Herbarium specimens reveal long-term decline in pollination services since in the 1970s

Bofeng Song[1,2], Heidi Zimmer[3], Mark Clements[3], Demetra Rakosy[4,5,6], Tiffany Knight[5,6,7,8], Joanne Bennett[9,1]*

1. Fenner School of Environment & Society, The Australian National University, Canberra, Australian Capital Territory, Australia
2. School of Biological Sciences, The University of Western Australia, Perth, WA,Australia
3. Centre for Australian National Biodiversity Research (Joint Venture Between Parks Australia and CSIRO), GPO Box 1700, Canberra, ACT, 2601, Australia
4. Thünen-Institute of Biodiversity, Braunschweig, Germany
5. German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany
6. Department of Community Ecology, Helmholtz Centre for Environmental Research—UFZ, Leipzig, Germany
7. Department of Science and Conservation, National Tropical Botanical Garden, 19 Kalāheo, HI, USA
8. Institute of Biology, Martin Luther University Halle-Wittenberg, Halle, Germany
9. Gulbali Institute, Charles Sturt University, Elizabeth Mitchell Drive, Albury, NSW, Australia

Author Email and Orcid

Bofeng Song: bofeng.song@research.uwa.edu.au (0009-0000-2000-2036)

Heidi Zimmer: heidi.zimmer@csiro.au (0000-0002-8496-7360)

Mark Clements: maclem1917@gmail.com (0000-0001-7478-5064)

Demetra Rakosy: demetra.rakosy@gmail.com (0000-0001-8010-4990)

Tiffany Knight: tiffany.knight@idiv.de (0000-0003-0318-1567)

Joanne Bennett: joabennett@csu.edu.au (0000-0002-7883-3577)

*Corresponding author: e.roseicapilla@gmail.com

Abstracts

Anthropogenic change has resulted in pollinator decline and altered plant-pollinator interactions. This may drive widespread declines in pollination and reproductive success of plants, yet few datasets allow us to track changes in pollination services over time. Herbaria provide a unique opportunity to assess pollination services across broad spatial and temporal scales, and the associated spatiotemporal anthropogenic change. We quantified changes in pollination services to the orchid genus *Caladenia* over the past century, a period of rapid land-use intensification and climate change in Australia. Examining 10,494 *Caladenia* flowers preserved at the Australian National Herbarium showed a reduction in pollination services totaling > 60 % over the whole study period, with rapid declines occurring post 1970. Declines in pollination services occurred across species pollinated by different taxa and threat status. Sexually deceptive species had more pronounced declines in pollinator services. Historical land-use change, and rising temperatures varied by region and were significant predictors of pollination service decline. Our findings provide rare evidence of declines in pollination services modulated by pollination syndrome and demonstrate the value of herbarium collections in understanding global change.

Key words: Orchidaceae, pollination, food deception, sexual deception, herbarium.

Introduction

Pollination is vital to the reproduction of ~90 % of flowering plants (Rodger et al., 2021). Global evidence suggests that pollinators may be particularly vulnerable to human disturbance (Potts et al., 2016), raising concerns that this reduction in pollinator services and associated reductions in plant reproductive success can lead to extinctions, reductions in plant diversity and shifts in plant composition towards less pollinator dependent plant species. Indeed, on a global scale, plant reproduction has been shown to be more pollen-limited in areas with high-intensity land use (Bennett et al., 2020). There is growing evidence that high intensity farming practices characterized by reduced floral diversity, fragment habitats and heavy reliance on synthetic inputs such as pesticides are having detrimental effects on pollinators and pollination (Goulson, 2013). Climate change, and its interactions with agricultural intensification, poses an existential threat to pollination services (Settele et al., 2016). Changes total rainfall can influence numbers of flowers and nectar volume (Kuppler and Kotowska, 2021), while changes to timing of rainfall can influence flowering phenology (Van Dyke and Kraft, 2025). Most evidence of disrupted pollinator services is found in studies that compare across plant populations or across relatively short time periods in well studied regions. Direct evidence of declines in pollination services across longer time periods, relevant for understanding shifts in land-use and climate are rare (Rakosy et al., 2023).

Herbaria hold collections spanning decades or centuries, which can be used to document spatial and temporal changes in pollination services (Rakosy et al., 2023). Data on rates of pollen transfer and ovary fertilization across multiple species and spatial scales has so far been rarely assessed (Rakosy et al., 2023). The family Orchidaceae is well-represented within herbaria worldwide. Orchidaceae encapsulates extraordinary floral diversity, corresponding to their diverse and often highly specialized pollination systems (Cozzolino and Widmer, 2005). Pollinator attraction relies on rewards in 54% of orchid species, and deceit in 46% of species, with orchids generally forming highly specialized relationships with individual pollination species (Ackerman et al., 2023). Orchids, with a few exceptions, package pollen grains into pollinia that can be released through pollinator contact. The removal of the leaves an empty clinandrium (i.e. the part of the orchid column which houses the pollinia) which means pollen collection via a vector can be observed even in dried specimens. For example, historical pollinarium removal rates were assessed for in *Pterygodium catholicum*, collected on Signal Hill, South Africa, from the late 19th century to 1950, revealing a decline over time (Pauw and Hawkins, 2011).

The Australian orchid genus *Caladenia* is relatively well represented across space and time in herbaria. There are around 288 species of *Caladenia* (Jones, 2021), including 137 nationally threatened species (DCCEEW, 2025), more than any other orchid genus in Australia. The genus encapsulates diverse pollination strategies, including self-compatibility, food and sexual deception, and strategies intermediate among these (e.g., attracting pollinators using sexual deception but also providing tiny amounts of sugar on the labellum) (Phillips et al., 2020a, Phillips et al., 2023). Thynnid wasps and bees are key pollinators, with the former common in food and sex-deception, and the latter in food deception. Using specimens at the Australian National Herbarium (ANH) from the 1920s to today, we assessed long-term changes in pollination services of *Caladenia* species. We compared this with potential drivers of change, including climate (deviations in temperature, total rainfall and rainfall seasonality) and human land-use intensity/footprint and whether observed changes were modulated by pollination strategy, pollinator taxonomic groups or threat status.

Methods

We accessed 2,125 herbarium specimen sheets and examined 10,494 *Caladenia* flowers from the collection at the ANH. The dataset for this study included a total of 25 species. These species were selected because they were the most well represented in the herbarium (each had more than 10 sheets) and represent different pollination strategies and major pollinator groups.

Assessment of pollination services success

For each herbarium sheet, flower was labeled sequentially. Location information (latitude and longitude) and year of collection for each specimen was recorded from the specimen label. Only fully open flowers, accessible to potential insect visitors, were considered in this study. For open flowers we determined if pollinia were completely or partially absent from the clinandrium (where the anther is located) as evidence of pollination services for male reproduction. For partially removed pollinia, we determined whether the removal was likely insect-related or caused by human handling. Pollinia breakage caused by insects is typically characterized by irregular or messy partial removal, consistent with the action of insect mouthparts or feet. Conversely, pollinia breakage caused by human handling was identified by distinct patterns such as tweezer punctures or straight cuts. In rare cases, damage could also occur during the mounting process, such as when cotton threads used during specimen preparation adhered to the anther caps. These criteria ensured that we could reliably distinguish between insect-related and human-related damage during our assessments.

To cross-validate data on pollinia removal, we also collected information on pollination services to female reproductive parts. Specifically, we recorded pollen was present on the stigmatic surface as supporting evidence of pollinator visitation, or if there was evidence of ovary fertilization assessed via a clear enlargement of the ovary's width (Figure S1). We also recorded if insect parts were present on the stigma, but this data was not used in analysis. All lines of evidence of pollination services were highly correlated. Most of the data was evidence for services to male reproduction N = 5861 (pollinium removal), with N = 954 records of pollination services to female reproduction (ovary fertilization and pollen on stigmas).

Pollination Strategy and Taxonomic Specialization

For each species, we determined subgenera, pollination strategy, and major pollinators based on the literature (Table S2). The dataset comprised one self-pollinating species (*C. alata*), 15 food-deceptive species, and 9 sexually deceptive species. For the analysis of pollination strategies, species with sexual deception and food deception were represented across the full dataset (1925–2020), while the self-pollinating species only had sufficient data starting from 1980. In *Caladenia*, there were three main ecological specializations: species that were primarily pollinated by either bees, wasps, or flies. Species for which specialization could not be determined or where uncertain (e.g. multiple pollinators were indicated but unknow) were excluded from analysis

Threat status

Species were denoted as threatened if they were listed regionally or nationally on the species profile and threat database under the Environment Protection and Biodiversity Conservation Act 1999 (DCCEEW, 2025) . If not listed they were assigned as unthreatened.

Data Analysis

To examine changes in pollination services through time, across all species, for pollinator dependent species (e.g. all species except self-compatible) and for species with differing pollination strategies and major pollinator taxonomic groups, we used GAMM (Generalized Additive Mixed Models) fitted using the *mgcv* package (Wood, 2001)) in R (R Core Team, 2025). To account for phylogenetic effects and species-specific variability, nested random effects were included in the models. Specifically, the random effects were defined as subgenera (Subgenus) as a random intercept and species nested within subgenera (Species | Subgenus) to capture within-group variation. The full dataset spanned from 1887 to 2020 and included 10,241 accessible flowers (Figure S2); however, due to the small sample size prior to 1925, the focus of the analysis was on the period from 1925 to 2020 (n = 10,178). To evaluate differences in pollination services percentages across pollination strategies, a one-way analysis of variance (ANOVA) was conducted. Post-hoc Tukey HSD tests were performed to compare the mean differences between self-pollinating, food-deceptive, and sexually deceptive species. A Kruskal-Wallis test was performed to assess differences in the median pollination services among pollinator groups (bees, wasps, and flies) during specific time periods. Post-hoc comparisons were conducted to evaluate pairwise differences between groups.

Segmented regression analysis, applied to subsets of the data, was also performed to identify data-driven breakpoints in the temporal trends of pollination services. Using the *segmented* package in R, this method allowed for the detection of significant shifts in trends and the estimation of breakpoints in a data-driven manner (Muggeo, 2008). This analysis was applied not only to the overall dataset but also to subsets categorized by pollination strategies and taxonomic specialization. Additionally, segmented regression was independently conducted for each pollination strategy (e.g., self-pollination, food deception, sexual deception) and major pollinator groups (e.g., bees, wasps, flies), enabling the identification of subgroup-specific breakpoints and temporal trends. By detecting year-specific breakpoints and assessing trend changes within each subgroup, this segmented regression approach provided a complementary perspective to GAMM.

To explore potential correlations between changes in pollination services with climate, we extracted data from the Bureau of Meteorology (BOM, 2024b, BOM, 2024a) on temperature and rainfall anomalies for specimen using the location and year of study. Climate anomalies are a measure of the deviations in mean baseline conditions. For rainfall in addition to the annual deviation in rainfall for the collection location, we placed records into the seasonal rainfall zones of Australia, and extracted rainfall anomalies for the dominate periods of rainfall for that location, summer or winter respectively. We used GLM (Generalized Linear Model) to account for temporal trends across the study period.

Land-use intensity was taken from the human footprint index, which is a remotely sensed composite of the extent of human impact on the environment scaled from 0 to 1 (Venter et al., 2016). The index weights human pressures including the extent of built environment and infrastructure, human population density, light pollution and extent of crops and pastures based on their impact on the environment (Venter et al., 2016). The *raster* package in R was used to process and extract spatial raster data for the human footprint index, enabling precise alignment of spatial data with corresponding specimen locations (Hijmans et al., 2015). The *sf* package facilitated the handling and manipulation of spatial vector data, such as specimen collection points, ensuring accurate integration of geographic and environmental datasets (Pebesma, 2018). A GLM with a Gaussian distribution and identity link function was applied to assess the effects of year, human footprint index, and their interaction on pollination services within the human-footprint model.

Results

Overview of *Caladenia* pollination services

The full dataset spanned from 1887 to 2020 (Figure S2). Due to the small sample size prior to 1925, we focused our main analysis on the period 1925 to 2020 (*n* = 10,115) but see supplementary material for the full dataset analysis. Pollination services GAMM identified a significant relationship between pollination service and year (F = 3174, R^2(adj) = 0.742, EDF = 8.936, p < 0.001), with an estimated decline in pollination service between the 1925 to 2020 of 61 %. Segmented regression identified 1977 (± 5.6 years) as a significant breakpoint in pollination services. Before 1977, there was no statistically significant relationship observed between year and pollination services (t = 1.352, SE = 0.0013, df = 79, *p* = 0.180). After 1977, a significant negative relationship was observed, with pollination services declining by 0.76% annually (t = -4.609, SE = 0.0020, df = 79, *p* < 0.001).

Investigation of different pollination strategy and ecological specialization

Mean pollination service differed between species with according to pollination strategy (F(2, 10066) = 7.39, p < 0.001). Sexually deceptive species exhibited the highest median pollination services, while self-pollinating species had the lowest. Pairwise comparisons revealed a significant difference in pollination services between sexual deception and food deception, whereas other comparisons were not significant. (Table S1).

The relationship between pollination services and year differed markedly across pollination strategy (F(2, 9950) = 14.42, $p < 0.001$). For food-deceptive species (n = 10,131 sampled flowers), there was an estimated overall decline in pollination services between 1925 to 2020 of 58% (F(8.96, 10122) = 2065, EDF = 8.956, R^2(adj) = 0.635, $p < 0.001$). A significant breakpoint occurred at 1976 (± 6.38 years). Before 1976, pollination services showed no significant relationship with year (t = 1.159, 95% CI: −0.002 to 0.006, $R^2 = 0.033$, p = 0.250). After 1976, pollination services showed a significant relative decline rate of 0.68% per year (t = −4.230, 95% CI: −0.010 to −0.004, $R^2 = 0.281$, $p < 0.001$) (Figure 1a).

For sexually deceptive species (n = 1,671 sampled flowers, one species), there was an estimated overall decline of 99.32% between 1925 to 2016 (there was insufficient replication in 2020 to calculate the % decline) (F(8.61, 9) = 126.3, EDF = 8.61, R^2(adj) = 0.392, p < 0.001). A significant breakpoint occurred at 1988 (± 8.42 years). Before 1988, pollination services showed no significant relationship with year (t = −0.960, 95% CI: −0.00820 to 0.00288, $R^2 = 0.033$, p = 0.341). After 1988, pollination services showed a significant relative decline rate of 1.76% per year (t = −2.932, 95% CI: −0.02959 to −0.00558, $R^2 = 0.326$, p < 0.01) (Figure 1b).

For self-pollinating species (n = 199 sampled flowers), there was a significant relationship between pollination services and year (F(8.99, 197) = 556.9, EDF = 8.97, R^2(adj) = 0.440, p < 0.001). Segmented regression identified a breakpoint in 1994 (±4.2 years) but it was not significant, and the relationship between pollination services remained similar across periods (Figure 1c).

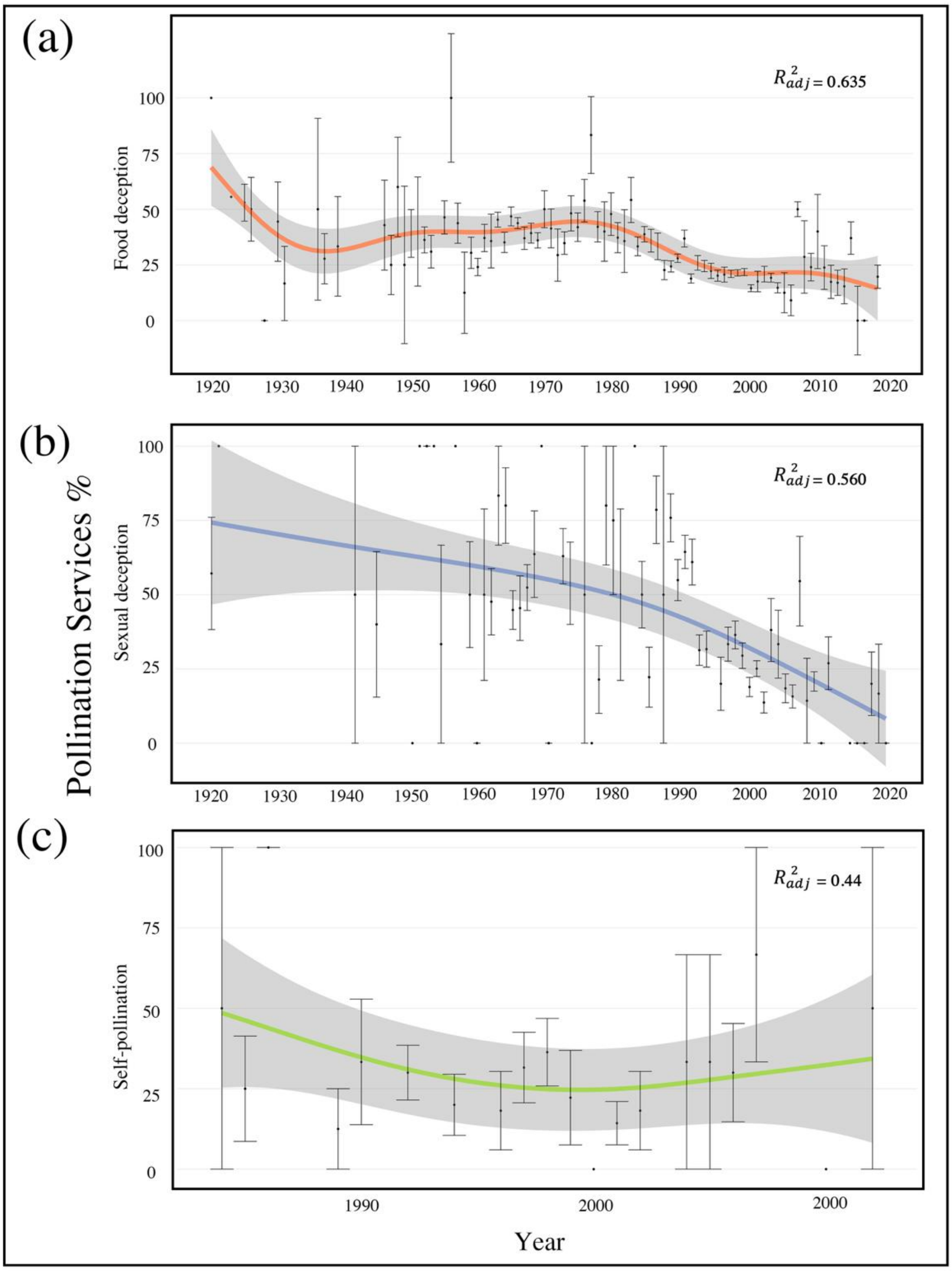

Figure 1. Historical trends of pollination service over time for different pollination strategy. (a) represents the trend for food-deceptive species, (b) represents the trend for sexually deceptive species, and (c) represents the trend for self-pollinating species. Black data points and error bars indicate the average pollination service success and standard error for each year. The colored lines represent the predicted trend for each pollination strategy based

on a GAMM, with the grey shaded area showing the 95% confidence intervals for these predictions.

A Kruskal-Wallis test showed significant differences in median pollination services among wasps, bees, and flies (taxonomic groups), identified as the primary pollinator group from published texts (see Table S2) across the whole period ($X^2 = 16.023$, df = 2, $p < 0.001$). Pairwise Wilcoxon rank-sum tests with Benjamini-Hochberg correction indicated marginally higher pollination services for species pollinated primarily by bees compared to wasps (W = 7,470,868, $p = 0.05$), while species pollinated by flies and wasps did not differ significantly (W = 4,348,442, $p = 0.657$). Likewise, pollination services for *Caladenia* pollinated by bees and flies were not significantly different (W = 2,541,630, $p = 0.236$).

For the period 1925–2020, pollination services were estimated to have declined by 51.6% for species pollinated by wasps, 61.7% for species pollinated by bees, and 50.7% for species pollinated by flies. The relationship between pollination services and year was significant for all groups: wasps (n = 2,698, EDF = 8.85, F = 644, R^2(adj) = 0.678, $p < 0.001$), bees (n = 7,394, EDF = 8.894, F = 2792, R^2(adj) = 0.773, $p < 0.001$), and flies (n = 1,043, EDF = 8.677, F = 378.9, R^2(adj) = 0.760, $p < 0.001$) (Figure S3).

For species pollinated by wasps, a breakpoint occurred in 1983 (±7.53 years). Before 1983, there was no significant relationship between pollination services and year (t = 0.176, 95% CI: −0.005 to 0.006, $p = 0.860$). After 1983, pollination services showed a significant annual decline of 1.35% per year (t = −3.36, 95% CI: −0.022 to −0.006, $R^2 = 0.250$, $p < 0.01$).

For species pollinated by bees, a significant breakpoint was identified at 1977 (±8.69 years). Before this breakpoint, pollination services showed no significant relationship with year (t = 0.301, 95% CI: −0.003 to 0.004, p = 0.764). After 1977, pollination services showed a significant annual decline of 0.66% per year (t = −3.45, 95% CI: −0.010 to −0.003, R^2 = 0.237, $p < 0.01$).

For the one species pollinated by flies, a breakpoint was identified in 1948 (±44.77 years). Before this breakpoint, pollination services showed no significant change (t = 0.290, 95% CI: −0.084 to 0.112, p = 0.773). After 1948, pollination services showed a significant annual decline of 0.72% per year (t = −4.41, 95% CI: −0.010 to −0.004, R^2 = 0.241, $p < 0.001$).

The decline in pollination service was similar across threat status. For listed species (n = 2975), the total decline from 1925 to 2020 was 63.2% (R^2 = 0.70, edf = 8.87, F = 774.1, $p <$ 0.001), while for unlisted species (n = 7202), the total decline was 58.52% (R^2 = 0.771, edf = 8.87, F = 2654, $p < 0.001$) (Fig. S4). There was an interaction term between year and threat status (SE = 0.001, t = 3.015, $p < 0.05$) indicating that while the average rates of decline were comparable, the shape or timing of change in pollination differed between listed and unlisted species. But breakpoint analysis showed overlapping breaks. In listed species, the breakpoint occurred in 1983 (±18.2 years), where there was no significant relationship between pollination services and year prior to the breakpoint (t = −0.87, 95% CI: −0.008 to 0.003, p = 0.385) and after there was a significant decline of 0.789% per year (t = −2.29, 95% CI: −0.015 to −0.001, R^2 = 0.229, $p < 0.05$). In unlisted species, the breakpoint occurred 1977 (±4.2 years), before the breakpoint there was a significant positive relationship between pollination services (t = 2.70, 95% CI: 0.001 to 0.006, p = 0.008), after 1977, pollination services declined by 0.805% per year (t = −5.61, 95% CI: −0.011 to −0.005, $R^2 = 0.402$, $p < 0.001$).

Environmental predictors of pollination services

Using GLM, we found a significant negative correlation between temperature anomaly and pollination services (t = -5.72, SE = 0.025, df = 84, $p < 0.001$), with pollination services decreasing by approximately 0.145 for every 1° C increase in temperature anomaly.

Pollination services were not correlated with annual rainfall anomalies (t = 0.253, SE = 0.001, df = 84, $p = 0.801$). Pollination services were not correlated with rainfall anomalies in the dominate rainfall period of collection location, which were summer (t = –0.966, SE = 0.001, df =6, p = 0.338) and winter (t = 0.916, SE =0.001, p = 0.363).

Human footprint had a significant relationship with pollination services, where areas with higher human footprint had significantly lower pollination services compared to those with a lower human footprint (estimate = 0.0002, t = 2.28, $p = 0.023$) (Table S3, Figure S5). Using a GLM with an interaction term, we found a significant interaction between human footprint and year on pollination services, where environments with a lower human footprint experienced a greater decline in pollination services over time (estimate = 9.071e-05, t = 2.26, $p = 0.024$) (Table S3, Figure S5).

Discussion

Pollination services for *Caladenia* have experienced a decline since the 1970s. This decline was modulated by pollination strategy, with species relying on sexual deception showing the fastest rate of decline, followed by food deception, while the self-pollinating species did not exhibit a decline. Species pollinated by different pollinator taxa experienced similar declines, but our result highlight that more data is required to answer this question. Decline in pollination services for *Caladenia* was correlated with increased temperature, indicating a potential impact of climate change on pollination services. Increased human footprint was also associated with a lower mean pollination service for *Caladenia* when considering data across all years. There was also an interaction between time and human footprint, with orchids in less human-impacted sites experiencing greater declines in pollination service though time. This suggests that widespread environmental changes, such as climate, may be the primary drivers behind declines in pollination services for orchids but other environmental factors for which data is unobtainable are also likely at play.

Pollination services to the single self-pollinating species showed no distinct temporal patterns, which may reflect its reduced vulnerability to fluctuations in pollinator populations or may simply reflect the limited sample size in this study for this pollination strategy, especially before 1980. There are risks associated with relying on self-pollination, as self-pollination can lead to reduced genetic diversity, increasing the risk of genetic drift and inbreeding depression (Goodwillie et al., 2005). Therefore, while self-pollination may currently provide reproductive insurance, it could reduce adaptive capacity (Jersáková et al., 2006, Patt et al., 1989), which may represent a future risk to these species, particularly under severe ecological pressures such as climate change.

Sexually deceptive *Caladenia* species showed the greatest decline in pollination services compared to other pollination strategies. Sexual deception is common among orchid species and involves the production of sex pheromones and/or engaging in physical mimicry to attract specific pollinators (Schiestl et al., 2003, Peakall, 2023). Sexually deceptive species may be more vulnerable to ecological changes due to their high rates of ecological specialization, including higher rates of one-to-one pollinator specialization compared to other orchids (Ackerman et al., 2023), as demonstrated for *Caladenia huegelii* (Phillips et al., 2015). A compounding influence on pollination services to sexually deceptive species, and particularly relevant for threatened species of *Caladenia*, is plant population size. Per plant reproductive rates are typically higher in smaller populations, likely because there are only a small number of pollinators, and they learn to ignore the deceptive flowers (Phillips et al., 2024). We were unable to account for plant population size in our study as these data were not consistently recorded with herbarium specimens. A further consideration is the additional layer of specialization caused by reliance on male insects for pollination. It remains unclear how sex differences in sensitivity to disturbance may affect pollination services to these species and this may be a future frontier in pollination ecology.

Food-deceptive orchids are generally thought to dependent on a wider variety of pollinators, although they can still have specific (one-to-one) pollinator relationships (Ackerman et al. 2023). Compared to sexually deceptive species relatively little is known about the pollinators of food-deceptive *Caladenia*, but they have been shown to have specialized relationships with pollinators or pollinator groups (Phillips and Batley, 2020, Phillips et al., 2020b, Reiter et al., 2019a, Reiter et al., 2019b). Most sexually deceptive species are known to exploit male thynnine wasps (Phillips et al., 2023). Non-sexually deceptive species in the genus are associated with a range of taxa including solitary bees, nectar-feeding pompilid wasps, and nectar-seeking thynnine wasps, which suggests that shifts in pollination strategy between food and sexually deception can occur without changing pollinator family (Phillips et al., 2023).

We found similar overall declines in pollination services by the different taxonomic groups considered, but more data is needed to address this question. The information on the identify of pollinators for our orchid species is scattered, in many cases scare and collected via disparate methods. Greater research into the pollination ecology of plants and their pollinators is urgently needed, particularly given the substantial taxonomic gaps and limited ecological knowledge for many species. This is especially true for fly pollinators, where information on species identity, ecology, and specialization remains scarce. Alarmingly, species are being lost before they are even described or their ecological roles understood (Skaldina and Blande, 2025).

Our results suggest broad-scale drivers are responsible for declines in pollination services since the 1970s. Areas with higher human land use intensity had lower pollination services overall, but recent declines in service are occurring at a higher rate in areas that are under lower land-use intensity. Climate is a possible driver for contemporary declines in pollination services in less disturbed regions. Here we did find a correlative relationship between temperature anomaly and decline in pollination services. Climate change can affect the interaction between plants and their pollinators in multiple ways. Temperature rises can disrupt the synchrony between plant flowering time and insect emergence (Hutchings et al., 2018), but on the other hand, Alquichire-Rojas et al. (2024) found that warmer temperatures can increase early season pollinator activity and/or duration of foraging. Australia has warmed by ~1.5 °C per year since records began in 1910, with a marked rise from the 1950s onward. Since the 1970s, shifting climate drivers like ENSO, IOD, and a strengthening SAM superimposed over increased mean temperatures have intensified and prolonged extreme heat events nationwide (CSIRO and BOM, 2024). These changes are likely to affect pollination services. In support, extreme temperatures in Australia have been shown to affect the activity of solitary bees, decreasing the duration of their active foraging periods, which may decrease pollination services to plants (Rader et al., 2013).

While we found no significant correlation between pollination services and rainfall anomaly, correlations between rainfall and flowering have been identified for orchids in Australia and elsewhere (Wells et al., 1998, Kéry and Gregg, 2004, Jasinge et al., 2018a), as has the potential for rainfall impacts pollinator populations and pollination services (Brundrett, 2019). Another possible driver of changes to pollination services, related to climate change, is changed fire regimes. High fire frequency, high fire severity, out of season fire and substrate fires have been identified as threats to Australian ecosystems (Keith et al., 2022), with season of burn having demonstrated effects for orchid growth and survival (Jasinge et al., 2018b, Thomsen et al., 2024). While a single fire had no effect on the pollination of *Caladenia tesselata* (Phillips et al., 2024), correlation between fire regime and orchid pollination services is an area for further research.

Mean pollination services across all years was lower in areas under greater land-use intensity, suggesting historical land-use change has impacted pollination services to orchids. In Australia, coastal regions are hotspots for orchid and pollinator abundance and diversity due to the richer soils and higher rainfall (Henseler et al., 2019). Coastal regions in Australia are also hotspots for human activity, including urbanization and agricultural intensification (Henseler et al., 2019). Increases in land-use intensity may have resulted in habitat loss for pollinators, with potential consequences for pollination services (Wenzel et al., 2020). Furthermore, land-use change was associated with increases in pesticide and herbicide use, which are also linked to declines in pollinator populations (Watanabe, 2014).

In this study we were unable to test for the effects of pesticides directly due to a lack of available data. However, the sharp decline in pollination services detected since the 1970s reflects the uptick in pesticide registration in Australia between the 1960s to 1980s (Brain and Anderson, 2019). Together, the effects of climate, land-use, and pesticide use could collectively undermine pollination services and ultimately impact the reproductive success of plants. Species dependent on specific environmental conditions or on specific pollinator taxa for pollination, which is common among orchids, may be particularly vulnerable to the effects of anthropogenic change making orchid sentinels for the effects of global change on pollination services (Thomas et al., 2004). In addition to the threats to pollination services, herbariums themselves also face potential risks. Particularly in the United States and Southern countries, many herbariums are experiencing budget cuts or are being closed. However, our study reaffirms the vital role of museum and herbarium collections in understanding and mitigating the effects of global change on biodiversity and its critical contribution it makes to makes to society (Bartomeus et al., 2019, Rakosy et al., 2023).

Pollination services play a vital role in the maintenance of terrestrial ecosystems globally and are under threat from the intensification of human activities. Orchids represent an important part of global plant diversity, and their unique pollination strategies and specialization of pollinator groups make them sentinels of change for other ecologically and economically important plant species. This study documented a major decline in pollination services over the continental landmass of Australia. We identified a tipping point in pollination services starting in the 1900s and maybe earlier for fly pollinated species. Our study indicates a major overarching driver is responsible for pollination service decline, such as rising temperatures and historical land-use change.

Data accessibility statement: The relevant data and code used in this study is available on GitHub (https://github.com/Song-Bofeng/Caladenia-Pollination-Services-Song-et-al-).

Author contributions:

Conceptualization: JMB, TMK, DR

Methodology: HZ, MC

Data collection: BS

Formal analysis: BS

Visualization: BS

Writing – original draft: BS

Writing – review & editing: JMB, HZ, TMK, DR

Supervision: JMB, HZ

Acknowledgements:

This research was supported by the Australia-Germany Joint Research Co-operation Scheme grant of J.M.B and T.M.K (project number 57654754), an initiative of Universities Australia and the German Academic Exchange Service (DAAD). J.M.B is supported by the Australian Research Council Australian Discovery Early Career Award (project number DE220100144) funded by the Australian Government.

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Supplementary material

Comparison between coastal and inland regions

Using the Botanical Districts of Australia (ANHSIR, 2024) we compared specimens collected from coastal bioregions to inland bioregions. We found the mean pollination services in coastal areas was consistently higher than in inland areas across both time periods (Figure S5). However, the mean pollination services in both regions showed a similar decrease over time (Figure S6, Figure S7). A Tukey HSD test confirmed significant differences between coastal and inland regions during both periods (Figure S5). The linear mixed model results indicated that coastal areas consistently had higher pollination services percentages compared to inland areas (Estimate = 0.0429, t (19482) = -12.491, df = 19482, $p < 0.001$).

Between 1925 and 1970, pollination services in coastal areas were significantly higher than in inland areas (Figure S5). This may have been attributed to the more suitable ecological environments and more abundant pollinator resources in coastal regions (*32*). Pollination services rates in both coastal ($R^2 = 0.4175$, DF = 3486, F = 2499, $p < 0.001$) and inland ($R^2 = 0.3584$, DF = 4483, F = 2505, $p < 0.001$) areas exhibited a consistent downward trend from 1925 to 2020 (Figure S6 & S7). In coastal areas, the annual rate of decline was -0.5192%, while in inland areas, it was slightly lower at -0.3998%. Despite these differences in the rate of decline, coastal regions maintained higher overall pollination service levels compared to inland regions throughout the study period. These results emphasize that, although starting points and rates of decline differed between coastal and inland areas, the overall trends of decline were consistent across both regions over time. Which is probably closely related to the intensity of human activities in these areas. Urbanization, industrialization, and tourism development in coastal regions (Yapp, 1986) exacerbated habitat fragmentation and environmental pollution (Venter et al., 2016). These human activities directly impacted pollinator abundance and diversity, leading to a rapid reduction in pollination services. Such regional differences, between coastal and inland areas, were not only linked to human activities but also may have related to the greater fragility of coastal ecosystems. Thus, while initial pollination efficiency was higher in coastal areas, the fragility of their ecosystems may have contributed to a more rapid decline in pollination services.

Critical analysis limitations and strengths

Bias may occur in this study during the specimen collection stage. Uneven sampling is a well-known problem in herbarium use, as collectors tend to ignore seemingly uninteresting sites in favor of "valuable" sites. For example, sampling rates are higher in nature reserves including remnant vegetation, in otherwise cleared/agricultural landscapes. In addition, larger or taller plants may be selected for sampling within a population. Moreover, specimens collected are often concentrated in easily accessible or frequently visited sites (Lang et al., 2019). For example, for the specimens from eastern NSW covered by this study, there are only a few remaining small habitats, so people take samples repeatedly in the same locations. However, repeated sampling at certain sites also provides an advantage for this study. It provides time-series data for specific regions, enabling analysis of long-term trends in pollination services. This continuous data enhances the study’s ability to assess changes over time, adding robustness to conclusions about regional differences and the impact of human activities on pollination services.

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Supplementary Figures

Figure S1. Examples of morphological evidence for pollination success in *Caladenia dilatata*. (a) A fertilized specimen showing clear ovary enlargement and darkening, consistent with successful fruit initiation. (b) A specimen with damaged pollinia but no pollen deposited on the stigma, and the ovary remains unfertilized without visible enlargement.

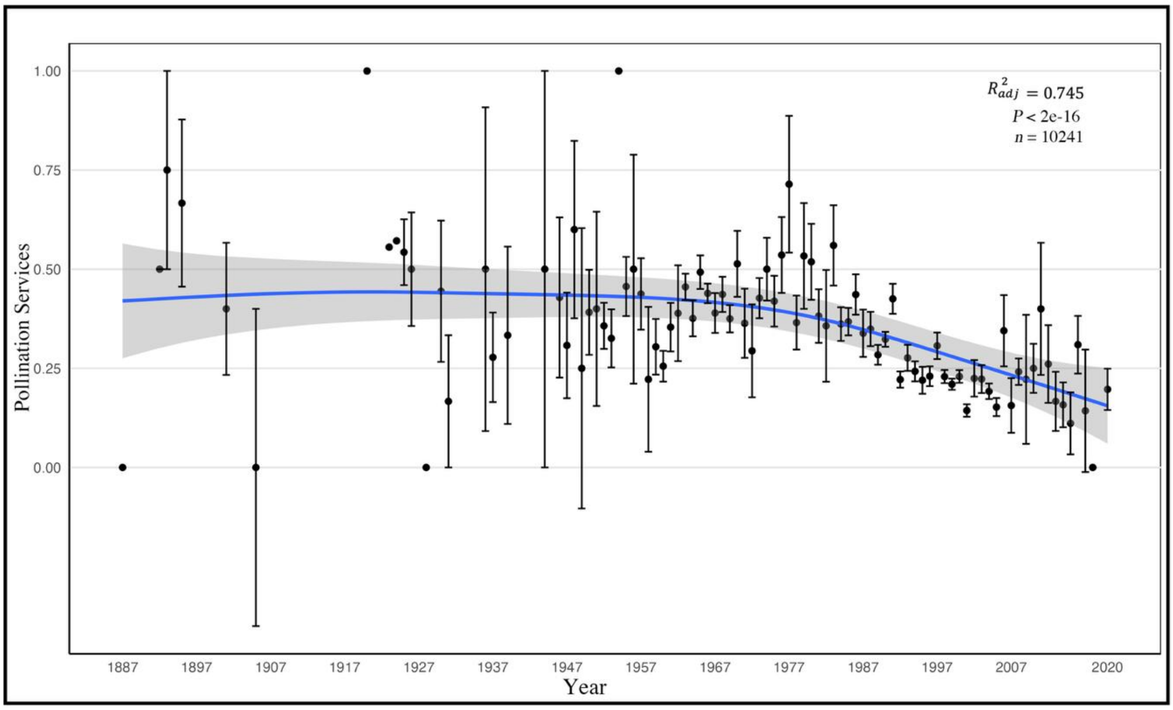

Figure S2. Historical trends in pollination services for *Caladenia* species (1887 – 2020).

The temporal trends in mean annual pollination services as proportion for *Caladenia* species based on generalized additive mixed models (GAMMs) with a Gaussian distribution, with error bars showing the standard error. The fitted blue line illustrates the modeled trend, and the gray shaded area denotes the 95% confidence interval. Statistical metrics are displayed in the top-right corner.

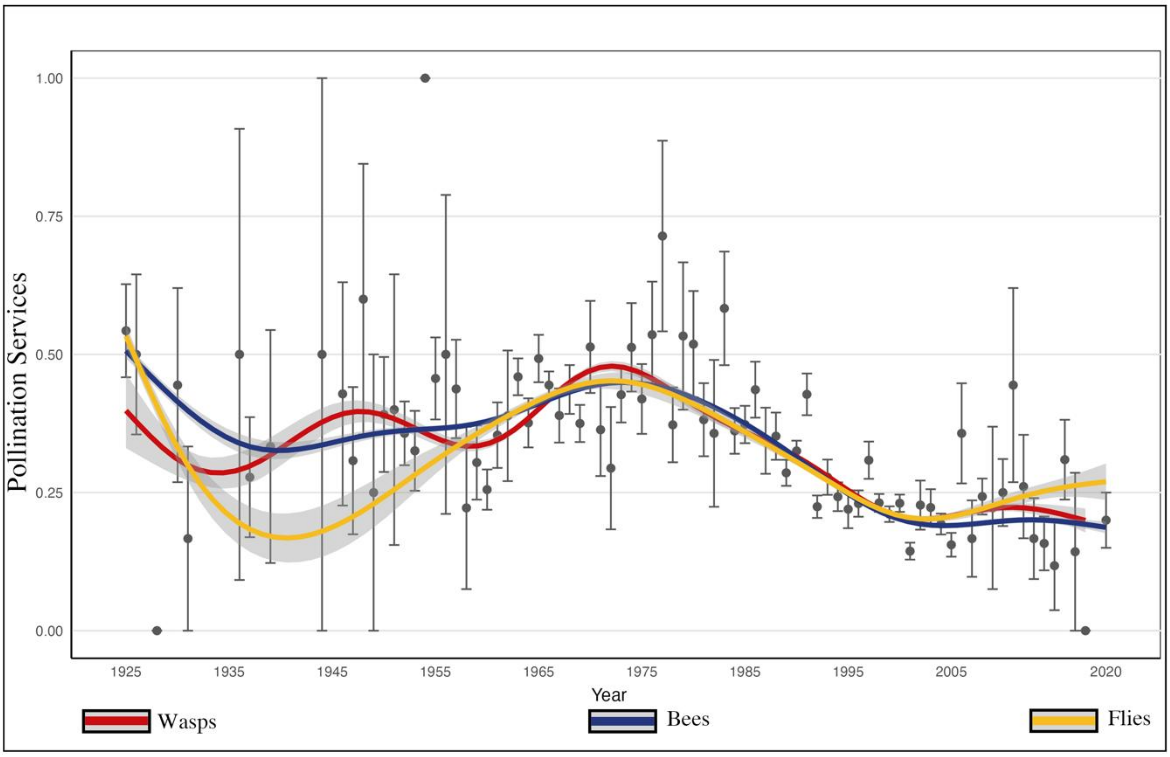

Figure S3. Temporal trends in pollination services (1925 – 2020) for *Caladenia* species primarily pollinated by either wasps, bees, or flies. Data points represent the mean annual pollination service per year as a proportion, with error bars showing the standard error. The colored lines depict the trends predicted by Generalized Additive Mixed Models (GAMMs) with a Gaussian distribution: the red line corresponds to wasps, the blue line to bees, and the yellow line to flies. The gray shaded regions around the trendlines indicate the 95% confidence intervals of the fitted models.

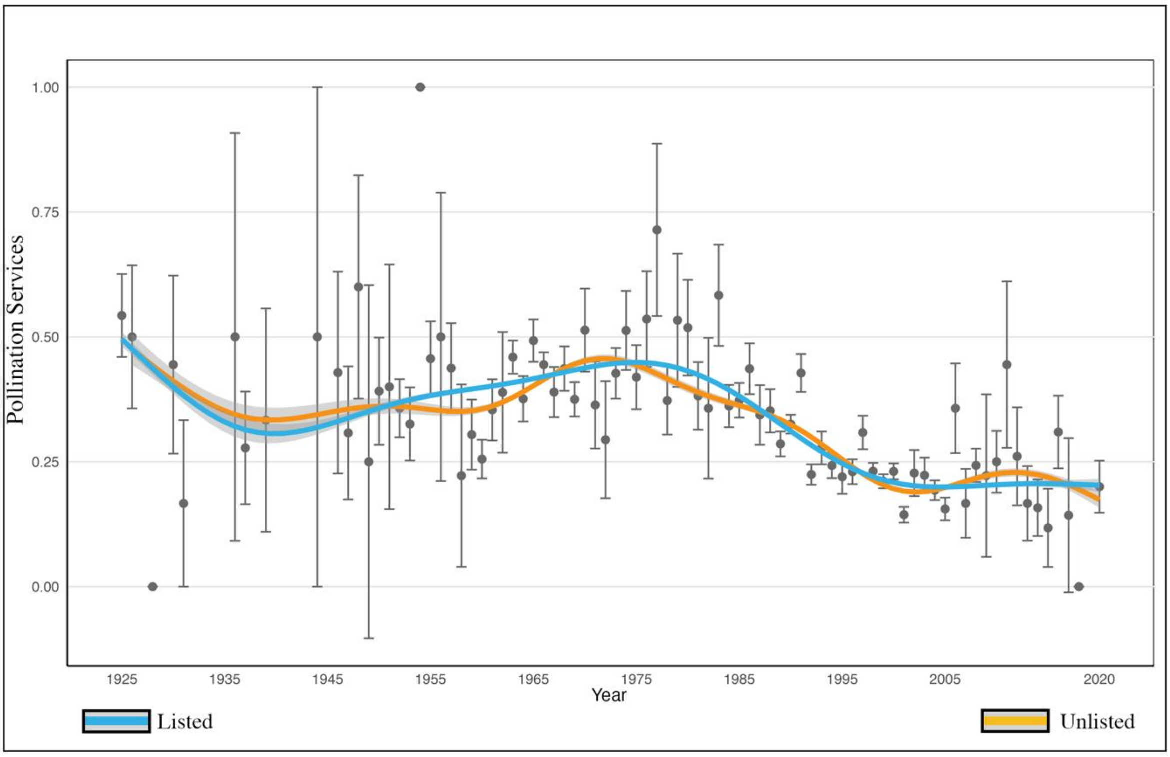

Figure S4. Temporal trends in pollination services (1925 – 2020) for *Caladenia* species by threat status. Data points represent the mean annual pollination service per year as a proportion, with error bars showing the standard error. The colored lines depict the trends predicted by Generalized Additive Mixed Models (GAMMs) with a Gaussian distribution: Blue lines show listed and orange unlisted species. The gray shaded regions around the trendlines indicate the 95% confidence intervals of the fitted models.

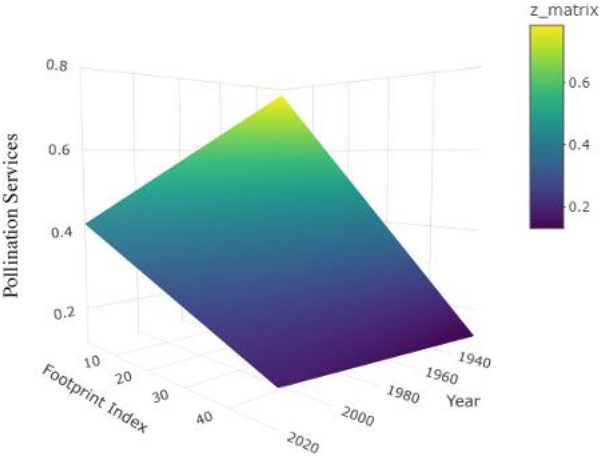

Figure S5. Three-dimensional interaction plot showing the effect of year and footprint index on predicted pollination services success. The Z-axis represents predicted pollination services, with higher values indicating more evidence of pollination service. The X-axis denotes the footprint index, which quantifies human impact on the environment, while the Y-axis represents the year. The color gradient, ranging from purple (low success) to yellow (high success), visualizes the combined effect of temporal changes and human impact on pollination services.

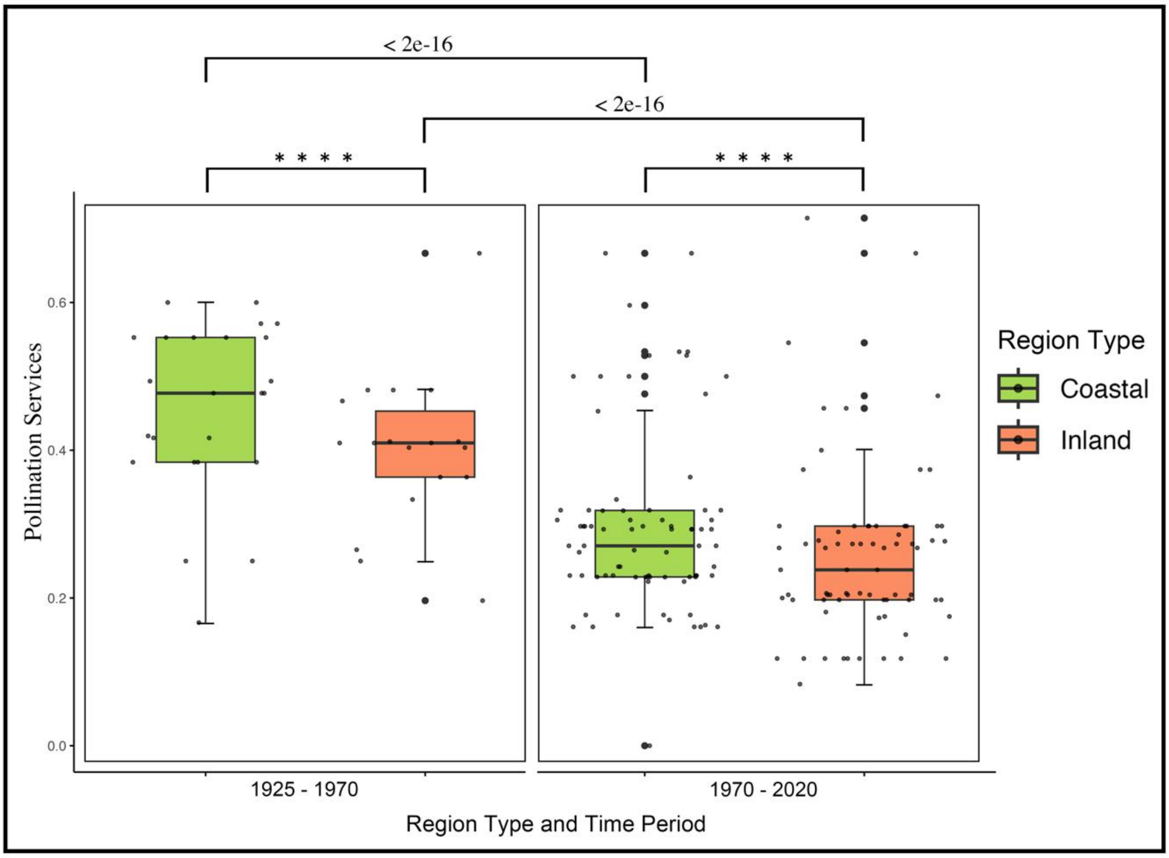

Figure S6. Comparison of pollination services in coastal and inland regions across two time periods (1925–1970 and 1970–2020). The figure illustrates the distribution of pollination services as a proportion in coastal (green) and inland (orange) regions. Each boxplot displays the median (thick black line), interquartile range (box), and data range excluding outliers (whiskers). Black dots represent individual data points. Statistically significant differences between coastal and inland regions within each time period are indicated by asterisks (****, $p < 0.0001$). The comparative analysis highlights temporal changes in pollination services success between these two region types.

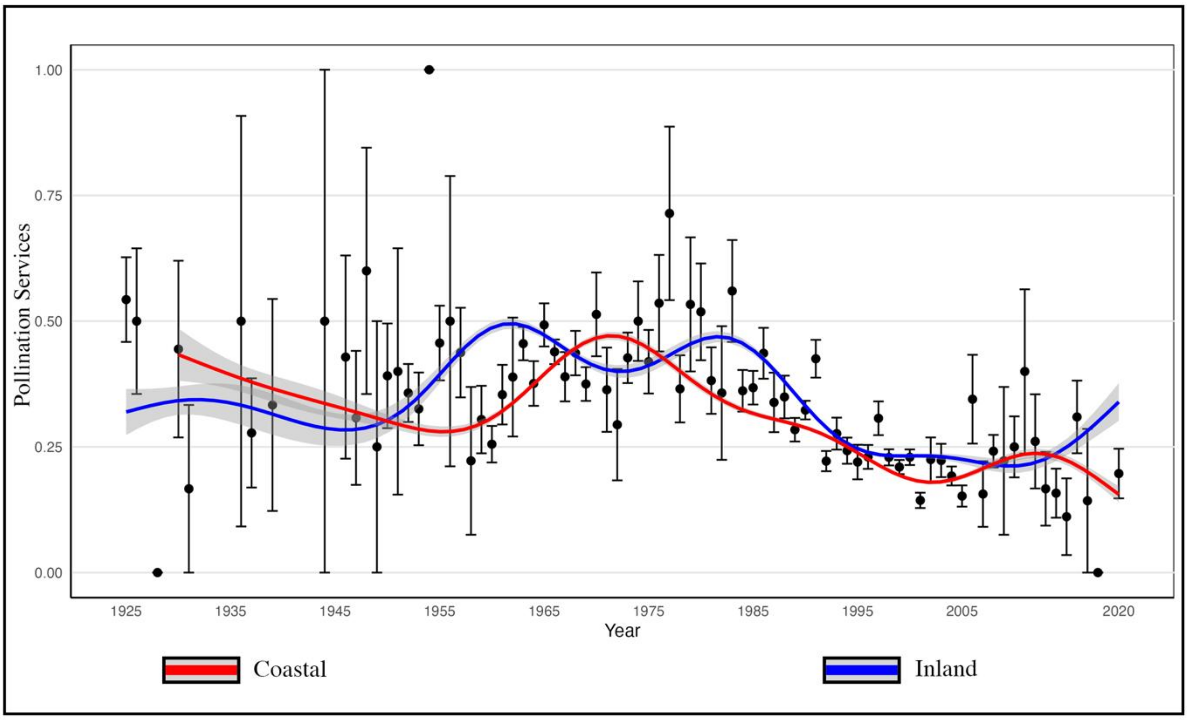

Figure S7. Temporal trends in pollination services success across coastal and inland regions from 1925 to 2020. The figure illustrates the temporal trends in pollination services as a proportion of individuals receiving pollination service for Caladenia species in coastal (red line) and inland (blue line) regions. Data points represent the mean annual pollination services success rates, with error bars showing the standard error of the mean. Smoothed trendlines were fitted using Generalized Additive Mixed Models (GAMMs), and the grey shading represents the 95% confidence intervals around the fitted trendlines. This comparison highlights differences in the temporal dynamics of pollination services between coastal and inland regions.

Supplementary Table

Table S1. Pairwise Comparisons of Pollination Services Among Pollination Syndromes Using t-tests. This table summarizes the results of pairwise t-tests assessing differences in pollination services among three pollination syndromes: self-pollinating, food-deceptive, and sexually deceptive species. The analysis includes t-values, p-values, and Cohen's d effect sizes for each comparison. No significant differences were observed between any pair of syndromes, indicating a lack of distinct differences in pollination services between these groups.

Comparison	t-value	*p*-value	Cohen's d
Self-pollinating *vs* Food-deceptive	-0.38	0.701	-0.03
Sexually deceptive *vs* Food-deceptive	3.67	0.000	0.103
Sexually deceptive *vs* Self-pollinating	1.74	0.083	0.132

Table S2. Detailed information on all study species. including sampled numbers, subgenera, pollination syndromes, and pollinator details. The table provides comprehensive details on the studied *Caladenia* and *Glossodia* species, as follows: the sampled number of specimens, their subgenus classification, pollination syndrome (*46*), and the corresponding pollinator species or groups (*17,53*). The pollination syndromes include food deception, sexual deception, and self-pollination, highlighting the diversity of reproductive strategies and associated pollinator groups.

Species Name	**Pollination Syndrome**	**Main pollinator**	**Subgenus**	**Sampled Number**	**Pollinators and references**
Caladenia alata	Self-pollination	NA	*Caladenia*	223	Self-pollination (Jones 2021).
C.alpina	Food Deception	Bee	*Stegostyla*	519	Small native bees (author obs. in Jones 2021).
C.capillata	Food deception	Multiple/NA	*Phlebochilus*	168	Multiple pollinator visitors (Kuiter 2015, 2016).
C.cardiochila	Sexual Deception	Wasp	*Calonema*	119	*Phymatothynnus* nr *nitidus* (Phillips et al. 2009); *Phymatothynnus victor* (Bates and Weber 1990).
C.carnea	Food Deception	Bee	*Caladenia*	1641	Native bees (Kuiter 2016, p. 156); *Trigonia* sp. (Adams et al. 1992) *Lasioglossum semipolitum*, *L. clelandi* (Farrington et al. 2009*), Homalictus* sp. (Phillips et al. 2009 [as suggested pollinator]), Sugarbag bees (*Tetragonula carbonaria*; Dyer et al. 2019); native bee (Morrison and Weston 1985).
C.catenata	Food Deception	Fly	*Caladenia*	282	Hoverfly (*Syrphus* sp.) (Uhlerr 1967); hoverfly (*Melangyna viridiceps*; Kuiter 2016 page 168; Kuiter 2017, p3); *Simosyrphus grandicornis* (Kuiter 2020 p. 56).
C.concinna	Sexual Deception	Wasp	*Calonema*	138	Thynnine wasps (*Aelothynnus generosus*; Bower 2001, 2008), *Aelothynnus* sp. (Hayashi 2016 cited by Reiter et al 2019).
C.cucullata	Food Deception	Multiple/NA	*Stegostyla*	807	Native bees and flower wasps (Phillips et al. 2009).
C.deformis	Food Deception	Bee	*Pheladenia*	393	Small native bees (*Lasioglossum (Chilalictus) hemichalceum* and *L. lanarium*; Kuiter 2016 p 161); small native bees (Jones 2021).
C.dilatata	Sexual Deception	Wasp	*Calonema*	282	*Lophocheilus anilitatis* (Kuiter et al. 2016, p24); *Thynnoides* (given in reference to "most members of the *C. dilatata* complex; Phillips et al. 2009); *Thynnoides* spp. (Stoutamire 1983).
C.filamentosa	Sexual Deception	Wasp	*Phlebochilus*	93	"?*Chilothynnus* sp." (Kuiter 2016 p. 52); thynnine wasps (Phillips et al. 2020).
C.fuscata	Food Deception	Bee	*Caladenia*	1192	Native bees (Bates 2011 [re subgenus Elevatae], Phillips et al. 2009); small bee *Lasioglossum* (*Chilalictus*) *hemichalceum* (Kuiter 2016, p. 157).
C.gracilis	Food Deception	Bee	*Stegostyla*	226	Native bees (Phillips et al. 2009); *Exoneura bicolor, Exoneurella lawsonii, Lasioglossum globosum, Hylaeus brevior* (Kuiter 2016 p. 158), hoverfly (Kuiter 2016, p. 169).
C.latifolia	Food Deception	Multiple/NA	*Elevatae*	562	Beetles, bee flies (*Comptosia maculosa, Sisyromia*) (Brown et al. 1997), hoverflies (*Malanogyna viridiceps*) (Brown et al. 1997), bees (*Leioproctus* sp.) (Brown et al. 1997), native bees (Bates 2011); small native bees (*Lasioglossum (Chilalictus) globosum*; Kuiter 2016); food deceptive noted by Dixon and Tremblay (2009).
C.moschata	Food Deception	Bee	*Stegostyla*	1128	*Lasioglossum hemichalceum* (Kuiter 2020, p. 54).
C.parva	Sexual Deception	Wasp	*Calonema*	144	*Lophocheilus anilitatus* (Kuiter 2016, p. 24); *Lophocheilus anilitatus* (Bower 2015).
C.patersonii	Food deception	Multiple/NA	*Calonema*	73	*Phymatothynnus* sp. 6 (Kuiter 2016, p. 48); Tiphiidae, Apidae, Colletidae and Halictidae in Hymenoptera; Calliphoridae, Tachinidae and Syrphidae in Diptera as visitors to the flower, but unsure if pollinators (Stoutamire 1983), food advertising noted by Stoutamire (1983).

C.phaeoclavia	Sexual Deception	Wasp	*Calonema*	234	*Lophocheilus anilitatus* (Bower 2015).
C.picta	Food Deception	NA	*Caladenia*	140	Morphology, based on Kuiter (2015, 2016).
C.praecox	Food Deception	Bee	*Stegostyla*	325	Bee (Shrestha et al. 2019)
C.reticulata	Sexual Deception	Wasp	*Calonema*	100	*Phymatothynnus* sp. (Jones 2021); *Phymatothynnus* spp., *Phymatothynnus* nr. *nitidus* 1 (Phillips et al. 2009); *Phymatothynnus nitidus* (Swarts et al. 2014)
C.tensa	Sexual Deception	Wasp	*Calonema*	59	Thynnine wasps; "*Thynnoides* sp. 1 ? *gracilis*" (Kuiter 2016 p. 26); *Thynnoides gracilis* species, *T. pugionatus* (Bird 2025).
C.tentaculata	Sexual Deception	Wasp	*Calonema*	599	*Thynnoides pugionatus* (Jones 2021); *Thynnoides* sp. 1 (Kuiter 2016 p. 25).
Glossodia major	Food Deception	Bee	*Glossodia*	865	Native bees (*Lasioglossum hiltacum*, *L. hemichalceum, L. lanarium, Exoneura bicolor*; Kuiter 2016 p. 164); native bees (Jones 2021).
G.minor	Food Deception	Bee	*Glossodia*	182	Small native bees (Jones 2021); *Lasioglossum calophyllae*, *L. hemichalceum*, (Kuiter 2016, p.166).

Table S2 References

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Table S3. Summary of Generalized Linear Model (GLM) Analysis on the Interaction Between Year and Human Footprint Index on Pollination Services. This table provides the estimated coefficients, standard errors, t-values, and p-values from the GLM model assessing the relationship between year, human footprint index, and their interaction on pollination services.

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	0.1403	0.01552	9.040	< 2e-16 ***
Year	-0.00688	0.0007804	-8.818	< 2e-16 ***
Footprint	0.0001821	0.0007972	2.284	0.0225 *
Year: Footprint	9.071e-05	0.0004015	2.259	0.0240 *