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Echoes of the past: niche evolution, range dynamics, and their coupling shape the distribution of species in the *Chrysanthemum zawadskii* species complex

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The distribution of species changes over time, and the current distribution of different species could result from distinct eco-evolutionary processes. Thus, investigating the spatiotemporal changes in the niche and geographic range of species is fundamental to understanding those processes and mechanisms shaping the current distributions of species. However, many studies only compared the current distribution and niche of the target species, ignoring the fact that the range shift of species is a dynamic process. Here, we reconstructed niche evolution and range dynamics of species to provide more information on related eco-evolutionary processes. We focused on a monophyletic species complex, *Chrysanthemum zawadskii* species complex, in which species occupy diverse habitats and exhibit different distribution patterns. Specifically, we investigated the niche breadth and overlap between lineages or species of the complex in geographic and environmental spaces. We then tested the phylogenetic signals for different climatic variables and estimated the niche of ancestral nodes on a time-calibrated phylogeny. Next, we used phyloclimatic modeling to reconstruct the dynamics of range shift for this complex. Our results show that this complex contains both specialist and generalist species, and niche diverges greatly among different species and intraspecific lineages of the complex. The moisture gradient may be the primary driver of the niche divergence of species in the complex. The reconstruction of ancestral distribution shows that this complex originated in the Qinling mountains and surrounding areas during the early Pliocene, and then diverged with the range expansion and niche evolution. Species of the complex have different range dynamics. Based on our findings, we propose that niche evolution, range dynamics, and their coupling shape the distribution of species, which provides insight into the eco-evolutionary processes that formed the current distribution of species in the *C. zawadskii* complex.

KEYWORDS

niche evolution, range dynamics, spatiotemporal coupling, species complex, eco-evolutionary process, phyloclimatic modeling, ecological niche modeling

1 Introduction

The ranges of species are dynamic owing to expansions, contractions, or shifts over space and time, which result from the evolutionary and ecological processes (Sheth et al., 2020; Bridle and Hoffmann, 2022; Rafajlović et al., 2022). Thus, different species, even those that are closely related, can have varying range sizes. Notably, it is crucial to distinguish between the drivers and consequences of changes in the range of species to understand the mechanisms of speciation and conserve biodiversity (Harnik et al., 2012; Saupe et al., 2015; Rafajlović et al., 2022). The niche is a core concept in ecology and evolution. It represents a set of ecological conditions affecting the survival and reproduction of species and is often used to explain the distribution, abundance, and diversification of species (Carscadden et al., 2020). As a critical component of the niche, niche breadth and its evolution are central to the explanations described above (Morin and Lechowicz, 2013; Slatyer et al., 2013). It is commonly assumed that the range of a species covaries with its niche breadth, but controversy over whether the range of a species is merely the spatial representation of its environmental tolerances remains (Harnik et al., 2012; Lancaster, 2022). Studying the range shifts between sister species is considered to be an ideal way to address these issues (Evans et al., 2009; Sheth et al., 2020). Some studies have measured the current range sizes of sister species and compared their niche breadths to understand the relationship between range changes and niche evolution of species (Kalkvik et al., 2012; Anacker and Strauss, 2014; Grossenbacher et al., 2014). However, the range shift of species is a dynamic process, and the current range of a species reflects the consequences of this process (Bridle and Hoffmann, 2022). Studies on identifying such a macroecological pattern provide little information on the underlying evolutionary and ecological processes (Sheth et al., 2020; Lancaster, 2022), and more knowledge of niche evolution and range dynamics is merited.

In recent decades, many hypotheses have been proposed to deduce possible mechanisms for variations in the range of different species, such as the oscillation hypothesis, climate variability hypothesis, and ecological opportunity hypothesis among others (Stevens, 1989; Hardy and Otto, 2014; Wellborn and Langerhans, 2015; Torres-Martínez et al., 2021; Lancaster, 2022). A key difference between these hypotheses is whether niche evolution or range expansion is the driver or the consequence. From this perspective, the relevant hypotheses can be divided into two categories. First is the niche breadth–range size hypothesis, which posits that increased niche breadth is the cause of range expansion, and second is the range size–niche breadth hypothesis, which suggests that increased niche breadth could just be the consequence of range expansion (Lancaster, 2022). Notably, both those hypotheses could oversimplify the processes that underlie variations in the range of a species. Lancaster (2022) thus proposed the range shift–niche breadth hypothesis, which posits that niche breadth evolves under eco-evolutionary processes during range expansion. Clearly, more study is required to reconstruct the historical dynamics of both the range and niche of species in a phylogenetic framework to understand the processes and mechanisms that shape the current distributions of species and to test the above hypotheses.

Ecological niche modeling (ENM) is one of the commonly used methods to deduce the potential distribution of species (Waltari et al., 2007; Maguire et al., 2015). In recent decades, ENM has developed rapidly, and many modeling methods, such as random forest, MaxEnt, and boosted regression trees, have been proposed (Sillero et al., 2021). Nonetheless, such an approach assumes that the niche of species is conserved, so that it is usually limited to shallow evolutionary timescales, e.g., mid-Holocene, Last Glacial Maximum, and Last Interglacial (Culshaw et al., 2021; Guillory and Brown, 2021). Since the niche of species is often regarded as evolving during speciation, it is necessary to consider the evolution of niche when reconstructing the historical distribution of species over deeper timescales. Fortunately, a solution that combines ENMs and phylogenetic analyses (also known as phyloclimatic modeling) has been proposed to solve this problem (Yesson and Culham, 2006). This method assumes that niches of species are not static over evolutionary time and reconstructs the ancestral niches of the target species based on climate data and phylogenetic information. Those ancestral niches could be converted into ancestral niche models which are projected into paleo-climate layers to estimate the ancestral geographic ranges of species (Yesson and Culham, 2006; Evans et al., 2009; Smith and Donoghue, 2010; Guillory and Brown, 2021). Therefore, we can use the results of both phyloclimatic modeling and ancestral niche reconstruction across evolutionary timescales to deduce the possible agents for changes in the range of species. In addition, we need to consider the effects of historical biogeographic processes on range dynamics of species and niche evolution to better understand the underlying eco-evolutionary processes that shape the distribution of species (Brown and Maurer, 1989; Ruggiero et al., 1998; Reed, 2003; Hoorn et al., 2010; Smith and Donoghue, 2010; Favre et al., 2015; Li et al., 2017; Yamamoto et al., 2017; Bridle and Hoffmann, 2022).

A species complex that contains several closely related species is well suited to explore the processes and mechanisms that underlie the range shifts and niche evolution of species because its species have a most recent common ancestor, usually occur in diverse habitats, and exhibit different distribution patterns (Pinheiro et al., 2018). In this study, we focused on the *Chrysanthemum zawadskii* species complex, which has a well-resolved phylogeny and traceable evolutionary history (Lu et al., 2022). Previous studies have shown that the *C. zawadskii* complex is a monophyletic group that consists of seven narrowly or widely distributed species in China (Shen et al., 2021; Lu et al., 2022). The narrowly distributed species, such as *C. hypargyrum* and *C. oreastrum*, typically occur in alpine habitats, while widespread species occur in diverse habitats (Lu et al., 2022). Phylogenetically, four geographic lineages of *C. hypargyrum* and *C. oreastrum* resided in basal clades of the phylogenetic tree, which occur in Qinling and its neighboring mountains (Lu et al., 2022). Another late-diverging large lineage, the core *C. zawadskii* complex, is composed of four widespread species (*C. zawadskii*, *C. maximowiczii*, *C. naktongense*, and *C. chanetii*) and a narrowly distributed *C. mongolicum* (Figure 1). Notably, the complex trends to expand toward high latitudes and results in large-range and small-range species with different habitats, which suggests that the distributions of species could covary with niche shifts during the expansion and evolution. However, the eco-evolutionary processes

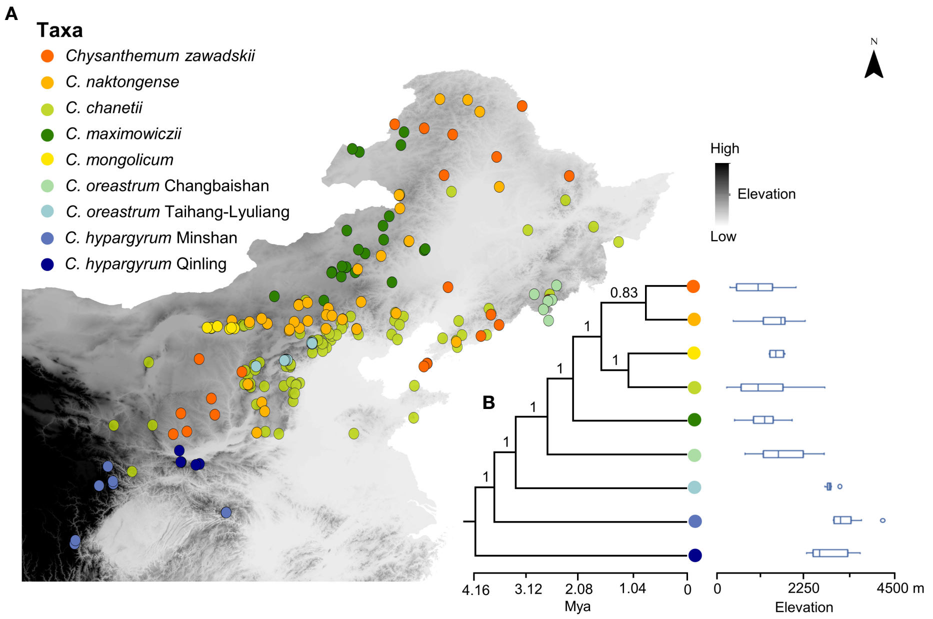

FIGURE 1
(A) Geographic localities of species within the *Chrysanthemum zawadskii* species complex in China. Grey shading indicates the elevation gradient, and darker colors represent higher elevation. **(B)** Phylogenetic relationships of the *C. zawadskii* complex species and different elevation ranges of the species. Colored circles represent different species and intraspecific lineages of this complex. Numbers at the nodes refer to Bayesian posterior probability. The geographic coordinates of each locality are listed in Table S1.

or mechanisms that underlie the range expansion and niche shifts at the lineage or species level of the complex remain unknown.

In this study, we investigated the spatiotemporal variations in niche and geographic range of the *C. zawadskii* complex in a phylogenetic context to test the hypothesis that geographic range is not merely a proxy for niche breadth of species, while niche evolution, range dynamics or their coupling jointly shape the current distribution of species. Our goals were to address the following questions: 1) whether the niches of species evolve over time in the complex, and what is their evolutionary tendency to specialize or generalize? 2) what are the main climatic factors driving the divergence of niches in the complex? and 3) what are the historical dynamics of range shifts of the complex at multiple evolutionary scales? In particular, we first investigated the niche breadths and overlaps between lineages or species in the complex. Secondly, we tested phylogenetic signals for different climatic variables and estimated the ancestral niches at multiple phylogenetic levels. We then used phyloclimatic modeling to reconstruct the dynamics of range shifts of this complex. Finally, we explored the processes of range shifts and niche evolution and their relative importance in the distribution and diversification of the *C. zawadskii* complex.

2 Materials and methods

2.1 Data collection

We collected occurrence records of the *Chrysanthemum zawadskii* complex from our field surveys and relevant databases, such as the Chinese Virtual Herbarium and the Global Biodiversity Information Facility (Figure 2). All the occurrences were manually checked to remove incorrect records and records without herbarium images. To conduct ENM analyses, duplicate records per raster cell (2.5 arc-minute) were filtered out with ENMtools *v.* 1.4.3 (Warren et al., 2010). In addition, the records of four widespread species (i.e., *C. zawadskii*, *C. maximowiczii*, *C. naktongense*, and *C. chanetii*) were further thinned using the ‘spThin’ *v.* 0.2.0 R package (Aiello-Lammens et al., 2015) in R v. 4.1.3 (R Core Team, 2022) to keep pairwise distances between the records greater than 10 km for avoiding spatial sampling biases. Overall, we retained 197 points of occurrence that covered the entire distribution range of this complex in China (Table S1, Figure 1).

We extracted 19 current climatic variables from WorldClim *v.* 1.4 at 2.5 arc-minute resolution (Hijmans et al., 2005) for ENM analyses and reduced the geographical extent of climatic layers to our study area. To avoid potential multicollinearity effects, we calculated Pearson’s correlation coefficients between the climatic variables with ENMTools. We then selected four relatively independent variables (Pearson’s coefficient < 0.8), including annual mean temperature, temperature annual range, annual precipitation, and precipitation seasonality, for further analyses (Table 1).

2.2 Ecological niche modeling

To provide potential distributions of species for subsequent niche comparisons, we generated ENMs for each species and lineage of the complex. According to the phylogeny of the *C.*

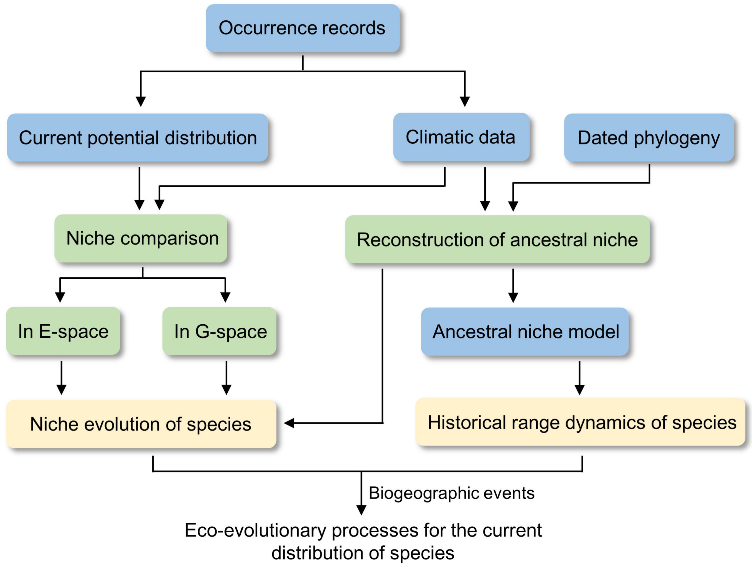

FIGURE 2
General workflow of the niche comparison and phyloclimatic modeling in this study. E-space and G-space indicate environmental space and geographic space.

zawadskii complex (Lu et al., 2022), each of two narrowly distributed species, *C. oreastrum* and *C. hypargyrum*, contains two distinct geographical lineages. Therefore, we conducted ENM analyses for both species and intraspecific lineages in this study (Figure 2). We here chose the well-tuned boosted regression trees (BRT) model, which is regarded as one of the top modeling algorithms for ENM analyses (Valavi et al., 2022). We first generated 10,000 pseudo-absences for this complex based on the "random" strategy in our study area with the 'biomod2' *v.* 4.1.2 R package (Thuiller et al., 2022). Second, we tuned BRT models for each species and lineage of the complex. In detail, three hyperparameters of the BRT model (i.e., "interaction.depth", "shrinkage", and "n.trees") were tuned following the guide of Elith et al. (2008) in the 'SDMtune' *v.* 1.1.6 R package (Vignali et al., 2020). We set five alternative values for "interaction.depth" (1, 3, 5, 7, 9) and three values for "shrinkage" (0.001, 0.005, 0.01), and values of "n.trees" were set at a range from 5,000 to 10,000 in increments of 500. We selected the best combination of those hyperparameters according to the area under the receiver operator characteristic curve (AUC) metric. After model tuning,

TABLE 1 Information on climate variables used in this study.

Variable description	Abbreviation	Resolution	Source
Climatic variables used for ENMs			
annual mean temperature	AMT	2.5 arc-minute	WorldClim 1.4
temperature annual range	TAR	2.5 arc-minute	WorldClim 1.4
annual precipitation	AP	2.5 arc-minute	WorldClim 1.4
precipitation seasonality	PS	2.5 arc-minute	WorldClim 1.4
Climatic variables used for niche comparison and ancestral niche reconstruction			
mean annual temperature	MAT	scale-free	ClimateAP 2.20
mean warmest month temperature	MWMT	scale-free	ClimateAP 2.20
mean coldest month temperature	MCMT	scale-free	ClimateAP 2.20
continentality	TD	scale-free	ClimateAP 2.20
mean annual precipitation	MAP	scale-free	ClimateAP 2.20
annual heat: moisture index	AHM	scale-free	ClimateAP 2.20
degree-days below 0°C	DD<0	scale-free	ClimateAP 2.20

(Continued)

TABLE 1 Continued

Variable description	Abbreviation	Resolution	Source
degree-days above 5°C	DD>5	scale-free	ClimateAP 2.20
degree-days below 18°C	DD<18	scale-free	ClimateAP 2.20
degree-days above 18°C	DD>18	scale-free	ClimateAP 2.20
the number of frost-free days	NFFD	scale-free	ClimateAP 2.20
precipitation as snow	PAS	scale-free	ClimateAP 2.20
extreme minimum temperature over 30 years	EMT	scale-free	ClimateAP 2.20
extreme maximum temperature over 30 years	EXT	scale-free	ClimateAP 2.20
Hargreaves reference evaporation	Eref	scale-free	ClimateAP 2.20
Hargreaves climatic moisture deficit	CMD	scale-free	ClimateAP 2.20
Climatic variables used for phyloclimatic modeling			
annual mean temperature	AMT	2.5 arc-minute	Oscillayers
temperature annual range	TAR	2.5 arc-minute	Oscillayers
annual precipitation	AP	2.5 arc-minute	Oscillayers
precipitation seasonality	PS	2.5 arc-minute	Oscillayers

Climatic variables obtained from WorldClim 1.4 and ClimateAP *v.* 2.20 are at the current period. Paleo-climatic layers downloaded from Oscillayers dataset are at seven past time points (3.79 Mya, 3.36 Mya, 2.74 Mya, 2.24 Mya, 1.68 Mya, 1.15 Mya, and 0.80 Mya).

we finally conducted BRT models for each species and lineage to predict their current potential distributions in 'biomod2'. More specifically, we set other model parameters as default values ("distribution": bernoulli; "bag.fraction": 0.5) in 'biomod2' and ran the well-tuned BRT model for each species or lineage with ten replicates of cross-validation. Each replicate of models was trained with 80% of the occurrences and tested based on the remaining data. We assessed the performance of each model according to the true skill statistic (TSS) and AUC metrics. Given that TSS values > 0.7 indicate high model performances, we chose the models whose TSS values are greater than 0.7 to generate the ensemble model for each species or lineage to make subsequent projections. The ensemble models of each species or lineage were generated by using the probability-weighted mean method, and then those ensemble models were projected into the current climatic layers to predict the potential geographic distribution of species in this complex.

2.3 Niche comparison

To compare the niches among different species or lineages of this complex, we quantified their niche overlap and breadth from two different perspectives: in environmental space (E-space) and geographic space (G-space), respectively (Figure 2). Niche comparison in G-space is based on geographic ranges of species which are often inferred by ENMs in many studies, while niche comparison in E-space often uses the environmental information obtained directly from the occurrence locations to quantify the niches of species (Brown and Carnaval, 2019).

For niche comparisons in G-space, we first quantified the niche breadth of each species or lineage using Levins' *B* metric, and a higher *B* value represents a broader ecological niche (Levins, 1968). Then, niche overlap between different species was estimated by Schoener's *D* metric (Schoener, 1968) in which high *D* values indicate that different species may occupy similar niches. It is important to note that the niche overlap and niche breadth in G-space could be overestimated if the areas with very low habitat suitability were included in the calculation (Rödder and Engler, 2011). Thus, we need a threshold to determine the presence or absence of species per raster cell. The "maximizing the sum of sensitivity and specificity" (maxSSS) statistic is regarded as a well-performing threshold selection method for transforming suitability continuous predictions to binary outputs (Liu C. et al., 2013). As a result, we calculated the maxSSS value for each species or lineage with the 'dismo' *v.* 1.3-5 R package (Hijmans et al., 2022), and the habitat suitability value per raster cell below the maxSSS value was set to 0. Finally, we estimated Levins' *B* and Schoener's *D* based on the binary suitability maps of species and lineages with the 'ENMtools' *v.* 1.0.6 R package (Warren et al., 2021).

We then compared the niches among different species or lineages in E-space. As the Hutchinsonian niche concept describes the niche of a species as an n-dimensional hypervolume, we here used the functional richness (*FRic*) metric to quantify the niche breadth of species in E-space. *FRic* is defined as the amount of functional space occupied by the species, and it can be calculated by using probabilistic hypervolumes in trait space (Carmona et al., 2019). Given that some species of the complex, such as *C. chanetii*, *C. naktongense*, and *C. oreastrum* often occur at different elevations on the same mountain, we consider that data from WorldClim may not reflect the niche differences of those species. Therefore, we used ClimateAP *v.* 2.20 which integrates the local elevation information of species to provide climatic variables with increased spatial accuracy (Wang et al., 2017). We obtained 16 scale-free climatic variables (Table 1) using ClimateAP based on the latitude, longitude, and altitude of species occurrences. We then performed principal component analysis (PCA) for those 16 climatic variables to summarize these variables on two principal component axes with the 'FactoMineR' *v.* 2.6 R package (Lê et al., 2008). We calculated the *FRic* value for each species and lineage by the 'TPD' *v.* 1.1.0 R package (Carmona et al., 2019) according to the values of PC1 and PC2. To estimate niche overlaps between the species pairs in E-space, we selected the PCA-env approach based on climatic data of presence records and background points (Broennimann et al., 2012). We generated a minimum convex polygon (MCP) for each species or lineage and then defined the geographical backgrounds as MCPs with a one-degree width buffer area. We randomly selected 1,000 points for each species in the background areas and obtained the climatic data of these background points in ClimateAP. We subsequently estimated Schoener's *D* and tested the niche similarity for different species pairs in the 'ecospat' *v.* 3.4 R package (Di Cola et al., 2017). In detail, the niche similarity of each species pair was assessed with 1000 randomization tests. Those tests generated a null distribution based on Schoener's *D* values between a species and background points of another species in the pair. If the Schoener's *D* values of the null distribution are significantly lower than that of the target species pair, these two species may share similar niches than expected by chance.

2.4 Phylogeny reconstruction and divergence time estimation

To reconstruct a dated phylogeny at the species level, we downloaded a set of nuclear loci that included 100 exons with the highest number of parsimony-informative sites (Lu et al., 2022). Because there is no fossil data for *Chrysanthemum* species, we reconstructed the species tree using the uncorrelated relaxed clock model in *BEAST *v.* 1.8.4 (Suchard et al., 2018) with the clock rate of $8.37 \times 10^{-4} - 2.61 \times 10^{-3}$ substitutions/site/million years. This clock rate is based on the standard rate of nucleotide substitution for the Asteraceae (Kay et al., 2006) and three years of the generation time for species of this complex. We selected substitution models based on the Bayesian Information Criterion with ModelFinder (Kalyaanamoorthy et al., 2017), and the optimal model was TN + F + G4. We used the Yule process as the species tree prior and selected the Piecewise linear and constant root as the population size model. We ran two independent analyses with 1×10^7 Markov chain Monte Carlo generations based on a random starting tree, and the trees were sampled every 1,000 generations. The results of these two runs were merged using LogCombiner *v.* 1.8.4 (Suchard et al., 2018), and then the convergence of these results was evaluated with Tracer *v.* 1.7 (Rambaut et al., 2018). Finally, a maximum clade credibility tree was summarized by TreeAnnotator *v.* 1.8.4 (Suchard et al., 2018).

2.5 Reconstructions of ancestral niche and historical distribution

To reconstruct the ancestral niche of the complex, we first tested the phylogenetic signal for the 16 climatic variables obtained from ClimateAP based on the dated species tree in the 'phylosignal' *v.* 1.3 R package (Keck et al., 2016). Three metrics, including Moran's *I*, Blomberg's *K*, and Pagel's λ, were calculated, and the significance of these metrics was assessed by 1,000 randomization tests. Moran's $I = 0$ indicates that a trait evolved under Brownian motion (BM); $I < 0$ indicates no phylogenetic signal, and $I > 0$ suggests that the related species have more similar traits. Similarly, Bloomberg's *K* of 1 indicates that trait distribution follows BM; $K < 1$ indicates no phylogenetic signal, and $K > 1$ implies that the traits of related species are more similar than those predicted under BM. Pagel's λ usually ranges between 0 and 1; $\lambda = 1$ also indicates that the trait evolved according to the phylogeny, and $\lambda = 0$ indicates no phylogenetic signal. However, λ can > 1 when a trait of a related species is more similar than expected under BM (Münkemüller et al., 2012). We then tested the optimal model of niche evolution for those 16 climatic variables using the 'geiger' *v.* 2.0.10 R package (Harmon et al., 2008). Four models including BM, Ornstein–Uhlenbeck (OU), Early Burst (EB), and White Noise (WN) were selected, and we used the Akaike's Information Corrected Criterion (AICc) value to evaluate model performance. The BM model was the optimal model for all variables (Table S2). Finally, we selected the BM model to estimate the ancestral niches under a maximum likelihood framework by the 'phytools' *v.* 1.2-0 R package (Revell, 2012).

After reconstructing the ancestral niche of species in the complex, we further used phyloclimatic modeling to estimate the ancestral distribution ranges of those species for exploring their historical shifts in ranges (Figure 2). Firstly, we obtained the paleo-climatic data of the same four climatic variables that were used in previous ENM analyses at seven past time periods (i.e., 3.79 Mya, 3.36 Mya, 2.74 Mya, 2.24 Mya, 1.68 Mya, 1.15 Mya, and 0.80 Mya) from the Oscillayers datasets for phyloclimatic modeling (Gamisch, 2019). We focused on those seven time periods because they correspond to the divergence times of species in the complex. All of those variables were at 2.5 arc-minute, and their geographical extents were also reduced to our research area (Table 1). Next, we constructed Bioclim models for each species and lineage of the complex using their current occurrences and climate data in the 'machuruku' *v.* 1.8.3 R package (Guillory and Brown, 2021). The niches of species were described by three parameters including the mean, standard deviation, and skewness of climatic variables, and those parameters were used as inputs for subsequent analyses. We then estimated ancestral climatic parameters of species based on the dated phylogeny and those climatic parameters. Finally, we converted those ancestral climatic parameters into ancestral niche models of species with the 'machuruku'. All those niche models were projected into corresponding paleo-climate layers of the above seven time periods to reconstruct the ancestral geographic ranges of species in the complex, and those ancestral ranges were converted to binary suitability maps with the 'machuruku'.

3 Results

3.1 ENMs and niche comparisons

The AUC and TSS values of all the ENMs were greater than 0.90 (Table S3), indicating that all the models performed well. The ENM results for most of the species and lineages in the current period were consistent with their actual distribution in China, except for *C. hypargyrum* Qinling lineage and *C. oreastrum* Taihang-Lyuliang lineage (Figures 1, S1). In addition, the maxSSS values of those species varied from 0.305 (*C. zawadskii*) to 0.742 (*C. mongolicum*). Given that BRT models were not effective for those two lineages, we did not estimate their niche breadth in G-space. The Levins' B values in G-space for other taxa of this complex showed that narrowly distributed species possessed lower Levins' B values than widespread species (Table S3). The estimations of niche breadth for all species and lineages in E-space also obtained similar results. Species with wider ranges of distribution, such as *C. zawadskii*, *C. naktongense*, and *C. chanetii*, had higher *FRic* values, and the *FRic* values of some narrowly distributed species or lineages were even less than one-tenth of the former (Figure 3).

Analyses of niche overlap in the E-space suggested that the niche differentiation greatly varied among the taxa of this complex in which the Schoener's D values ranged from 0 to 0.462 (Table 2). The niche overlaps between the three widespread species (*C. zawadskii*, *C. naktongense*, and *C. chanetii*) were relatively high (D = 0.279 to 0.462). Moreover, the niche similarity tests showed that *C. chanetii* and *C. zawadskii* possessed significantly more similar environmental conditions than expected by chance ($p < 0.05$, Table S4). Schoener's D values between intraspecific lineages of two narrowly distributed species, i.e., *C. hypargyrum* and *C. oreastrum*, were relatively low (D = 0 to 0.089). Meanwhile, the results of the niche similarity tests suggested that Schoener's D values between intraspecific lineages of those two species were not significantly higher than that of the null distribution (Table S4). *C. maximowiczii*, a species that occurs in grasslands, showed relatively low niche overlap with other species. Similarly, another endemic species, *C. mongolicum*, also had little or no overlap with other species. Interestingly, the niche overlap in G-space showed a similar pattern to that in the E-space (Table S5).

3.2 Divergence time and niche evolution

The mean divergence times of the main nodes (Figures 1, S2) estimated under a relaxed clock model were similar to those estimated by Lu et al. (2022). In particular, the *C. hypargyrum* Qinling lineage diverged first about 4.16 million years ago (Mya), and other lineages or species have then emerged since the mid-Pliocene (ca. 3.78 Mya, Figure S2). Based on Moran's I, Blomberg's K, and Pagel's λ, we detected statistically significant phylogenetic signals for three of the 16 climatic variables, including the annual heat: moisture index, precipitation as snow, and Hargreaves climatic moisture deficit (Table 3). We identified the BM model as the evolution model that best fits these climatic variables according to the AICc statistics (Table S2). The results of

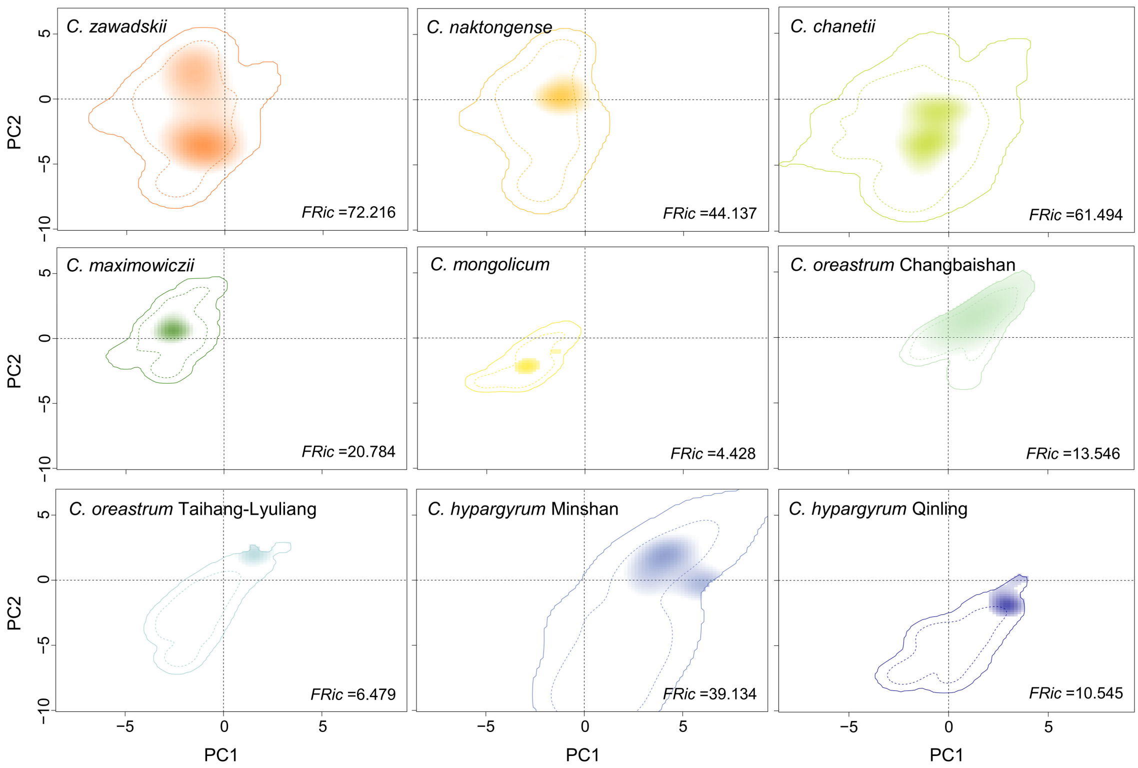

FIGURE 3
Climatic conditions occupied by different species and intraspecific lineages of the *Chrysanthemum zawadskii* complex in environmental space. The solid and dashed contour lines represent 100% and 50% of the background environments, respectively. The tint-to-dark shading of each species or intraspecific lineage shows the density of the occurrences by cell. *FRic* indicates the Functional richness metric.

TABLE 2 The Schoener's *D* values between species and lineages of the *Chrysanthemum zawadskii* species complex in E-space.

	Cza	Cna	Cmo	Cch	Cma	Cor-CBS	Cor-TL	Chy-MS
Cna	0.279							
Cmo	0.006	0.004						
Cch	**0.462**	0.326	0.011					
Cma	0.057	0.109	0.051	0.051				
Cor-CBS	0.121	0.116	0.000	0.196	0.018			
Cor-TL	0.020	0.000	0.000	**0.131**	0.000	0.033		
Chy-MS	0.005	0.000	0.000	0.045	0.000	0.089	**0.012**	
Chy-QL	0.000	0.000	0.000	0.022	0.000	0.000	0.000	0.034

E-space, environmental space; Cza, *C. zawadskii*; Cna, *C. naktongense*; Cmo, *C. mongolicum*; Cch, *C. chanetii*; Cma, *C. maximowiczii*; Cor-CBS, *C. oreastrum* Changbaishan lineage; Cor-TL, *C. oreastrum* Taihang-Lyuliang lineage; Chy-MS, *C. hypargyrum* Minshan lineage; Chy-QL, *C. hypargyrum* Qinling lineage.
Bolded values represent species pairs that share similar niches than expected by chance ($p < 0.05$).

ancestral state estimation under the BM model suggested that there is niche divergence between the four early-diverged alpine lineages and the core *C. zawadskii* complex (Figure 4). In comparison to the alpine lineages, the species of core *C. zawadskii* complex have evolved toward climatic conditions with less precipitation and higher temperature (Figures 4, S3). The kernel density plots in E-space also suggested that there was differentiation in the climatic conditions occupied by different species (Figure S4).

3.3 Changes in the geographic range of the complex across evolutionary times

Our results of phyloclimatic modeling showed that this complex originated in the Qinling mountains and its surrounding areas during the early Pliocene (Figures 5, 6). These results also showed that this complex diverged with its expansion to northern China along mountain ranges (Figures 6, S5). Additionally, the

TABLE 3 Phylogenetic signals tested for 16 climatic variables using three different metrics.

	Moran's *I*	*P* value	Bloomberg's *K*	*P* value	Pagel's λ	*P* value
Temperature related variables						
MAT	-0.118	0.447	0.652	0.497	$4.110E^{-05}$	1.0
MWMT	-0.048	0.049	0.805	0.226	$4.110E^{-05}$	1.0
MCMT	-0.160	0.735	0.544	0.702	$4.110E^{-05}$	1.0
TD	-0.121	0.389	0.603	0.526	$4.110E^{-05}$	1.0
DD<0	-0.161	0.755	0.548	0.671	$4.110E^{-05}$	1.0
DD>5	-0.053	0.089	0.791	0.272	$4.110E^{-05}$	1.0
DD<18	-0.125	0.484	0.643	0.512	$4.110E^{-05}$	1.0
DD>18	-0.067	0.139	0.757	0.288	$4.110E^{-05}$	1.0
NFFD	-0.091	0.247	0.706	0.407	$4.110E^{-05}$	1.0
EMT	-0.164	0.763	0.532	0.716	$4.110E^{-05}$	1.0
EXT	-0.061	0.084	0.735	0.380	$4.110E^{-05}$	1.0
Precipitation related variables						
MAP	-0.078	0.145	0.945	0.087	0.923	0.890
PAS	-0.057	0.138	0.898	0.139	**1.237**	0.022
Eref	-0.092	0.214	0.826	0.235	$4.110E^{-05}$	1.0
CMD	-0.075	0.150	**1.102**	0.042	1.193	0.134
Temperature and precipitation related variable						
AHM	-0.063	0.095	**1.280**	0.019	**1.227**	0.027

See Table 1 for abbreviations of climatic variables. Values that indicate significant phylogenetic signals are in bold ($p < 0.05$).

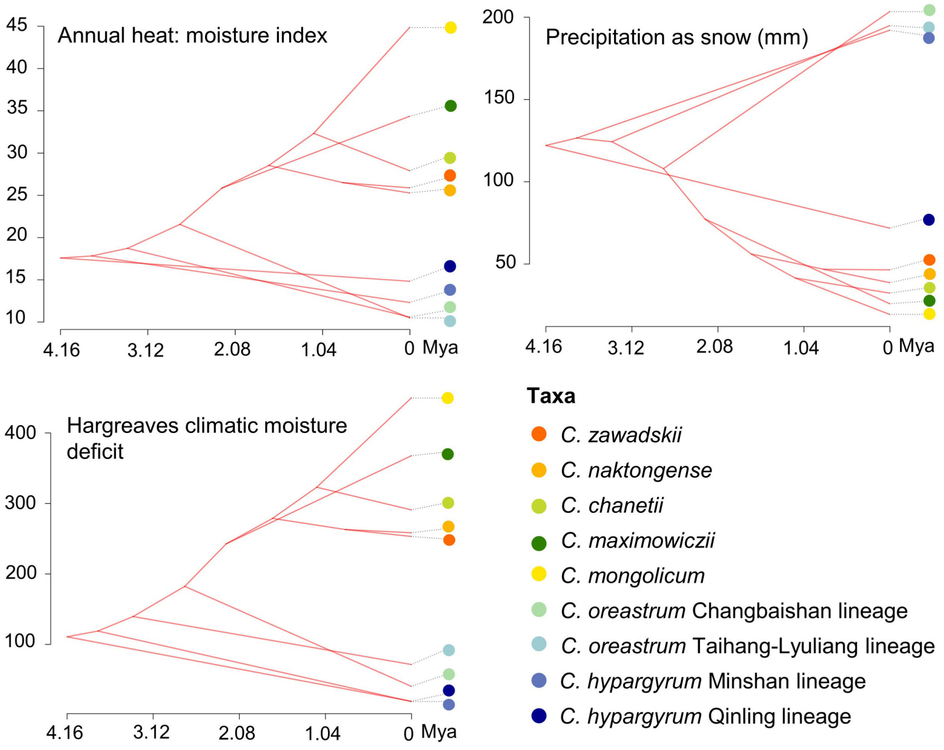

FIGURE 4
Reconstruction of the ancestral niches for different species and intraspecific lineages of *Chrysanthemum zawadskii* complex in environmental space. Colored circles represent different species and intraspecific lineages of this complex.

geographical ranges of *C. hypargyrum* and *C. oreastrum* showed little change and seem to have contracted over evolutionary time (Figure 5). For example, the suitable habitats of these alpine lineages decreased from 2.24 Mya to the present, except for the *C. oreastrum* Taihang-Lyuliang lineage. In contrast, there were several range expansions for the core *C. zawadskii* complex during its diversification (Figure 6). From 2.74 to 2.24 Mya, we detected a large shift in the geographical range of the core *C. zawadskii* complex. Another two range expansions occurred at 1.68 Mya and 1.15 Mya for the core *C. zawadskii* complex. We then checked the response curves and statistical values of four climatic variables for the core *C. zawadskii* complex at four different past

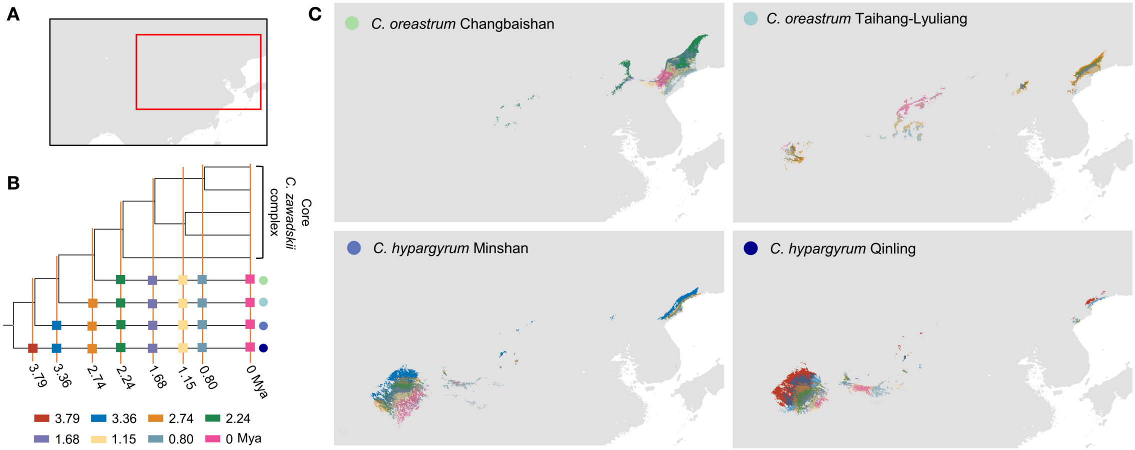

FIGURE 5
Reconstructions of the ancestral area of narrowly distributed alpine lineages of the *Chrysanthemum zawadskii* complex. **(A)** A map shows areas in this study. **(B)** The phylogenetic tree was used to reconstruct the ancestral niche and distribution, with eight past time periods that were focused on in this study. **(C)** Dynamics of ancestral distribution for those four alpine lineages of this complex. Colored circles and rectangles represent different intraspecific lineages of this complex and different past time periods, respectively.

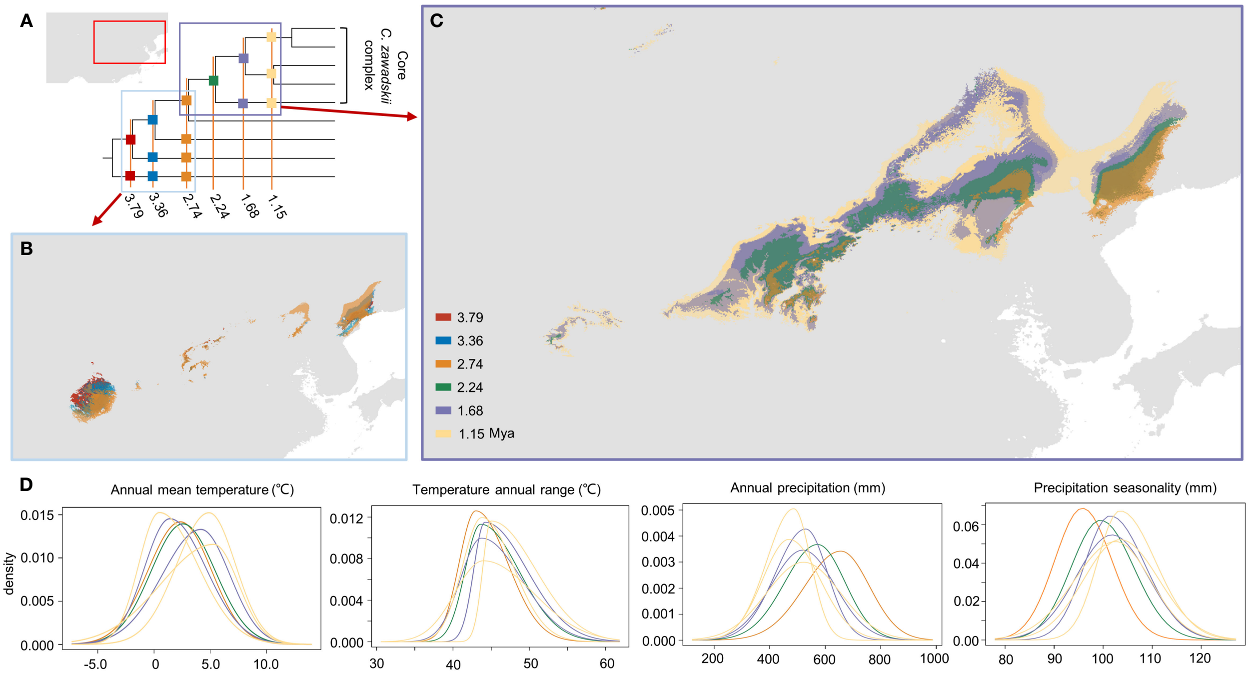

FIGURE 6
Dynamics of range and niche breadth of species in the *Chrysanthemum zawadskii* complex. **(A)** The phylogenetic tree was used to reconstruct the ancestral niches and ranges, and the map inset at the top left shows the study areas in this work. **(B)** Ancestral area reconstruction of this complex on the first three past time periods (in the blue rectangle: 3.79 Mya, 3.36 Mya, and 2.74 Mya). **(C)** Range shifts of the core *C. zawadskii* complex across four past time periods (in the purple rectangle: 2.74 Mya, 2.24 Mya, 1.68 Mya, and 1.15 Mya). **(D)** Response curves of four climate variables across four past time periods (2.74 Mya, 2.24 Mya, 1.68 Mya, and 1.15 Mya). Colored rectangles and curved lines correspond to different past time periods, separately.

periods (Figure 6, Table 4). The 95% confidence interval of those climatic variables indicated that the niche breadth of the core *C. zawadskii* complex did not increase obviously from 2.74 to 2.24 Mya (Figure 6, Table 4). Notably, the temperature-related climatic variables had high confidence interval overlap, and their mean values showed little difference between the above two past periods. Conversely, the mean values of the precipitation variables changed more clearly. In addition, as the core *C. zawadskii* complex diversified, the mean values and 95% confidence interval of those climatic variables greatly varied among species of the core complex.

4 Discussion

4.1 Closely related yet different: phylogenetic relatedness and niche divergence among species of the *C. zawadskii* complex

According to our findings, the territories of Qinling Mountains showed favorable environmental conditions to host the ancestor of *C. zawadskii* complex in the early Pliocene, making this region

TABLE 4 Statistical values of the response curves of four climate variables for the core *Chrysanthemum zawadskii* complex across four past time periods.

Period	Annual mean temperature			Temperature annual range			Annual precipitation			Precipitation seasonality		
	Mean	LCL	UCL	Mean	LCL	UCL	Mean	LCL	UCL	Mean	LCL	UCL
2.74 Mya	2.253	-1.997	6.786	44.570	39.249	50.044	635.028	480.670	858.484	96.052	86.804	106.101
2.24 Mya	2.612	-1.859	7.327	45.981	39.976	50.862	557.341	406.183	778.631	100.099	89.323	111.452
1.68 Mya	3.479	-1.478	8.269	45.727	39.074	52.063	520.077	361.617	771.220	101.860	88.810	114.821
	2.158	-2.079	7.004	47.384	41.640	52.692	506.179	365.582	691.923	102.930	92.688	114.166
1.15 Mya	3.317	-2.696	8.793	46.221	38.206	54.868	522.022	353.421	823.704	101.541	87.274	114.936
	4.473	0.107	8.647	45.030	39.119	51.745	483.088	327.634	710.626	103.829	89.820	117.894
	1.719	-2.291	6.689	48.711	43.224	54.433	458.133	327.604	609.892	105.592	95.878	116.701

LCL, 95% lower confidence limit; UCL, 95% upper confidence limit.

eligible as probable land where *C. hypargyrum*, *C. oreastrum*, and the core *C. zawadskii* complex might have evolved. The formation of four alpine geographic lineages could result from mountain uplifts, such as those that took place 4.1–3.4 Mya for the Minshan Mountains and 5.3–3.6 Mya and 2.6 Mya for the Taihang Mountains, and the resultant geographical barriers between alpine populations since the early Pliocene (Zhang et al., 2005; Gong, 2010; Shi et al., 2020). In addition, species of the complex have a relatively weak ability to disperse owing to their achenes that lack pappi or wings (Shi et al., 2011). Both geographical barriers and limited dispersal capacity restricted the gene flow between alpine populations or lineages, and then local selection and/or drift facilitated the formation of four alpine lineages.

Notably, although these alpine lineages have diverged, they still prefer habitats with relatively humid climate conditions and low mean warmest month temperature (Figures 4, S3), which suggests their phylogenetic niche conservatism in some niche axes. Unlike alpine lineages, species of the core *C. zawadskii* complex can tolerate hotter and drier environmental conditions. The ancestral niche estimations indicate that the variables related to precipitation exhibit more pronounced divergence within the complex than those of the temperature factors (Figure 4, Table 3). In fact, the relative importance of temperature and precipitation in driving the distribution and diversification of species is not identical among different plant taxa (Moles et al., 2014; Häkkinen et al., 2022). A recent study indicated that many plants tend to adapt to novel precipitation regimes, whether wetter or drier, rather than adapting to hotter or colder climates, suggesting the importance of precipitation in the niche evolution of species (Häkkinen et al., 2022). In this study, we can deduce that niche differentiation within the complex might be primarily driven by the moisture gradient. According to our results, the common progenitor of the core *C. zawadskii* complex split from the alpine lineages at approximately 2.73 Mya, and then its distribution range extended to the Chinese Loess Plateau (CLP) and surrounding areas (Figure 6). Previous studies showed that there was a major change in the precipitation gradient on the CLP during the Pliocene-Quaternary boundary, and the climate became dry and cold (Wu et al., 2007; Nie et al., 2013; Peng et al., 2018). The progenitors of the core *C. zawadskii* complex could have quickly adapted to such a change and then expanded into drier habitats. Additionally, analyses of paleosol pollen assemblages from the CLP suggested that open habitats increased during this period (Hui et al., 2021). Species of this complex generally occur in open habitats, such as grassland, slope, and forest edges (Shi et al., 2011), and such changes could provide more ecological opportunities for range expansion and diversification of the core *C. zawadskii* complex.

4.2 Evolution of niches: from specialist to generalist or vice versa

Comparative analyses of niches showed that there exists a distinct niche divergence among species of the complex (Table 2, Figure 3). Interspecific variations in the phenotypic traits, habitats, and distribution ranges of the *C. zawadskii* complex implied that niche evolution occurred (Lu et al., 2022). Multiple niche analyses in this study supported that shifts in niche breadth occurred in the complex. For decades, there was a consensus that specialization is an evolutionary dead end (Moran, 1988; Schluter, 2000; Vamosi et al., 2014). Nonetheless, a growing number of studies have indicated that such a “consensus” might not be general, and that it is possible to transition from specialists to generalists (Armbruster and Baldwin, 1998; Dennis et al., 2011; Donoghue and Edwards, 2014; Vamosi et al., 2014; Day et al., 2016; Sexton et al., 2017; Rombaut et al., 2022). Within this complex, early divergent alpine lineages possess narrow niches, and they are more likely to be specialists than generalists. Another small-range species, *C. mongolicum*, also has a narrow niche, and it is sympatric with its sister species, *C. chanetii* with a large range (Lu et al., 2022). Taking together the findings described above and the climatic tolerances of ancestral nodes under the phylogenetic framework, we found that specialists can be converted to generalists and vice versa in this complex. Notably, niche comparison in G-space could be affected by the results of ENMs, so such comparisons may not be applicable to some rare species. By comparison, niche comparisons in E-space based on the environmental information of occurrence locations appear to be more stable and reliable.

Climate variability is often regarded as a critical factor in determining the niche breadth of a species (Quintero and Wiens, 2013). Many studies examined the relationship among species range, niche breadth, and habitat climate variability, and they found that species that originated from regions with variable climates could evolve broader niche breadths than their allied species in stable habitats (Stevens, 1989; Addo-Bediako et al., 2000; Quintero and Wiens, 2013; Pintor et al., 2015; Li et al., 2016; Mumladze et al., 2017). Reconstruction of ancestral niche indicated that species of the core *C. zawadskii* complex have evolved broader niche breadths since 2.24 Mya (Figure 6). During the early Pleistocene (2.2–1.7 Mya), the East Asian summer monsoon (EASM) gradually intensified in the CLP (Hui et al., 2021), and the dramatic seasonal climatic fluctuations in this region enhanced the niche breadth of the core *C. zawadskii* complex. Nonetheless, the alpine lineages did not evolve increased niches or undergo range expansion (Figure 5). We hypothesized that alpine lineages could survive *in situ* mountain refugia with stable climates and adapt to alpine habitats rather than expanding to lower altitudes because of the geographical barriers and their limited ability to disperse (Bai et al., 2010; Zhao et al., 2013; Guo et al., 2014).

4.3 Coupled changes between range size and niche breadth in the evolution of *C. zawadskii* complex

Speciation is usually a lengthy process with niche evolution and range changes (Stankowski and Ravinet, 2021), and the current pattern of distribution and niche of species represents the consequences of this process. When we integrate snapshots of niches and ranges of species across different historical periods, the complete picture of an eco-evolutionary process that shapes species distribution can be reconstructed. The progenitor of this complex probably adapted to relatively cold climates and diverged from the other *Chrysanthemum* lineages with the uplift of Qinba mountains since the late Miocene (Liu J. et al., 2013; Meng, 2017; Shi et al., 2020; Lu et al., 2022). Subsequently, the complex spread west- and northwards along the mountain ranges to northern China, and then rode the rising mountains and occupied alpine habitats. Some lineages (*C. hypargyrum* and *C. oreastrum*) adapted to survive *in situ*, and others expanded into drier climates in northern China since the early Pleistocene. Changes in vegetation and the EASM evolution in the CLP during the early Pleistocene enhanced broader niches and larger range sizes of the core *C. zawadskii* complex.

The spatiotemporal dynamics of the niches and ranges of the *C. zawadskii* complex indicate that the coupled changes between ranges and niches drive the range expansion of the complex, which is more consistent with the range shift-niche breadth hypothesis (Lancaster, 2022). Climate fluctuation and the decrease of interspecific competition since the Pleistocene provided an opportunity for this herbaceous species complex to expand its range (Wu et al., 2007; Nie et al., 2013; Peng et al., 2018; Hui et al., 2021), and the niche breadth increased in pace with the expansion of its range into areas that have a highly variable climate, which further promoted the range expansion. Notably, even though the species are closely related, the patterns of range shifts are diverse across taxa of the complex, which suggests that historical biogeographic processes also affect the distribution of species.

In sum, by integrating the findings from phyloclimatic modeling, niche comparisons, and biogeographic analyses, we can better understand the processes and mechanisms behind the changes in geographic range and niche evolution. Nonetheless, the reconstruction of ancestral distribution ranges by phyloclimatic modeling is still in the early developmental phase, and some factors, such as the reliability of paleoclimatic data and robustness of phylogeny, could dramatically influence the results (Gamisch, 2019; Rivera et al., 2020; Guillory and Brown, 2021). Although we weighed and chose the appropriate climatic variables for the complex in the current period, we could not say that the paleoclimatic data of the same variables are the best fit for estimating the ancestral distribution of the target species. In addition, we here focused on the niche of species on a larger scale, but microhabitats could also influence the niche differentiation of species and their distribution (Lawson et al., 2014). Therefore, we need to consider more factors that affect niche evolution and range dynamics of species and incorporate more data in our future works.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

W-XL and G-YR conceived the ideas. W-XL, Z-ZW and X-YH collected the data. W-XL designed methodology and analyzed the data. W-XL and G-YR led the writing of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1250491/full#supplementary-material

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