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RESEARCH ARTICLE

Niche Dynamics Under Current and Future Climates of South African Plants in France

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Correspondence: Mohamad Abdallah (mhmad.abdallah1@gmail.com)**Received:** 3 March 2026 | **Revised:** 28 April 2026 | **Accepted:** 1 June 2026**Keywords:** biogeographic origin | climate change | France | niche dynamics | non-analogue climates | plant invasions | risk assessment

ABSTRACT

Aim: While climatic niche dynamics of invasive plants have been increasingly studied worldwide, comparative assessments disentangling niche conservatism from expansion into analogue and non-analogue climates remain very limited in France. Here, the climatic niche dynamics of four South African plant species established in France were quantified, and spatial changes in climatic availability across France were estimated to support invasion risk assessment and management prioritisation.

Location: France.

Taxon: Angiosperms (*Arctotheca calendula*, *Carpobrotus acinaciformis*, *Carpobrotus edulis* and *Oxalis pes-caprae*).

Methods: We quantified climatic niche overlap, stability, expansion and pioneering between native and introduced ranges using ordination-based niche dynamics metrics, including Schoener's *D* and niche equivalency and similarity tests. Future climatic availability was projected under emission scenarios to estimate spatial turnover, distinguishing areas of climatic retention, loss, and gain.

Results: Climatic niche overlap between native and introduced ranges was limited to moderate, yet niche stability within analogue climates was consistently high, indicating overall climatic niche conservatism. Species responses differed markedly. *Oxalis pes-caprae* showed the strongest conservatism, with full niche equivalency across ranges. In contrast, *A. calendula*, *C. acinaciformis*, and *C. edulis* exhibited partial niche shifts. Notably, *A. calendula* and *C. edulis* demonstrated significant niche pioneering, expanding into wetter and more climatically stable environments in France relative to their native South African ranges. Future projections revealed substantial spatial turnover, with concurrent contractions of currently suitable areas and emergence of newly suitable territories, particularly for species exhibiting greater niche flexibility.

Main Conclusions: South African plant species exhibit both niche conservatism and divergence in France, reflecting species-specific strategies shaping invasion dynamics. Climatic pre-adaptations alone do not determine niche outcomes; ecological traits and native niche breadth likely contribute to niche differentiation across ranges. Effective management requires moving beyond generic approaches toward species- and scenario-specific strategies that consider the timing and magnitude of each species' redistribution.

1 | Introduction

Climate change is increasingly shaping patterns and processes of plant invasions worldwide (Bellard et al. 2018). By altering temperature regimes and precipitation patterns, it changes the environmental conditions that can both facilitate the establishment and spread of invasive plants in some areas while constraining their success in others (Merow et al. 2017; Newbold et al. 2020; Cao Pinna et al. 2024). As climate change is expected to alter plant invasions, new challenges related to their management are likely to arise (Beaury et al. 2020). Hence, early detection and prevention remain the most effective and cost-efficient strategies for averting widespread invasions (Essl et al. 2020). Once an exotic species becomes widespread, management and control efforts require long-term policy decisions that are often expensive and time-intensive (Love et al. 2018). Therefore, focusing on species that are already established but not yet causing major impacts is crucial, as these taxa represent a critical window for implementing effective management strategies.

Following introduction into a new region, one of the main determinants of an exotic species' establishment success is habitat suitability, which depends largely on climatic conditions, resource availability and disturbance regimes (Liu et al. 2020; Broennimann et al. 2021). When the realised climatic niche of an exotic species (i.e., the range of climates it occupies while maintaining stable or positive population growth) in the introduced range closely matches that of its native range (the 'climate matching' hypothesis), the species is considered to exhibit niche conservatism (Morente-López et al. 2023; Riera et al. 2025; Rönnfeldt et al. 2026). Conversely, if the realised climatic niche (hereafter, 'climatic niche') in the introduced range differs from that in the native range, for example, through an expansion or contraction of its limits, the species has undergone a niche shift (Carlin et al. 2023; Ángel-Vallejo et al. 2024; Lozano et al. 2026).

When evaluating climate matching to assess invasion potential, the existence of analogue climates between native and invasive regions is essential for accurately assessing species' responses to ongoing and future environmental change. Analogue climates are climatic conditions supporting a species in the introduced range that are similar to those in the species' native range. In contrast, non-analogue climates represent different climatic conditions in the introduced range that were not available in the species' native range (Carlin et al. 2023). Non-analogue climates may hide niche shifts but also niche conservatism (Fenollosa et al. 2025). Several studies have chosen not to investigate niche shifts under non-analogue climates because shifts resulting from rapid evolution cannot be distinguished from those arising from an underestimation of the fundamental niche (Petitpierre et al. 2012; Guisan et al. 2012; Liu et al. 2020). While distinguishing between these two types of niche shifts is important to determine exotic species potential expansion with novel environmental conditions, excluding non-analogue climates does not necessarily reveal their underlying causes and may reduce the accuracy of environmental niche models, as well as hinder interpretation of the ongoing impacts of invasions (Atwater et al. 2018; D'Amen and Azzurro 2020; Pili et al. 2020).

The invasive success of exotic species depends on specific functional traits (van Kleunen et al. 2010) as well as introduction

history and biogeographic origins (Cao Pinna et al. 2021). The biogeographic origin of a species can serve as a proxy for the climatic pre-adaptations of different source pools due to climate matching (Atwater et al. 2018; Cao Pinna et al. 2021; Sychrová et al. 2022). This pattern highlights the importance of considering biogeographic origins when evaluating plant invasions, as it provides critical insights into niche dynamics and improves the prediction of invasion risk across spatial and temporal scales. Species originating from Mediterranean-type climatic regions, for example, might already be adapted to warm, dry summers and mild, wet winters, making them more likely to establish and spread in regions with similar climate regimes (Deitch et al. 2017; Rivas-Martínez et al. 2017; Cao Pinna et al. 2025). However, small differences in niche breadth and functional traits might explain why not all species with similar biogeographic origins become invasive (Bujan et al. 2021; Sychrová et al. 2022). In this regard, comparing multiple species with shared native distribution might contribute to understanding the drivers of invasion potential, especially when exploring climate change impacts on distribution shifts.

The present study examines different plant species native to the Cape Region of South Africa that are present in France. France provides an ideal setting to investigate climatic niche dynamics with regard to species' biogeographic origins, as it spans a diverse array of climatic zones, encompassing Mediterranean, continental, oceanic and mountainous climatic regions along steep bioclimatic gradients over short distances (Hertzog et al. 2025). Although climatic niche dynamics of invasive plants have been increasingly studied globally, comparative analyses within France's diverse climatic context remain limited (but see Gallien et al. 2016; Christina et al. 2020, 2023). Moreover, these studies focused exclusively on single invasive species and did not consider species' biogeographic origins, neither when evaluating niche dynamics nor when examining whether introduced populations occupy climatic conditions similar to, or novel relative to, those in their native ranges. Addressing this gap, the present study aims to evaluate how climate shapes the invasion potential of South African plant species in France (hereafter referring to Metropolitan France, i.e., the European part of the country, excluding overseas territories), with implications for anticipating future invasion hotspots under climate change. Specifically, the study will:

1. Quantify and compare the climatic niches of South African plant species across their native (South Africa) and introduced (France) ranges to detect niche shifts or conservatism and assess whether they occupy analogue or novel climatic conditions in France.
2. Quantify spatial changes in climatic niche availability for these species across France under different climate scenarios for 2030 and 2050.
3. Assess changes in the geographic extent of areas across France that share climatic conditions with the current invaded niche under the assessed climate scenarios, providing spatially explicit outputs to support invasion risk assessment and guide evidence-based national management planning and prioritisation.

TABLE 1 | Family, status, and description of the four studied plant species.

Species	Family	Description
<i>Arctotheca calendula</i>	Asteraceae	Herbaceous annual or perennial plant with a stoloniferous growth habit, a basal rosette of lobed, woolly leaves and bright yellow daisy-like flowers. It thrives in sandy or disturbed soils and is tolerant to drought and high temperatures. Found for the first time around 1980 in the Hérault and Var Departments (France), it has become invasive in several Mediterranean and temperate regions, where it rapidly colonises roadsides, pastures and coastal dunes, forming dense mats that outcompete native vegetation and alter community composition (Vivant 1980; Sakhraoui et al. 2024; Cal-IPC 2025).
<i>Carpobrotus acinaciformis</i>	Aizoaceae	This succulent perennial plant forms dense mats with long, trailing stems and thick, triangular leaves. It produces large, showy magenta flowers and reproduces both vegetatively and through seeds. Dated back to Europe around the 1700s, it has become invasive in many Mediterranean coastal areas including France, displacing native dune vegetation and altering soil properties (Campoy et al. 2018; Novoa et al. 2023; Canavan et al. 2025).
<i>Carpobrotus edulis</i>	Aizoaceae	A mat-forming succulent with thick, triangular leaves and large yellow flowers that often turn pinkish with age. It spreads vigorously through stolons and rooting nodes, enabling rapid colonisation of sandy and coastal habitats. Widely planted in the European Mediterranean coastal areas since 1700's for erosion control, it has become one of the most aggressive coastal invaders in the Mediterranean and Atlantic regions, where it suppresses native vegetation and alters soil pH and nutrient dynamics (Campoy et al. 2018; Canavan et al. 2025).
<i>Oxalis pes-caprae</i>	Oxalidaceae	Native to South Africa, <i>Oxalis pes-caprae</i> was first registered in Europe around the 1700s. Since then, it has successfully invaded the Mediterranean basin and various temperate zones, thriving in disturbed and anthropogenic habitats such as roadsides, agricultural fields, and coastal areas. Its ability to form dense, monodominant carpets allows it to suppress native flora, alter soil nutrient cycles and hinder ecosystem recovery after disturbance (Papini et al. 2017; González-Moreno et al. 2015; Malfa et al. 2025).

2 | Materials and Methods

2.1 | Species Selection and Occurrence Data

Four South African exotic plant species were selected (Table 1) based on the *Classification des impacts environnementaux des Espèces Végétales Exotiques Résidentes en France métropolitaine* (CLEVER) project, a French national initiative that compiled literature review and botanist-validated observation data from the National Botanical Conservatories across France to assess the environmental impacts of exotic plant species established in France using the EICAT/EICAT+ framework (de Solan et al. 2024; de Solan et al. 2026). The selection of the four species from that list focused on taxa sharing common biogeographic origin with moderate, well-documented ecological impacts and confirmed establishment in France. Occurrence records for the selected species in both their native (South Africa) and introduced ranges (France) were compiled via the ‘rgbif’ package (Chamberlain et al. 2025), from the Global Biodiversity Information Facility (GBIF, accessed October 2025), which includes registers from French national platforms such as the Inventaire National du Patrimoine Naturel (INPN), the Conservatoire Botanique National (CBN) and the Muséum national d'Histoire naturelle (MNHN) databases. GBIF provides a large volume of occurrence data, but these records are often prone to sampling bias and errors in

geographical, temporal, and taxonomic representation, which can result in spurious estimates of species' niches and occurrences (Marcer et al. 2022). To mitigate these issues, a multi-step data cleaning and filtering protocol was implemented (Kass et al. 2025). This procedure aims to flag potentially erroneous records by checking for proximity to known geographic artefacts (e.g., the centroids of administrative regions and biodiversity institutions), identifying spatial outliers and duplicate records, and detecting coordinates with suspicious values or formatting inconsistencies. Additionally, following standard practices, spatial thinning of 0.1 km was applied to remove pseudo-replicates. These steps substantially reduced the number of records while improving dataset reliability, resulting in a more balanced and reliable dataset that better reflects the species' actual distribution for subsequent analyses (Figure 1).

2.2 | Environmental Variables and Selected Scenarios

Nineteen bioclimatic variables were obtained from the WorldClim v2.1 database (Fick and Hijmans 2017), representing current climatic conditions for the 1970–2000 climatological baseline, at a spatial resolution of 2.5 arc-minutes (~5 km at the equator). Variables were cropped and masked to the spatial

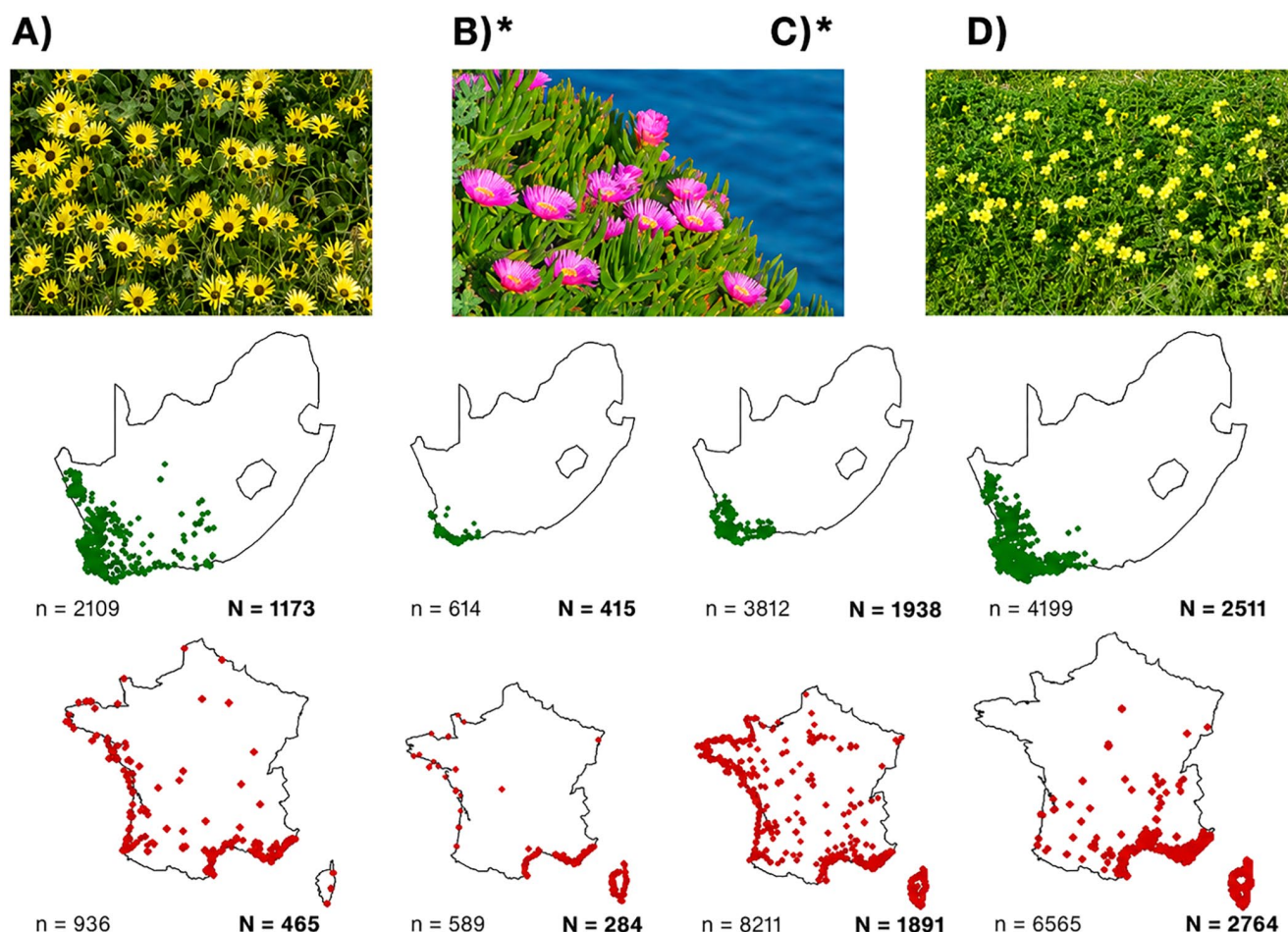


FIGURE 1 | Occurrences of (A) *Arctotheca calendula*, (B) *Carpobrotus acinaciformis*, (C) *Carpobrotus edulis* and (D) *Oxalis pes-caprae* in their native range (South Africa, green) and introduced range (France, red). Lowercase *n* indicates the number of records before data cleaning and spatial thinning, whereas uppercase *N* indicates the number of records after cleaning and thinning. Only *N* were used for map display and subsequent statistical analyses. *Due to ongoing debates regarding the taxonomy and identification of *Carpobrotus* species and the hybrid complex (Canavan et al. 2025), we included both *C. edulis* and *C. acinaciformis* to ensure clarity and comprehensive mapping.

extents of France and South Africa using country boundaries derived from GADM v4.1 shapefiles. To reduce multicollinearity and improve model interpretability, pairwise Pearson correlation coefficients were calculated using background environmental values, retaining only variables with $|r| < 0.7$. This resulted in a final set of eight bioclimatic variables: BIO2 (Mean Diurnal Range, °C), BIO7 (Temperature Annual Range, °C), BIO8 (Mean Temperature of the Wettest Quarter, °C), BIO13 (Precipitation of the Wettest Month, mm), BIO14 (Precipitation of the Driest Month, mm), BIO15 (Precipitation Seasonality, %), BIO18 (Precipitation of the Warmest Quarter, mm) and BIO19 (Precipitation of the Coldest Quarter, mm).

Future climate projections were restricted to France and included two Shared Socioeconomic Pathways (SSPs) from the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report: *SSP2-4.5*, representing a moderate development pathway with intermediate population and land-use changes, and *SSP5-8.5*, representing a high-emissions, fossil-fueled scenario with rapid socioeconomic development. These pathways allow consideration of both climatic impacts and human-induced changes that could influence species

invasions, providing useful context for management strategies. Projections were obtained for two time horizons, 2021–2040 (hereafter ‘2030’) and 2041–2060 (hereafter ‘2050’), at the same spatial resolution. Climatic data were derived from the CMIP6 ensemble using the IPSL-CM6A-LR climate model, a standard configuration developed by the Institut Pierre-Simon Laplace Climate Modelling Centre (IPSL-CMC) (Bonnet et al. 2021). This model is widely used in French national climate projections and forms a core part of adaptation assessments conducted by institutions such as Météo-France and the Institut national de recherche pour l’agriculture, l’alimentation et l’environnement (INRAE).

2.3 | Climatic Niche Conservatism

2.3.1 | Assessing Climatic Niche Conservatism

For each species, an environmental principal component analysis (*PCA-env*) approach (Broennimann et al. 2012) was calibrated using the pooled environmental backgrounds from the species’ native and introduced ranges. *PCA-env*

is widely regarded as a gold standard for assessing climatic niche conservatism (Liu et al. 2020). The scores of the first two PCA axes were used to create a two-dimensional climatic space, which was divided into a 100×100 grid (Petitpierre et al. 2012; Guisan et al. 2014). Smoothed occupancy of climatic conditions in this space was estimated using the species' occurrences and the environmental PCA scores for both ranges, implemented with the 'ecospat' R package (Di Cola et al. 2017). The resulting smoothed occupancies of climatic conditions across both ranges were used to calculate representative metrics of climatic niche conservatism (see below), using an intersection threshold of 10% to remove marginal climatic conditions and considering only the 90% most common environments shared between the native and introduced ranges, ensuring that metrics were calculated in the common environmental space.

2.3.2 | Climatic Niche Conservatism Components

Niche overlap was quantified using Schoener's *D*, which measures the overlap in niche occupancy between the native and introduced ranges and varies from 0 (no overlap) to 1 (complete overlap) (Schoener 1970; reviewed in Warren et al. 2008). To facilitate a more objective interpretation of overlap values, the framework proposed by Rödder and Engler (2011) was adopted, classifying niche overlap into five categories: 0–0.2 (no or very limited overlap), 0.2–0.4 (low overlap), 0.4–0.6 (moderate overlap), 0.6–0.8 (high overlap), and 0.8–1.0 (very high overlap). To test the statistical significance of niche overlap (Schoener's *D*), niche equivalency and similarity tests were performed, comparing the overlap between the two observed niches with overlaps generated from simulated niches. The equivalency test assesses whether two niches are more or less equivalent than expected by chance by randomly reallocating all occurrences between the two ranges. The similarity test evaluates whether the observed niche overlap between two ranges differs from the overlap expected when occurrence density grids are randomly shifted within the background environment (Warren et al. 2008, 2010; Broennimann et al. 2012; Di Cola et al. 2017). To ensure robust statistical inference, each test was based on 1000 simulations. For both tests, one-sided hypotheses of niche divergence (shift) and niche conservatism were assessed; for the similarity test, randomisations were performed by shifting each niche independently. For both the equivalency and similarity tests, a significant *p* value (≤ 0.05) indicates that the two niches are either less (niche divergence) or more (niche conservatism) equivalent or similar than expected under random expectations.

The remaining components were calculated by partitioning the climatic niche into analogue and non-analogue conditions. For analogue climatic conditions (i.e., environments available in both native and introduced ranges), stability (*S*; conditions available in both ranges and occupied in both), expansion (*E*; conditions available in both ranges but occupied only in the introduced range) and unfilling (*U*; conditions available in both ranges but occupied only in the native range) were quantified (Petitpierre et al. 2012; Guisan et al. 2014). For non-analogue climatic conditions (i.e., environments available in only one range), pioneering (*P*; conditions occupied in the introduced range but unavailable in the native range) and abandonment

(*A*; conditions occupied in the native range but unavailable in the introduced range, calculated for illustrative purposes) were also quantified (Atwater et al. 2018). All metrics were weighted by the smoothed occupancy densities (*z.uncor*) in the corresponding range. For analogue metrics (*U*, *S*, *E*), the proportional contribution of each component was calculated relative to the total analogue niche volume ($U + S + E$), whereas *P* and *A* were weighted according to introduced- and native-range climate commonness, respectively. Additionally, maps were generated to visualise niche dynamics across both analogue and non-analogue climatic conditions, as well as the distribution of species occurrences along key bioclimatic variables. Analyses were performed following the 'ecospat' package (Di Cola et al. 2017) and functions provided by Dr. Blaise Petitpierre (Riera et al. 2025).

2.4 | Future Climatic Niche Availability

PCA-env analyses were calibrated separately for each of the four assessed species. For each species, the environmental dataset was constructed by combining values of eight retained bioclimatic variables extracted from the current climatic background of the native (South Africa) and current climatic conditions observed in species' native occurrences and current, 2030- and 2050-time horizons in introduced (France) ranges and in species' invaded occurrences. Two independent *PCA-env* analyses were conducted per species, corresponding to the SSP2-4.5 and SSP5-8.5 climate scenarios, using the *dudi.pca()* function in the 'ade4' R package (Dray and Dufour 2007). The first three principal components were retained to summarise the dominant climatic gradients, with the first two axes defining a two-dimensional climatic space onto which current and future climatic conditions where PCA coordinates have been extracted using the *get_pca_ind()* function from the 'factoextra' R package. The species' climatic native and invaded niche and climatic conditions in native and introduced regions were delineated using a kernel density estimation (KDE), applied in PCA space using the *kde()* function from the 'ks' R package (Di Cola et al. 2017) using 99% contour levels (Blonder et al. 2014), resulting in polygons representing climatic envelopes. For each grid cell, future climatic conditions were classified as falling inside (available) or outside (unavailable) the polygon representing the species' introduced climatic niche. Following established niche dynamics concepts (Petitpierre et al. 2012; Guisan et al. 2014; Broennimann et al. 2012, 2021), each grid cell was assigned to one of five categories by comparing current and future classifications within the PCA-based climatic space (Figure S1) and then within the geographic space using the 'terra' R package (Hijmans et al. 2026), each grid cell having a unique PCA and geographical coordinates. The five categories were classified as follows:

- i. PA: Persistently Available (Areas of the introduced range that currently have, and are projected to retain under climate change, a suitable climate for the species),
- ii. PU: Persistently Unavailable (Areas within the introduced range that are currently unsuitable for the species and are projected to remain unsuitable under future climate conditions),

- iii. AG: Availability Gain (Areas that are unsuitable under current climate conditions but become suitable under projected future climates),
- iv. AL: Availability Loss (Areas that are suitable under current climate conditions but become unsuitable under projected future climates), or
- v. UC: Uncertain (Marginal areas showing inconsistent climatic suitability over the three time periods, for example, inside in the present and 2050 but outside in intermediary 2030 period, or vice versa).

These classifications describe changes in climatic analogy relative to the currently realised invaded niche and do not represent predictions of species occurrence.

3 | Results

3.1 | Climatic Niche Conservatism Components

Schoener's niche overlap values indicated very limited to low climatic niche overlap between the native (South Africa) and introduced (France) ranges of the four species, with *Carpobrotus acinaciformis* exhibiting the lowest overlap (Table 2). The niche similarity test did not support niche divergence for any of the assessed species ($p > 0.05$), whereas niche conservatism was supported for all four species ($p \leq 0.05$). Nevertheless, the niche equivalency test between native and introduced ranges rejected full statistical equivalence for *Arctotheca calendula*, *Carpobrotus acinaciformis*, and *Carpobrotus edulis* ($p \leq 0.05$). Conversely, *Oxalis pes-caprae* showed significant niche equivalency between the two ranges ($p \leq 0.05$) (Table 2).

Species' niches were further examined to assess climatic niche dynamics components under both analogue and non-analogue climatic conditions (Figure 2). Within analogue climatic space, niche stability (S) was high for all species, representing the largest proportion, with *Oxalis pes-caprae* exhibiting the highest S , that is, retained the greatest fraction of its analogue niche between South Africa and France. Overall, niche expansion (E) was higher than niche unfilling (U), which was negligible or absent across all species, with *Carpobrotus edulis* exhibiting the highest E and no detectable U . Within non-analogue climatic space, pioneering (P) differed markedly among species. *Arctotheca calendula* showed the highest occupation of climatic conditions in France that are unavailable in South Africa, whereas *Oxalis pes-caprae* exhibited no pioneering ($p = 0$) (Table 2).

3.2 | Principal Component Analysis of Species Occurrences

To examine the distribution of species occurrences across native and introduced ranges along key bioclimatic variables, PCA-*env* analyses were conducted separately for each of the four following species.

3.2.1 | *Arctotheca calendula*

Occurrences of *A. calendula* in the native (South Africa) and introduced (France) ranges occupied distinct regions of the climatic space defined by the first two PCA axes, which together explained 79.78% of the total variance (Figure 3A). PC1 (53.57%) described a gradient from climates with higher temperature variability (negative scores; higher mean diurnal temperature range and warmer wet-season conditions, BIO2 and BIO8) to wetter climates (positive scores; higher precipitation in the driest and wettest months, BIO14 and BIO13). PC2 (26.21%) captured seasonal climatic variation, contrasting climates with higher temperature annual range and precipitation of the warmest quarter (BIO7, BIO18) with those characterised by higher precipitation seasonality and precipitation of the coldest month (BIO15, BIO19). Native-range occurrences were predominantly associated with higher temperature-related and seasonal variability (BIO2, BIO7, BIO8 and BIO15), whereas introduced-range occurrences clustered in climates with higher precipitation across seasons (BIO13, BIO14, BIO18 and BIO19). Together, these patterns indicate that *A. calendula* is expanding from more climatically variable and seasonally structured environments in South Africa toward wetter and less seasonally constrained conditions in France.

3.2.2 | *Carpobrotus acinaciformis*

For *C. acinaciformis*, the first two PCA axes explained 63.5% of the total climatic variation (PC1 = 32.81%, PC2 = 30.69%; Figure 3B). Occurrences showed partial separation in the PCA environmental space, with substantial overlap along both axes. PC1 represented a gradient from hotter and wetter summer conditions (positive scores; BIO7 and BIO18) to regions with more variable winter conditions (negative scores; BIO15 and BIO19), whereas PC2 captured variation in precipitation and temperature during wet periods, contrasting with wetter conditions in the driest and warmest months (positive scores; BIO14 and

TABLE 2 | Niche overlap (Schoener's D), p values from niche similarity (Sim) and equivalency (Eq) tests indicating niche conservatism (C) or divergence (D) and percentages of climatic niche conservatism components between native and introduced ranges.

Species	Overlap	Sim (C)	Sim (D)	Eq (C)	Eq (D)	S (%)	E (%)	U (%)	P (%)
<i>Arctotheca calendula</i>	0.13	0.02	0.94	1.00	<0.01	86	13	1	42
<i>Carpobrotus acinaciformis</i>	0.11	0.01	1.00	0.69	0.02	83	16	1	2
<i>Carpobrotus edulis</i>	0.15	0.03	0.98	0.29	0.01	81	19	0	22
<i>Oxalis pes-caprae</i>	0.26	0.02	0.98	0.01	0.13	97	1	2	0

Note: Significant values ($p \leq 0.05$) are shown in bold. Stability (S), expansion (E), and unfilling (U) were calculated within analogue climatic space, whereas pioneering (P) was calculated within non-analogue climatic space.

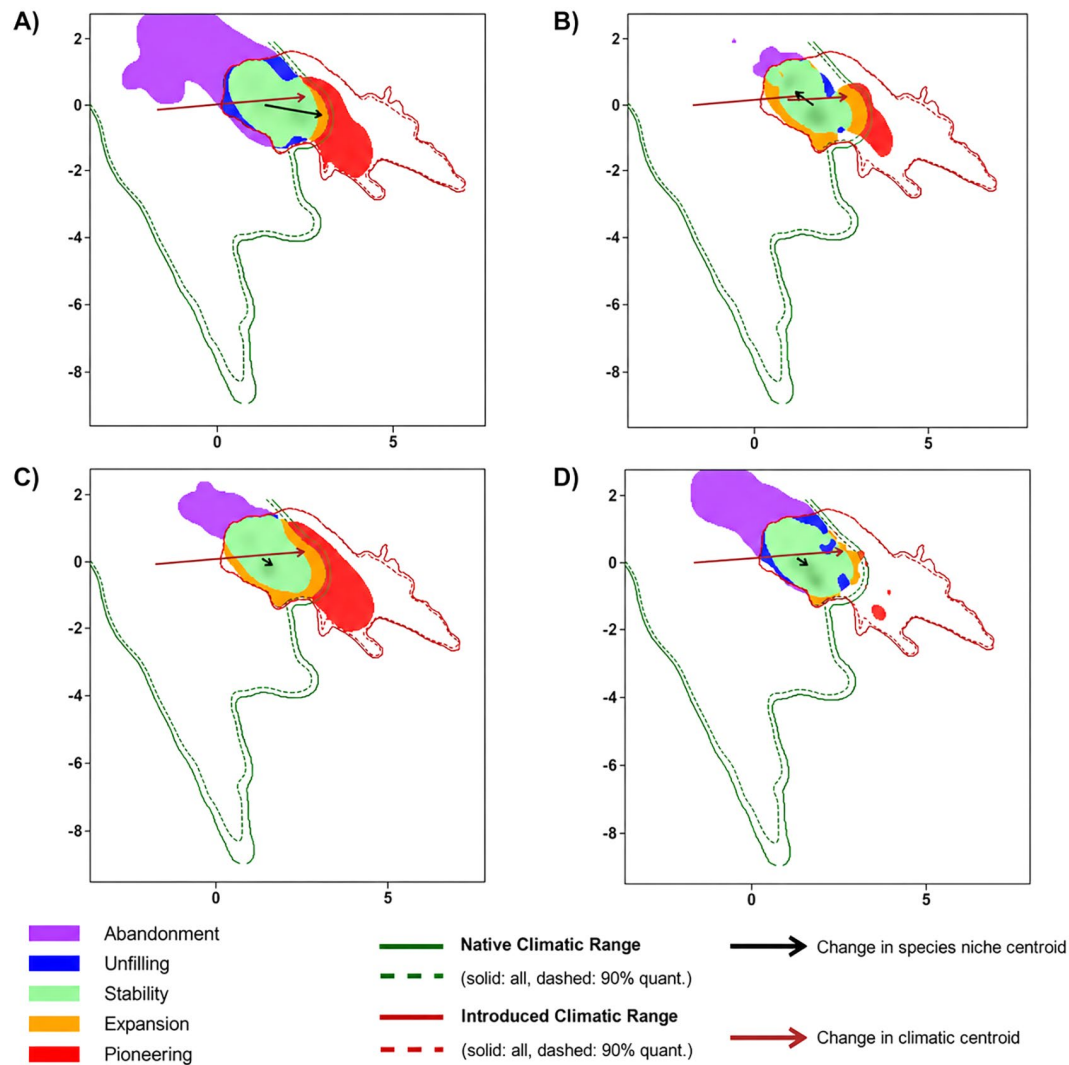


FIGURE 2 | Climatic niche of (A) *Arctotheca calendula*, (B) *Carpobrotus acinaciformis*, (C) *Carpobrotus edulis* and (D) *Oxalis pes-caprae* between the native (South Africa) and introduced (France) ranges in reduced ordination space (principal component analysis axes). Solid and dashed contour lines represent the intersection of 90% and 100% of available environments in the native (green) and introduced (red) ranges, encompassing both analogue and non-analogue climatic conditions.

BIO18) from warmer wet-season environments (negative scores; BIO8). Native-range occurrences were mainly associated with higher BIO15, BIO13 and BIO19, as well as cooler conditions during the wettest quarter (BIO8). In contrast, introduced-range occurrences were associated with a higher temperature annual range and increased precipitation during the warmest and driest periods (BIO7, BIO18, BIO14). Overall, this pattern suggests that *C. acinaciformis* occurs in cooler, seasonally wet environments with moderate precipitation variability in South Africa, whereas it has expanded into regions in France characterised by larger temperature fluctuations and wetter conditions during both warm and dry periods.

3.2.3 | *Carpobrotus edulis*

The first two PCA axes for *C. edulis* explained 66.8% of the total climatic variation (PC1 = 44.21%, PC2 = 28.11%; Figure 3C).

PC1 represented a gradient from regions with higher precipitation during the wettest (BIO13, BIO14) and warmest (BIO18) periods (positive scores) to areas with lower temperature variability and cooler wet-season conditions (negative scores; BIO2, BIO8). PC2 captured variation mainly associated with precipitation seasonality (BIO15) and precipitation during the coldest quarter (BIO19) (positive scores), contrasting with drier and warmer summer conditions (negative scores; BIO7, BIO14, BIO18). Native-range occurrences were associated with higher BIO2, BIO8 and BIO15 on the left side, whereas introduced-range occurrences were strongly associated with higher BIO13, BIO14, BIO18 and BIO19 on the right side. Overall, this pattern indicates that *C. edulis* occurs in more seasonally variable environments, with warmer wet-season temperatures and larger day-night temperature fluctuations in South Africa, whereas it has expanded into climates that are generally wetter year-round and more climatically stable in France.

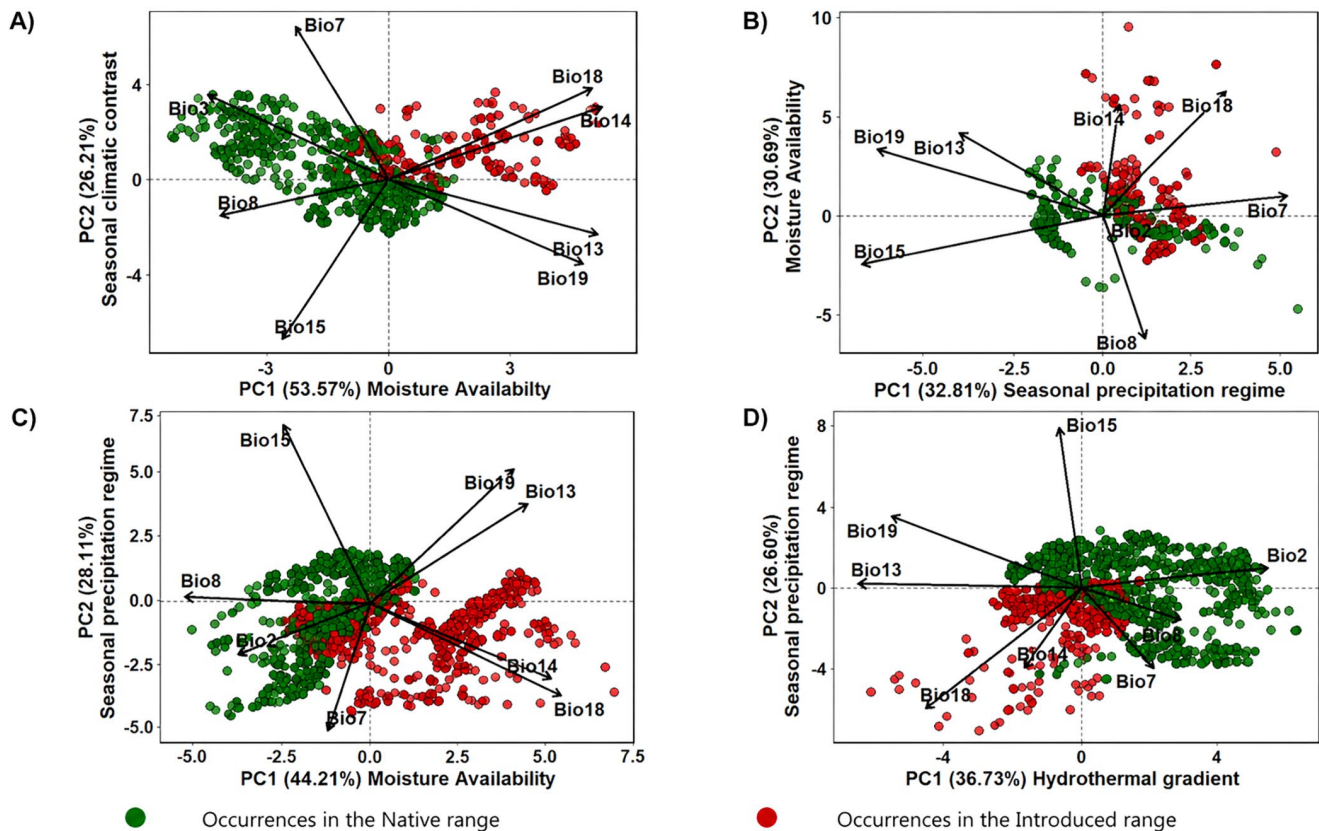


FIGURE 3 | Principal Component Analysis (PCA) showing the distribution of occurrences of (A) *Arctotheca calendula*, (B) *Carpobrotus acinaciformis*, (C) *Carpobrotus edulis* and (D) *Oxalis pes-caprae* in the native (South Africa; green) and introduced (France; red) ranges along key bioclimatic variables. Arrows indicate loadings of the eight bioclimatic variables on the first two PCA axes (PC1 and PC2), with the percentage of variance explained shown for each axis: BIO2 (Mean Diurnal Range, °C), BIO7 (Temperature Annual Range, °C), BIO8 (Mean Temperature of the Wettest Quarter, °C), BIO13 (Precipitation of the Wettest Month, mm), BIO14 (Precipitation of the Driest Month, mm), BIO15 (Precipitation Seasonality, %), BIO18 (Precipitation of the Warmest Quarter, mm) and BIO19 (Precipitation of the Coldest Quarter, mm).

3.2.4 | *Oxalis pes-caprae*

For *O. pes-caprae*, the first two PCA axes explained 63.33% of the total climatic variation (PC1 = 36.73%, PC2 = 26.60%; Figure 3D). PC1 represented a gradient from climates characterised by higher temperature variability and warmer conditions during the wettest quarter (positive scores; BIO2, BIO7, BIO8) to environments with higher precipitation across seasons (negative scores; BIO13, BIO18, BIO19). PC2 reflected variation in climatic seasonality, separating environments with stronger precipitation seasonality and higher precipitation during the coldest month (positive scores; BIO15, BIO19) from climates associated with warmer and wetter conditions during the warmest and driest periods (negative scores; BIO7, BIO14, BIO18). Native-range occurrences were mainly associated with higher BIO2, BIO8, BIO15 and BIO19, whereas introduced-range occurrences were more frequently associated with climates characterised by higher precipitation across seasons, particularly higher BIO13, BIO14 and BIO18. Overall, this pattern shows that native and introduced populations of *O. pes-caprae* occupy partially distinct portions of the climatic space defined by temperature variability, precipitation seasonality and year-round moisture conditions.

3.3 | Future Climatic Niche Availability

Spatial changes in climatic niche availability were assessed for the four assessed species for 2030 (2021–2040) and 2050 (2041–2060) under SSP2-4.5 and SSP5-8.5 scenarios within France.

3.3.1 | *Arctotheca calendula*

3.3.1.1 | SSP2-4.5 Scenario. By 2030, France encompasses extensive areas where climatic conditions remain persistently available (PA) for *A. calendula*, covering most of the country, with only limited areas of availability interruption in regions 2 (Bourgogne-Franche-Comté) and 4 (Centre-Val de Loire). By 2050, the spatial extent of PA climates contracts markedly, becoming largely confined to regions 2, 4, 6 (Grand Est) and 8 (Île-de-France). Areas classified as persistently unavailable (PU) also decrease by mid-century, although they continue to occupy substantial portions of regions 1 (Auvergne-Rhône-Alpes), 2, 4, 6, 8, 10 (Nouvelle-Aquitaine) and 13 (Provence-Alpes-Côte d'Azur). Conversely, areas experiencing a gain in climatic availability (AG) for *A. calendula* expand by both 2030 and 2050, particularly in regions 1, 3 (Bretagne), 9 (Normandie), and 10.

In contrast, areas undergoing a loss of climatic availability (AL) intensify toward mid-century, especially in regions 4, 6, 7 (Hauts-de-France), 10, 12 (Pays de la Loire) and 13. The net availability change ($NAC = AG - AL$) indicates a stronger contraction of the species' current climatic space by 2050 compared with 2030. Areas classified as uncertain (UC), reflecting temporal inconsistency in climatic availability across the current, 2030, and 2050 periods, are distributed throughout the country, with a notable concentration in region 8 (Figure 4A; Table 3).

3.3.1.2 | SSP5-8.5 Scenario. PA areas are widespread across most of the country in 2030, yet these areas shrink by 2050 remaining limited to very small patches in regions 4 and 8. PU is widespread in 2030 across regions 1, 2, 4, 8, 10, and 13, and though reduced by 2050, remains concentrated in these areas. AG increases by 2030, especially in regions 1, 3, 6, 9 and 10, and continues expanding in these regions by mid-century. AL also expands over time, concentrated in regions 2, 4, 6, 10 (Occitanie), 11, and 12. NAC indicates less overall contraction by 2050 than in 2030. UC areas appear across all regions except 4 and 12 (Figure 5A, Table 4).

3.3.2 | *Carpobrotus Aciniformis*

3.3.2.1 | SSP2-4.5 Scenario. PA areas are limited in 2030 and contract by 2050, persisting in regions 1, 5 (Corse), 6, 11, and 13. PU dominates most of France in 2030, except region 5, and remains extensive by 2050. AG areas occur mainly in regions 1, 11, and 13 by 2030, with smaller patches in regions 2, 3, 6, 7, and 9 (Normandie), expanding slightly by 2050. AL increases over time, mainly in regions 2, 4, 6, 9, 11, and 13. NAC shows moderate range contraction by 2030, continuing more gradually toward 2050. UC emerges mainly in regions 1, 8, 10, and 11 by 2050 (Figure 4B; Table 3).

3.3.2.2 | SSP5-8.5 Scenario. PA areas are more limited than under SSP2-4.5, occurring in the same core regions, with smaller patches in regions 2 and 4 by 2030, and contracts further by 2050. PU again dominates most of the country, except region 5, and despite a slight reduction, remains the largest class. AG appears in regions 2, 3, 6, 7 and 9 and expands slightly by mid-century, whereas AL also increases over time, concentrated in regions 2, 4, 6, 9, 11 and 13. NAC shows less range contraction by 2050 than by 2030. UC is mainly distributed across regions 1, 2, 6, 9, 10, and 11 (Figure 5B; Table 4).

3.3.3 | *Carpobrotus edulis*

3.3.3.1 | SSP2-4.5 Scenario. By 2030, PA covers ~50% of France, mainly in coastal regions 3, 7, 9, 11, and 13, as well as region 5, but contracts by 2050 to smaller patches in the same regions. PU is limited in 2030 to regions 1, 2, 4, 6, 10, 11, and 13, declines further by 2050, and remains absent from regions 5, 7, 9, and 12. AG increases by 2030 and expands across most regions, except 4 and 8, whereas AL is already substantial and intensifies by 2050, becoming the dominant dynamic with remaining patches in regions 7 and 9. NAC indicates a small contraction by 2030 that increases by 2050. UC appears in mid-century across most regions, except 4 and 8 (Figure 4C; Table 3).

3.3.3.2 | SSP5-8.5 Scenario. *C. edulis* shows relatively lower PA areas under SSP5-8.5 than under SSP2-4.5 (Table 4) by 2030, occurring broadly across the French landscape. However, these areas are projected to decrease by mid-century, becoming more spatially restricted. PU is substantial in 2030 but declines by 2050, persisting strictly in regions 1, 2, 4, 6, 11 and 13. AG is limited, mainly in regions 4, 8 and 12, with little change by mid-century, while AL is already pronounced in 2030 and increases slightly, becoming the second dominant dynamic. NAC indicates overall loss in both periods, stronger in 2030 than in 2050. UC persists by 2050, scattered across the landscape (Figure 5C; Table 4).

3.3.4 | *Oxalis pes-caprae*

3.3.4.1 | SSP2-4.5 Scenario. PA is limited and continues to decline toward mid-century, while remaining restricted to regions 1, 5, 10, 11 and 13. PU dominates most of the country in 2030 and, although it contracts by 2050, remains the largest class across the landscape, except for region 5. AG is present in regions 1, 3, 9, 11 and 13 and increases slightly by mid-century, particularly around regions 1 and 3. AL is limited but increases slightly over time, indicating a gradual rise in loss-related dynamics. Interestingly, NAC indicates a slight net availability expansion in 2030, followed by a slight net contraction by 2050. UC areas persist by mid-century, representing the lowest percentage among all assessed species (Figure 4D, Table 3).

3.3.4.2 | SSP5-8.5 Scenario. By 2030, *O. pes-caprae* maintains a limited extent of PS, which becomes even more restricted by mid-century, persisting predominantly in regions 1, 5, 11 and 13. PU covers most of the landscape in 2030 and, despite a slight contraction by 2050, remains the dominant suitability class across the metropolitan area. AG appears in regions 2, 3, 6, 7 and 10 and shows a slight increase toward mid-century. AL becomes more pronounced over time, especially in regions 2, 4, 6, 8, 11 and 13. As a result, and in contrast to the SSP2-4.5 scenario, NAC indicates a minor net availability contraction in 2030, followed by a moderate net expansion by 2050. UC areas will persist, scattered across the country by 2050 (Figure 5D, Table 4).

4 | Discussion

In the present study, the niche dynamics of four South African species (*A. calendula*, *C. acinaciformis*, *C. edulis* and *O. pes-caprae*) in France were quantified to determine whether they conserved their climatic niches or shifted to novel climatic conditions following their introduction. Comparisons between native (South Africa) and introduced (France) ranges under analogue climatic conditions revealed high levels of niche stability across all species, together with frequent but generally small-magnitude shifts, with very limited to low cases of climatic niche overlap. Low niche overlap (Schoener's *D*) values combined with high stability (*S*) of introduced niches (Table 2) are uncommon, but similar patterns have been reported in previous studies on non-native species (Pili et al. 2020; Montagnani et al. 2022; Riera et al. 2025; Lozano et al. 2026). For example, Montagnani et al. (2022) found high

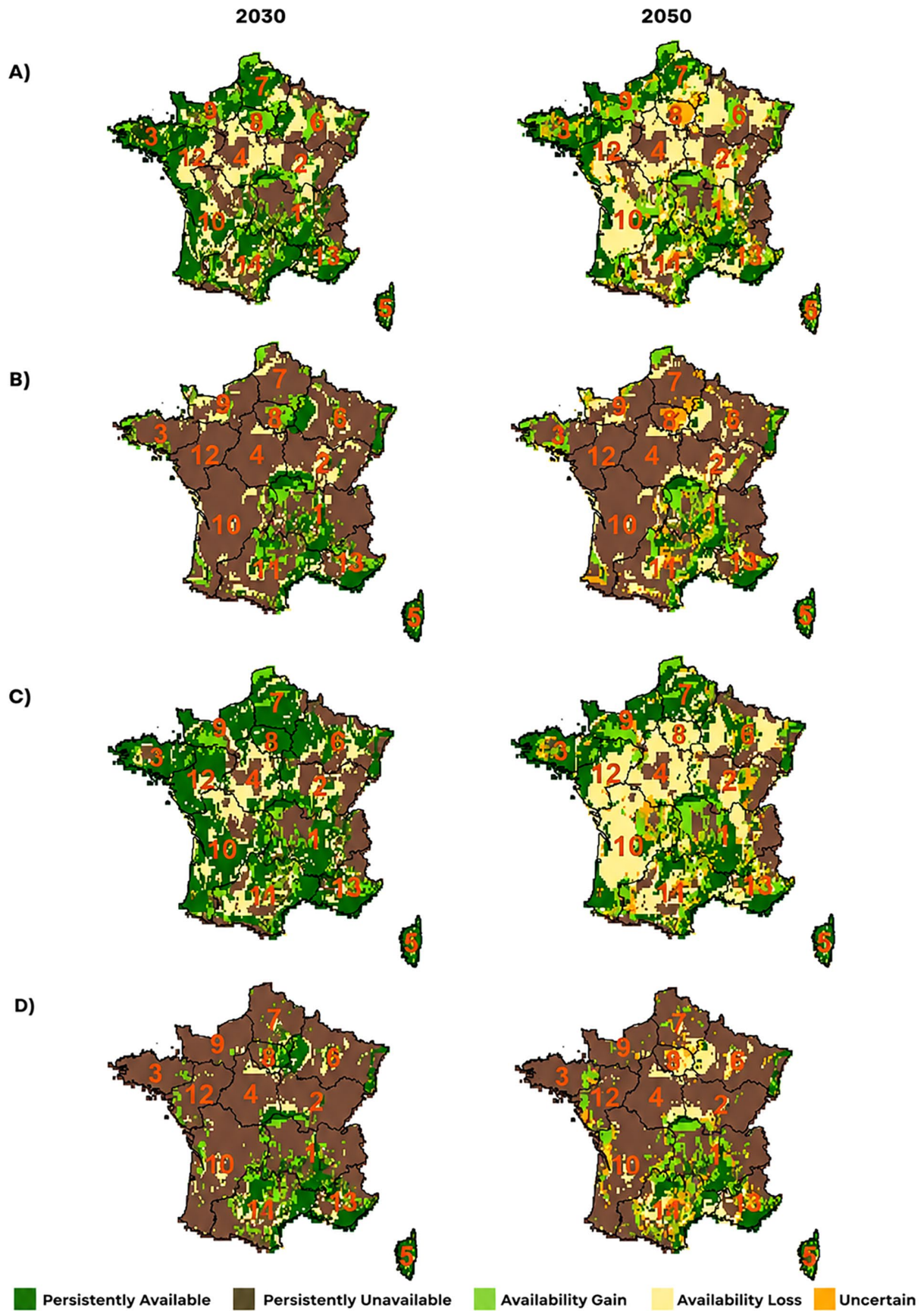


FIGURE 4 | Legend on next page.

FIGURE 4 | Spatial changes in the availability of climatic conditions analogous to the current invaded niche across France under the SSP2-4.5 scenario for (A) *Arctotheca calendula*, (B) *Carpobrotus acinaciformis*, (C) *Carpobrotus edulis* and (D) *Oxalis pes-caprae* in 2030 and 2050. Numbers refer to the 13 administrative regions of metropolitan France: (1) Auvergne-Rhône-Alpes; (2) Bourgogne-Franche-Comté; (3) Bretagne; (4) Centre-Val de Loire; (5) Corse; (6) Grand Est; (7) Hauts-de-France; (8) Île-de-France; (9) Normandie; (10) Nouvelle-Aquitaine; (11) Occitanie; (12) Pays de la Loire; (13) Provence-Alpes-Côte d'Azur.

S and very low Schoener's *D* values in the Asian vine *Pueraria lobata* (kudzu) introduced to Europe, indicating that the introduced niche is nested within the native one. Consistent with this pattern, our results show that although the climatic niche occupied by South African species in France is largely included within their native niche (high stability), the species use only a restricted subset of these native climatic conditions. Moreover, the climates occupied in France fall within suboptimal conditions relative to the native range, resulting in low niche overlap. Furthermore, while niche *S* was the dominant component of niche conservatism across all species under analogue climatic conditions, niche expansion (*E*) generally exceeded niche unfilling (*U*). Niche pioneering (*P*) also appears to contribute to the presence of *A. calendula* and *C. edulis* in France when considering non-analogue climatic conditions.

When analysing the climatic drivers of species presence in the native and introduced ranges, these two species are expanding into rainfall conditions during the summer months (BIO14,18) and more climatically stable environments, suggesting tolerance of climatic conditions not represented in the native range. A comparable pattern was reported for *C. edulis* in Spain, where Fenollosa and Munné-Bosch (2019) documented expansion into colder regions. Taken together, these findings suggest that *C. edulis* is not strictly constrained by the climatic limits of its South African origin, but instead exhibits niche flexibility that likely contributes to its successful establishment across Europe. These findings align with growing evidence that non-native plant species can expand into novel climatic conditions beyond those observed in their native distributions (D'Amen and Azzurro 2020; Pili et al. 2020; Carlin et al. 2023). One possible explanation is that many newly introduced species may expand either by acclimatising to new climatic conditions and other abiotic factors (Bujan et al. 2021; Abdallah et al. 2022) and/or by evolving novel local adaptations that enable them to spread beyond the environmental conditions of their native range (Colautti and Barrett 2013; Gallien et al. 2016). Besides, the capacity for greater expansion, and even niche pioneering, may be particularly pronounced in species with relatively narrow realised native climatic niches (Pili et al. 2020; Carlin et al. 2023; Riera et al. 2025).

The niche similarity test indicated climatic niche conservatism for the four assessed South African species in France. In contrast to the assumption that rapid local adaptation or acclimatisation promotes invasion success in non-native species (Colautti and Barrett 2013; Lancaster et al. 2015; Bujan et al. 2021), our results suggest that invasion success could be strongly associated with climatic niche conservatism but also with niche shift (Liu et al. 2020; Morente-López et al. 2023; Fenollosa et al. 2025; Riera et al. 2025; Rönnfeldt et al. 2026). The niche equivalency test, in contrast, showed that only three species (*A. calendula*,

C. acinaciformis and *C. edulis*) exhibited non-equivalent climatic niches between their native and introduced ranges. This suggests that, even though the introduced climatic space is not different enough from the native to reject niche conservatism, species do occupy somewhat different environmental conditions in the introduced area. Together, these results indicate that for those species, there are significant dynamics toward niche expansion and pioneering. However, the interpretation of niche dynamics within the *Carpobrotus* complex must be considered in light of the long-standing taxonomic uncertainty surrounding *C. edulis* and *C. acinaciformis*. Such taxonomic complexity may blur ecological boundaries between taxa and potentially enhance environmental tolerance through hybrid vigour or introgression. Future studies integrating genomic approaches with niche modelling would help disentangle the relative contributions of taxonomic uncertainty and hybridisation in shaping the invasion dynamics of the *Carpobrotus* complex.

In contrast to the patterns observed for the other species, *O. pes-caprae* exhibited a distinct niche dynamic. The niche equivalency test indicated full equivalence between its native and introduced climatic niches, and not expansion or pioneering. This strong climatic niche conservatism may be explained by the species' broad realised niche in its native range, which likely allows it to occupy suitable environments in the introduced range without requiring substantial expansion or pioneering (Cao Pinna et al. 2025). These results highlight that, while niche dynamics are not uniform across species, the South African species show both evidence of niche conservatism and dissimilarity in France. Such variation likely reflects species-specific invasion strategies, suggesting that climatic pre-adaptations, as inferred from biogeographic origin, are not the sole determinants of niche dynamics in non-native species. Species' ecological characteristics, eco-evolutionary mechanisms and native niche breadth may also represent key drivers of niche differentiation across ranges (Bates et al. 2020; Bujan et al. 2021; Sychrová et al. 2022; Cao Pinna et al. 2025).

Integrating knowledge of invasive species' climatic niche dynamics across spatio-temporal spaces enables researchers and environmental managers to forecast potential geographical invasion risks and identify areas where these species may enter, establish, spread and cause significant impacts. Our climate change projections also suggest species-specific responses under both SSP2-4.5 and SSP5-8.5 climatic scenarios. *Arctotheca calendula* and *C. edulis* emerge as the most climatically dynamic and potentially concerning under future scenarios, given their extensive current climatic occupancy and high projected turnover under both scenarios. Although their net availability declines by mid-century, the simultaneous occurrence of availability gains in western and transitional regions and losses in currently available areas indicates dynamic redistribution rather than simple contraction. In

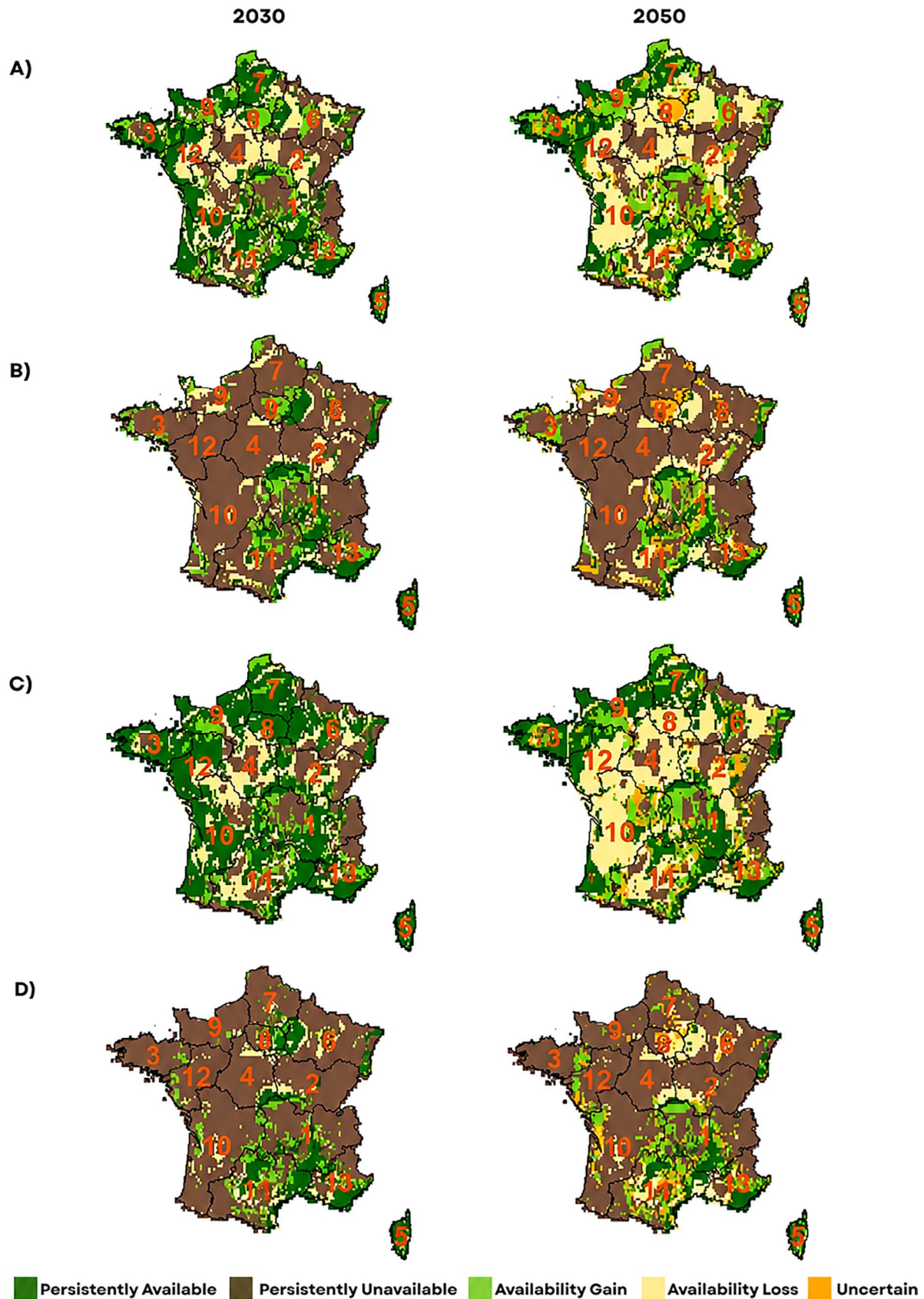


FIGURE 5 | Spatial changes in the availability of climatic conditions analogous to the current invaded niche across France under the SSP5-8.5 scenario for (A) *Arctotheca calendula*, (B) *Carpobrotus acinaciformis*, (C) *Carpobrotus edulis* and (D) *Oxalis pes-caprae* in 2030 and 2050. Numbers refer to the 13 administrative regions of metropolitan France: (1) Auvergne-Rhône-Alpes; (2) Bourgogne-Franche-Comté; (3) Bretagne; (4) Centre-Val de Loire; (5) Corse; (6) Grand Est; (7) Hauts-de-France; (8) Île-de-France; (9) Normandie; (10) Nouvelle-Aquitaine; (11) Occitanie; (12) Pays de la Loire; (13) Provence-Alpes-Côte d'Azur.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Climatic availability dynamics in principal component analysis (PCA) space under SSP2-4.5, comparing current conditions with projections for 2030 and 2050 for (A) *Arctotheca calendula*, (B) *Carpobrotus acinaciformis*, (C) *Carpobrotus edulis* and (D) *Oxalis pes-caprae* in the introduced range (France). Grid cells were classified as Persistently Available (inside both current and future climatic niches), Persistently Unavailable (outside in both periods), Availability Gain (outside under current conditions but inside in the future), Availability Loss (inside under current conditions but outside in the future) or Uncertain (marginal areas showing inconsistent climatic availability across time periods, for example, inside in the present and 2050 but outside in 2030, or vice versa).