Corporation	https://www.ibm.com/analytics/spss-statistics-software
Adobe Photoshop CS 5.0	Adobe Systems Incorporated	https://www.adobe.com/cn/products/photoshop.html
Other		
The classified information	Iplant	www.iplant.cn
Distribution data	Global Biodiversity Information Facility	www.gbif.org
Distribution data	National Plant Specimen Resource Center	NPSRC, www.cvh.ac.cn
Climate data	WorldClim version 2.1	www.worldclim.org
Drought index	SPEIbase v.2.6 at DIGITAL.CSIC	http://digital.csic.es/handle/10261/10002
Soil parameters	Harmonized World Soil Database	westdc.westgis.ac.cn/data/611f7d50-b419-4d14-b4dd-4a944b141175

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Daofeng Liu (liu19830222@163.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

Data reported in this paper will be shared by the lead contact upon request.

This paper does not report original code.

METHOD DETAILS

Taxa distribution data

The occurrence records from NPSRC and GBIF were used to generate taxa lists (Qian et al., 2018). We also fetched distribution data from investigational literature which describes the location information and habitat niche of wild *Lilium* through field study as supplement (for example, Du et al. (2013) and Liang et al. (2018)). The location and classified information (species, subspecies and varieties) were subsequently revised and uniformed according to Iplant (www.iplant.cn), an online website consolidating data from ai-Plants, Flora of China and Plant Photo Bank of China. To reflect the natural distribution of the wild *Lilium*, only the taxa described as initial species or subspecies in Iplant were selected. All observations collected on urban green spaces, botanical gardens and other sites before 1970 were excluded. As uneven sampling intensity would cause calculation bias (Dyderski et al., 2018), for each species, subspecies and varieties, we resampled the data within a 0.1° grid–one data point was selected within each grid cell. All the observations were transformed into spatial points in a WGS-84 spatial coordinates system. After resample, only the taxa with at least 5 specimens were selected for further data analysis.

Diverse distributions correspond to various environmental conditions, which affect the flowering period of plants. We compared the locations of all specimens with the plant distributions described on Iplant, and only selected the taxa with a fitting degree of more than 70%. We considered the flowering period information on Iplant as reliable data for the selected taxa since the geographical distribution of these taxa is basically consistent with the description on Iplant (Du et al., 2015). Finally, a database of Chinese *Lilium* was built after the data cleaning.

Climate data and soil parameters

We obtained the 0.5° grid (~1 km^2) monthly climate data (mean and maximum temperature) from WorldClim version 2.1 to quantify heat events for the period of 1970-2000. We also extracted the mean temperature of coldest quarter (TOC) from the WorldClim climatic layer to predict the cold tolerance of *Lilium*. For each taxon, climatic niche width was calculated as the range of environmental conditions between the minimum and the maximum temperatures found among the cells of each taxon distributions (Rolland and Salamin, 2016).

The Standardized Precipitation and Evapotranspiration Index (SPEI) is a multiscalar drought index which can quantify the onset, duration and magnitude of drought episodes based on climatic data (Vicente-Serrano et al., 2010a, 2010b). We downloaded the monthly SPEI dataset from SPEIbase v.2.6 at DIGITAL.CSIC (Consejo Superior de Investigaciones Científicas, http://digital.csic.es/handle/10261/10002) to quantified the severity of droughts. We read and converted the SPEI dataset based on its corresponding software which developed by Vicente-Serrano et al. (2010a), so that the March-August SPEI at 1-month time scale could be extracted in ArcGIS 10.2.

The soil parameters, including ECe and pH measured in a soil-water solution were obtained from Harmonized World Soil Database (HSWD), a 30 arc-second raster dataset with over 15,000 different soil mapping units that combines existing regional and national updates of soil information worldwide (Nachtergaele et al., 2012). We established connection between the ArcGIS layer and the soil attribute database relying on the data management toolbox in ArcGIS to explore the salt and alkali stresses suffered by wild lilies.

QUANTIFICATION AND STATISTICAL ANALYSIS

All the raster and vector data, including the WorldClim climatic layer, SPEI, ECe and pH parameters was extracted to the distribution point relying on the spatial analyst toolbox in ArcGIS. Microsoft Excel 2016 was used to tabulate the data and IBM SPSS Version 20.0 was used to carry out statistical analysis and generate the boxplot, scatter plot and bubble chart. For taxa with flowering period lasting two or three months, the average temperature of flowering period (TOF) corresponding to each specimen location was calculated firstly, while other data could be used directly for statistics analysis. All the figures were colored in Adobe Photoshop CS 5.0 to better visualize the relationship between *Lilium* and temperature conditions.

For temperature conditions, the distribution map was generated in ArcGIS by combining taxa distribution with the climatic zone map (Zhang and Yan, 2013). To visualize distance and relatedness among *Lilium* taxa, we applied a hierarchical cluster analysis based on squared Euclidean distance (Liu et al., 2010). The taxa were divided into different groups based on the similarity of their temperature conditions (median values of the TOC and mean TOF), and then the scatter plots were generated to visualize the relationship between the groups and their corresponding temperature conditions. For other environmental conditions, the boxplots were used to quantified the drought, salt and alkali stresses suffered by wild *Lilium*.

The lower quartile (LQ), median, and upper quartile (UQ) were determined for the TOF and the TOC. We considered the median values as tolerance indicator as they provided the taxon's central tendency to heat or cold conditions in their distributions. The taxa with median values of the mean TOF $> 25°C$ and the maximum TOF $> 30°C$ were predicted as being potentially tolerant to heat stress. For the TOC, the taxa with median values $\leq$ - 5°C were predicted as hardy varieties. To evaluate the results of our prediction, the number of specimens distributed in heat (the mean TOF $> 25°C$) or moderately warm (the mean TOF $\leq 25°C$) climate of predicted heat tolerant and non-tolerant taxa were calculated, then a Chi-square test in SPSS was performed. The same method was used in the prediction of cold tolerance. Besides, we used the median niche width of heat and cold tolerant taxa to assign taxa to two distinct categories: stenotypic and eurytopic tolerances. Taxa with a niche width smaller than the median were assigned to the stenotypic category, while a larger niche width were categorized as eurytopic category (Rolland and Salamin, 2016).