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RESEARCH ARTICLE

European mistletoe shares a similar demographic strategy with non-parasitic plants

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Abstract

1. The demographic strategies of parasites are fundamental to their population dynamics, impacts, responses to environmental change and management. Parasitic plants are an economically important group of parasites that differ from non-parasitic plants in their unique resource acquisition mechanisms and various morphological and ecological adaptations. Though they are well-suited to demographic study, structured population models have rarely been applied to parasitic plants. Thus, whether or not parasitic plants also differ from non-parasitic plants in their demographic strategies remains poorly understood.
2. Using a 10-year dataset on European mistletoe (*Viscum album*) parasites, we quantified the relationship between mistletoe traits and vital rates. We used vital rate regressions to parameterise an integral projection model (IPM), from which we extracted time-based life history traits to quantify mistletoe's demographic strategy. To compare the demographic strategies of parasitic plants and non-parasitic plants, we performed a principal component analysis (PCA) of life-history traits for mistletoe, two other parasitic plants and 498 non-parasitic plant species.
3. We found that individual mistletoe growth rate and fruiting probability depend on mistletoe size, a proxy for mistletoe age. Fruiting probability also depends on the mistletoe's vertical position on the host, whereas mistletoe survival was independent of size and position. Mistletoe life-history traits were most sensitive to changes in individual mistletoe growth rate and then to survival, though generation time was also sensitive to changes in reproduction.
4. Contrary to our expectation, *V. album* and other parasitic plants placed centrally in our PCA of demographic strategies, near the centre of both the fast–slow continuum and reproductive strategy axis. This suggests that parasitic plants and non-parasitic plants share a similar demographic strategy, at least as summarised by our chosen life-history traits.
5. *Synthesis*. Our results suggest that the unique adaptations of parasitic plants do not prevent them from experiencing similar demographic constraints to

non-parasitic species. If parasitic plants exhibit unique responses to global change compared to non-parasites, there is insufficient evidence to suggest that this is driven by differences in life history. Our conclusions support a general view that population-level behaviour is similar between parasitic and non-parasitic plants.

KEYWORDS
hemiparasite, integral projection model (IPM), life history, macroparasite, parasitic plant, plant–plant interactions, principal component analysis (PCA), vital rates

1 | INTRODUCTION

Parasites have pervasive impacts on ecosystems, ranging from direct harm inflicted upon hosts to indirect interactions with the wider community (Schmid-Hempel, 2021). These impacts arise from parasite population dynamics, which are in turn influenced by parasite investment in vital rates (e.g. survival, reproduction) and the demographic strategies that emerge from them (Vicente et al., 2007). Demographic strategies are combinations of life history traits and can be classified along axes such as the fast–slow continuum (based on growth rate and longevity) and reproductive strategy (based on reproductive frequency and output) (Salguero-Gómez et al., 2016). Understanding the demographic strategies and life histories of parasites provides the context for modelling and managing their impacts.

The importance of parasite life histories is reflected in our approaches to modelling their dynamics. Despite the immense taxonomic diversity of parasites (Poulin & Morand, 2014), their population dynamics can be modelled using a life history-based classification into microparasites and macroparasites (Anderson & May, 1979). Whereas microparasites (e.g. viruses, bacteria, protists) typically reproduce directly within hosts, macroparasites (e.g. helminths, arthropods, parasitic plants) do not. Macroparasites have longer generation times (Anderson & May, 1979), and their effects on host fitness typically scale with the number of parasites present (intensity sensu Dobson & Hudson, 1992). As such, macroparasite population dynamics are usually modelled by tracking individual parasites (Grenfell & Keeling, 2007). To predict and manage the impacts of macroparasites, it is therefore useful to understand how individual-level factors influence their demographic strategies and population dynamics.

Variation among macroparasite individuals shapes their population-level effects by influencing vital rates such as survival, reproduction and transmission (Vindenes et al., 2008). Individual-level macroparasite traits like size, stage and age are important determinants of parasite vital rates (McCall et al., 2016; Mideo & Reece, 2012). For instance, the fecundity of Taeniidae tapeworms increases with size (Leung, 2022). Similarly, a macroparasite's location in its host can affect resource access and host responses, affecting its vital rates. For example, trematodes infecting *Hyla* tadpoles survive and transmit more effectively when they colonise the tadpole's head rather than the tail (Sears et al., 2013). Given their importance to vital rates and resource access, individual macroparasite traits such as body size have been proposed as candidates for focal variables in structured population models (Metcalf et al., 2016). Such models, for example, integral projection models (IPMs; Ellner et al., 2016; Merow et al., 2014), link individual-level traits to vital rates and subsequently to population dynamics and demographic strategies (Caswell, 2001; Ellner et al., 2016) and have only recently been applied to macroparasites (Bruijning et al., 2021; Wilber et al., 2016, 2021). Yet, these recent host–parasite structured population models typically quantify heterogeneity at the host level (e.g. infection intensity) rather than including individual macroparasite traits (Metcalf et al., 2016; Wilber et al., 2021).

Parasitic plants are an ideal group of macroparasites in which to quantify parasite population dynamics and demographic strategies using structured population models (Gilbert & Parker, 2023). Defined by their ability to grow in and on another ('host') plant, parasitic plants are an ecologically and economically important group (Press & Phoenix, 2005), comprising 13 independent lineages (Feild & Brodribb, 2005; Teixeira-Costa, 2021). Parasitic plants extract water and nutrients from their hosts via a physiological bridge called a haustorium (Teixeira-Costa, 2021; Yoshida et al., 2016). Many parasitic plants are large and conspicuous, relatively low in intensity, sessile, and in some cases, long-lived. These attributes allow the repeated measurement of individual parasites, facilitating long-term demographic studies.

Nonetheless, the demographic strategies of parasitic plants are understudied (Römer et al., 2023). Obligate parasitic plants are distinguished from non-parasitic plants via their: (1) haustorium for resource acquisition from a host, (2) dependence on hosts for survival and reproduction and (3) requirement to transmit to suitable new hosts. These differences in resource acquisition and other determinants of vital rates may result in parasitic plants investing differently in vital rates compared to non-parasitic species and thus different life history strategies. Hence, parasitic plants may occupy different regions of life history space, such as the fast–slow and reproductive strategies continua (Salguero-Gómez et al., 2016), compared to their non-parasitic counterparts. Moreover, selection pressures associated with a parasitic life cycle may have selected for different demographic strategies in parasitic plants (Gebauer et al., 2019; Salguero-Gómez et al., 2015, 2016; Tyree & Zimmermann, 2013; Viney & Cable, 2011; Zuber, 2004). For example, parasites face strict requirements to transmit before host death (Poulin, 1995), and so increased investment in early reproduction may have been favoured by natural selection. However, parasitic plants still share many life history constraints with non-parasitic species, so their demographic strategies may not be as exceptional as expected (Poulin, 1995).

To quantify the demographic strategy of a parasitic plant, we parameterised an integral projection model (IPM; Easterling et al., 2000) for European mistletoe (*Viscum album*). IPMs are structured population models which predict population dynamics by combining regressions of vital rates against individual traits (Merow et al., 2014). IPMs therefore incorporate individual trait heterogeneity unlike unstructured population models. Using a decade of annual censuses from Silwood Park, UK, we modelled survival, growth and reproduction as functions of parasite size and position on the host. We then estimated European mistletoe's life history traits (generation time, mean life expectancy, mean age at maturity, mean reproductive window) to compare its strategy with two other parasitic plants and 490 non-parasitic species along the fast–slow and reproductive strategy continua (Salguero-Gómez et al., 2016). Based on observations of other macroparasites described above, we hypothesised that (H1) parasite vital rates depend on individual-level parasite traits (size and position on the host), making an IPM a suitable approach for modelling parasite dynamics. Specifically, we expected that (H1a) survival decreases with size as larger individuals exert more stress on host branches, increasing the risk of snapping or embolism (Griebel et al., 2022). (H1b) Growth declines and fruiting increases with size as parasites shift investment towards reproduction in adulthood. (H1c) Survival decreases with position on the host due to embolism risk (Gebauer et al., 2019; Tyree & Zimmermann, 2013) and wind exposure, while (H1d) growth and fruiting increase with position on the host due to greater light access, as *V. album* is partially autotrophic. (H2) Parasite life history traits will be most sensitive to changes in reproduction and establishment, as the need to transmit between hosts is considered a key selection pressure for macroparasite life histories (Viney & Cable, 2011). (H3) Parasitic plants are expected to exhibit dissimilar demographic strategies from non-parasitic plants. Specifically, we hypothesise that parasitic plants will occupy the iteroparous end of the reproductive axis due to selection for frequent reproduction to optimise the probability of successful transmission. We expect that parasitic plants will place in the centre of the fast–slow continuum. While selection will favour increased longevity to optimise transmission success, host survival will necessarily limit parasite lifespan.

2 | MATERIALS AND METHODS

2.1 | Study species

To quantify the demographic strategy of a parasitic plant, we collected demographic data from a population of European mistletoes (*Viscum album* subspecies *album*), the only mistletoe native to Great Britain (Briggs, 2021). Mistletoes, aerial parasites of trees in the order Santalales, are a polyphyletic group of obligate stem macroparasites (Mathiasen et al., 2008) that use an endophytic haustorium to extract water, ions, and some carbon from the host (Zuber, 2004). European mistletoes (*Viscum album* subspp.) harm their hosts by reducing leaf nutrients (Daryaei & Moghadam, 2012), reducing host growth (Barbu, 2009) and increasing host mortality (Raftoyannis et al., 2015). As hemiparasites, mistletoes retain some photosynthetic capability (Mathiasen et al., 2008), such that light availability has the potential to influence resource acquisition.

Viscum album subspecies *album* (hereafter, 'European mistletoe') has a wide host range, documented to parasitise 452 angiosperm host tree taxa (Barney et al., 1998). European mistletoe grows annually via dichasial branching (Thomas et al., 2022), producing globose clumps of up to 2 m diameter, with a maximum lifespan of 27–30 years (Zuber, 2004). Seed dispersal between trees occurs by bird vectors, while intra-host transmission can occur via gravity ('seed rain'; Mellado & Zamora, 2016) and asexual vegetative reproduction via cortical strands under the bark (Thoday, 1951).

Once on a suitable host branch, European mistletoe seeds germinate and develop a primary haustorium to establish. After 2 years, the first leaves develop, and first flowering occurs at about 4–5 years (Zuber, 2004). European mistletoe parasites in Britain are easiest to track in the winter, when deciduous host leaves have fallen, also coinciding with berry ripening (Thomas et al., 2022). It is possible for several individual mistletoes to grow so close together as to appear like one clump (Thomas et al., 2022). However, over long periods as in our studies, close individuals that fruit or die in different years can be distinguished retrospectively. The ease of individual tracking (Aukema, 2003), the natural variation in size and mistletoe position (Zuber, 2004), and the strong correlation between size and age (Reid et al., 1995; Zuber, 2004) make European mistletoe an ideal macroparasite in which to test our hypotheses linking traits to vital rates and its demographic strategy.

2.2 | Demographic data collection

We collected demographic data on European mistletoe each winter (November–February) from December 2013 to December 2022 in Silwood Park, Berkshire, United Kingdom (51°24′33″N, 0°38′32″W, 55–70 m a.s.l.). As *V. album* grows primarily in May–June (Zuber, 2004), measuring mistletoe size at any point in winter gave the same indication of growth over the previous season. Each year, we took high-resolution photographs of the same individual host trees containing mistletoes (Canon DSLR, EOS 77D, 72ppi, Ōita, Japan) and assessed berry presence using a telescope (ATS 80, Swarovski Optik, Tyrol, Austria). As mistletoe clumps are roughly spherical, the orientation of the photo had little effect on estimates of size, but photographs were taken from the same position for each tree for consistent individual detection. To test (H1c-d) the effect of parasite position (height above-ground) on vital rates, we used a laser rangefinder (BL-X3 Bozily Golf, China) to measure the vertical positions of ~39% of individual mistletoes trigonometrically and the tree height, after including the observer's eye-height. We used ImageJ software (Schneider et al., 2012) to interpolate the positions of the remaining mistletoes. Together, we recorded 3394 observations of 740 mistletoe individuals (mean 273 per year, range 153–389) across 24 host trees from five genera: *Crataegus* ($n=1$ host tree), *Malus* ($n=2$), *Populus* ($n=3$), *Sorbus* ($n=1$) and *Tilia* ($n=17$). We censused all trees within Silwood Park that contained mistletoe in 2014–2016, but later excluded one host tree, as its high mistletoe density (>200) made it impossible to distinguish between individual parasites. We thank the Imperial College London facilities management team for granting permission to conduct this study at Silwood Park.

We used the images collected in the field to estimate size and vital rates for each mistletoe individual annually. We measured mistletoe size from images as the two-dimensional area of polygons drawn around mistletoe clumps using ImageJ software (Schneider et al., 2012). We used a standard 1 m stick as a reference for each tree to calibrate the measuring software. We corrected for the effect of distance from the observer on estimation of mistletoe area (see Supporting Information Section 3). Relative changes in size from 1 year to the next indicated mistletoe growth (or shrinkage). We measured mistletoe survival from the presence/absence of a mistletoe in 1 year compared to the next year. If individuals were missed for one or more years and then observed in a later year, we assigned them as having survived throughout that period. Some individual mistletoes were also obscured from view in some years such that their size could not be measured. In total, size could not be measured in 454 (~14.3%) of 3394 mistletoe observations, affecting at most 430 of 740 (58.1%) mistletoes in at least 1 year (Figure S1). Our results are insensitive to the exclusion of these individuals from our models (Table S2). Mistletoe sizes and positions had roughly symmetrical, unimodal distributions (Figure S2) and were independent of one another (Figure S3).

2.3 | Vital rate regressions

To test whether (H1) parasite size and vertical position on host affect mistletoe vital rates, we fitted vital rate regressions. Specifically, we used generalised linear mixed models (GLMMs) with a logit link function for survival and fruiting probability because they are binary variables. We modelled growth of surviving mistletoes via mixed effect models as inherent growth rate (IGR) using a Gaussian distribution (Lamont et al., 2023):

$$\mathrm{IGR} = \frac{z_{t+1} - z_t}{z_t}$$

where z_{t+1} and z_t are log-transformed area of a mistletoe individual in times t+1 and t, respectively.

Using IGR as a metric of parasite growth allowed us to compare growth as a function of size without confounding size in both predictor and response variables, as would occur with relative growth rate (RGR) (Lamont et al., 2023). We used mistletoe area and position on host as fixed effects in separate models, additive models and models with an interaction. We log-transformed area to reduce the skew of the mistletoe size distribution, and we also removed outliers (±3 standard deviations from the mean). We identified 11 individuals as outliers, and their removal did not impact the vital rate regressions chosen for use in the IPM. We further modelled survival as a quadratic function of size to allow for increased mortality in large individuals, such as due to increased mechanical stress on the host. To allow for a slowing down of growth as individuals increased in size, potential evidence of loss in vitality with age (Li et al., 2019), we also modelled IGR as a quadratic function of size. We incorporated individual mistletoe ID as a random effect in all models to control for variation due to repeat measurements on the same individual. Due to a lack of repeat measurements on some individuals, some mixed effect models were singular (i.e. the model could not reliably estimate random effect variance) and we therefore excluded them from the analysis (Table S1). To determine which parasite traits best predicted vital rates (H1), we manually selected models that had the lowest AIC scores (where ΔAIC >2; Table S1) (Merow et al., 2014). If AIC scores did not significantly differ between the best performing models (i.e. ΔAIC <2), the simplest model was chosen. This approach avoided implementing complex relationships into our IPM that there was insufficient statistical support for. We performed all regressions using the *lme4* package (Bates et al., 2015) in R (R Core Team, 2025). Model fit was evaluated via examination of residual distributions (Figure S5).

To tease apart expected density-dependent effects on mistletoe vital rates (Queijeiro-Bolanos et al., 2017), we also tested the relationship between infection intensity (number of mistletoes per host) and individual vital rates. We performed GLMMs (for survival and fruiting) and mixed effects models (for growth) of vital rates against log-transformed intensity (to reduce the skew of residuals). We tested the relationship between position on the host and intensity via a linear model to check for potential confounding.

2.4 | Integral projection model (IPM)

To test (H2) whether European mistletoe life history traits are most sensitive to reproduction, and (H3) whether, as parasitic plants, mistletoes exhibit a distinct demographic strategy from non-parasitic plants, we linked parasite traits to parasite population dynamics and extracted life history traits. To do so, we modelled the mistletoe life cycle via a size- and height-structured integral projection model (IPM) (Figure 2) (Easterling et al., 2000; Merow et al., 2014). Because both size and position on the host influenced mistletoe vital rates, we extended the standard single-trait IPM to incorporate these two state variables (Ellner & Rees, 2006; Rosen et al., 2025). Our IPM linked size z and position h distributions of individuals at time t, $n(z,h,t)$, to their size z' and position h' distributions in the following year t+1, $n(z',h',t+1)$, via the following overall structure:

$$n(z',h',t+1) = \int_{L_z}^{U_z}\int_{L_h}^{U_h} K(z',h',z,h)\cdot n(z,h,t)\,dh\,dz$$

$$= \int_{L_z}^{U_z}\int_{L_h}^{U_h} \left[P(z',z) + F(z',h',z,h)\right]\cdot n(z,h,t)\,dh\,dz$$

where the kernel K describes transition probabilities between states (sizes and positions) from one time point to the next. Kernel $K(z', h', z, h)$ is the sum of transitions due to survival and growth (given by sub-kernel $P(z', z)$) and sexual reproduction (given by sub-kernel $F(z', h', z, h)$) and integrated across the range of possible mistletoe sizes and positions on host of all individuals, from L_z (minimum size) to U_z (maximum size) and L_h (minimum height) to U_h (maximum height).

In accordance with our selected models, we modelled survival and growth transitions as size-dependent, growth as a quadratic function of size, and fruiting (fruit presence) as a function of both size and height. Individual mistletoe heights were assumed to be normally distributed and remained constant for each individual following recruitment. Despite not changing across the life cycle, implementing position as a covariate allowed its effects on fruiting to be incorporated into the model, similar to covariates such as crown illumination implemented in other IPMs (Metcalf et al., 2009). Although size was not a significant predictor of survival, we modelled survival as a function of size as IPMs require vital rates to be modelled as a function of a common variable. Growth of surviving individuals was incorporated into the IPM as a quadratic relationship between size in t and size in t+1 to allow for the slowing down of growth with age as found from our vital rate regressions. We used an exponential allometric relationship between size and number of berries produced, given that an individual fruited. This relationship was based on the growth form of *Viscum album* plants, which produce berries at terminal shoots (Thomas et al., 2022) between pairs of terminal leaves. As two new leaves form from each terminal bud in a dichasial branching pattern each year, leaf number, and thus berry number, grows exponentially with age (Briggs, 2021). As age is strongly correlated with size (log-transformed area, z), we assume that berry number $b(z)$ also increases exponentially with size (Figure S7):

$$b(z) = ke^{z}$$

We parameterised this relationship using the observation by Mellado and Zamora (2014) that *Viscum album* produces ~2000 berries per m^2 of mistletoe crop, such that constant $k = 0.2$.

We identified 'new recruits' as individuals with 1–3 leaf pairs that were too small to be observed in previous years. This size corresponds to an individual that is approximately 3 years old (Zuber, 2004), meaning these individuals have grown from berries produced 3 years earlier and younger individuals are unobservable. To account for individuals between 0 and 3 years of age, we estimated the total survival probability over the first 3 years as the number of new recruits in time t+3 divided by the number of berries produced in t (Lucas et al., 2008). We then assumed that the probability of survival over each of the first 3 years was constant ($s_0 = s_1 = s_2$) and therefore equal to the cube root of the total survival from seed to 3-year-old individuals. We also tried an alternative method to avoid this assumption, fixing λ, extrapolating survival of 1 and 2-year-olds (s_1, s_2) and back calculating seed establishment probability (s_0), but outputs from the resulting IPM were similar (see Supporting Information Section 9, Figure S11). We estimated the sizes of 1- and 2-year-olds by extrapolating the growth curves back from the smallest observed mistletoes, assumed to be 3 years old, to complete the life cycle. Sizes and positions of 1-year-old individuals were assumed to follow a normal distribution, which matches the observed distributions well (Figures S2 and S8). Overall, the sub-kernels $P(z', z)$ and $F(z', h', z, h)$ were structured as follows, with parameters and vital rate regressions defined in Table 1:

$$P(z', z) = s(z) \cdot G(z, z')$$

$$F(z', h', z, h) = f(z, h) \cdot b(z) \cdot s_0 \cdot c_z(z') \cdot c_h(h')$$

2.5 | Life history traits

To test (H3) whether European mistletoe exhibits a distinct life history strategy compared to non-parasitic plants, we estimated life history traits from our IPM. We discretised the IPM by imposing a mesh onto kernel K. To balance resolution with computational power, we used 50×50 mesh points for each state variable, producing a 2500×2500 mega-matrix for two state variables. Our outputs were largely insensitive to the number of mesh points used (Figure S10). We summarised European mistletoe's demographic strategy using life history traits expressed as rates per unit time (Stott et al., 2024), calculated using the *Rage* R package (Jones et al., 2022): generation time (T), mean life expectancy (η_e), mean age of maturity (L_α) and reproductive window ($L_{\alpha\text{-}\omega}$). We estimated generation time (T) as the number of years required for the population to increase by a factor of the net reproductive output, R_0 (Caswell, 2001), the mean number of offspring produced by an adult in their lifetime. To indicate how long a recruit would be expected to live, we estimated mean life expectancy (η_e) for the smallest individual in our model using a 'mixing distribution' (Ellner & Rees, 2006, p. 71). We estimated mean age at maturity (L_α) as the average age of first reproduction using a Markov chain approach (Caswell, 2001). As European mistletoes continue to reproduce up to death (Zuber, 2004), we estimated reproductive window ($L_{\alpha\text{-}\omega}$) as the difference between mean life expectancy and mean age at maturity.

To test whether European mistletoe life history was most sensitive to reproduction and establishment (H2), we performed a parameter-level sensitivity analysis. Parameter-level sensitivities describe the effects of small perturbations on model parameters (Caswell, 2001; Griffith, 2017) and indicate how altering one aspect of the parasite life cycle influences overall population dynamics (Ellner et al., 2016). We calculated parameter-level sensitivities of λ, R_0, T, η_e, L_α and $L_{\alpha\text{-}\omega}$ to each of the parameters in our vital rate regressions using a 'brute force method' (Morris & Doak, 2002). Specifically, we added a small amount (0.001) to each parameter while keeping all others unaltered and then created a new IPM using this value. We extracted IPM outputs (λ, R_0, T, η_e, L_α and $L_{\alpha\text{-}\omega}$) as before and calculated the sensitivity (s_x) as the relative change in each parameter compared to that from the original IPM:

$$s_x = \frac{\text{metric before change} - \text{metric after change}}{\text{parameter before perturbation} - \text{parameter after perturbation}} = \frac{\text{metric before change} - \text{metric after change}}{0.001}$$

TABLE 1 Vital rate parameters and models selected for use in integral projection model (IPM) describing the *Viscum album* life cycle.

Vital rate/parameter	Selected model	Parameters	Details of parameterisation
Survival *s(z)*	logit $[s(z)] = \beta_{s0} + \beta_{s1} z$	$\beta_{s0} = 1.81$ $\beta_{s1} = 0.0907$	Logistic regression
Growth *G(z, z′)*	$z' \sim N(\mu = \beta_{g0} + \beta_{g1} z + \beta_{g2} z^2, \sigma_g^2)$	$\beta_{g0} = 2.58$ $\beta_{g1} = 0.572$ $\beta_{g2} = 0.0163$ $\sigma_g = 0.566$	Linear regression
Fruiting probability *f(z, h)*	logit $[f(z,h)] = \beta_{f0} + \beta_{f1} z + \beta_{f2} h$	$\beta_{f0} = -8.68$ $\beta_{f1} = 1.00$ $\beta_{f2} = -0.0443$	Logistic regression
Berry production *b(z)*	$b(z) = ke^z$	k = 0.200	Estimated from Mellado and Zamora (2014)
Establishment probability s_0	Constant	$s_0 = 0.0500$	Estimated from as the cube root of total survival probability from 0 to 3 years
Recruit size $c_z(z')$	$z' \sim N(\mu_z, \sigma_z^2)$	$\mu_h = 1.003$ $\sigma_h = 0.500$	Normal distribution
Recruit position $c_h(h')$	$h' \sim N(\mu_h, \sigma_h^2)$	$\mu_z = 17.0$ $\sigma_z = 5.02$	Normal distribution

Note: For each vital rate, the selected model and associated parameters (for size/position-dependent vital rates) or constant value (for size-independent vital rates) are given. Size- and position-dependent models describe the relationships between parasite size and each vital rate, as plotted in Figure 1. We chose models based on significance of effects and AIC, log (Area). z = log(Area) in t, z' = log(Area) in t+1; h = height above-ground in t, h' = height above-ground in t+1; logit specifies a logistic link; parameters are given to three significant figures. See Table S1 for all vital rate regressions.

2.6 | Principal component analysis (PCA)

To compare (H3) European mistletoe's demographic strategy with those of other parasitic and non-parasitic plants, we performed a phylogenetic principal component analysis (pPCA) using life history traits (Salguero-Gómez et al., 2016). We extracted matrix population models (MPMs) from the COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2015) using the *RCompadre* R package (Jones et al., 2022). We filtered chosen models following a set of criteria to ensure comparability, to remove duplicates and ensure all matrices were useable (see Supporting Information Section 15), resulting in 509 species each with a single MPM. Using a list of all families known to contain parasitic plants (Nickrent, 2020), we found two further species in our dataset that are parasitic: *Thesium subsucculentum* (Santalaceae) and *Pedicularis furbishiae* (Orobanchaceae). MPMs from these root hemiparasites in COMPADRE were originally sourced from Albert Gamboa et al. (2009) and Menges (1990), respectively.

For each MPM, we calculated generation time (T), mean life expectancy (η_e) from the first non-propagule stage, mean age at maturity (L_α) and reproductive window ($L_{\alpha\text{-}\omega}$). We log-transformed these life history traits (Figure S14) and removed outliers (±1.5 IQR) because principal component analysis (PCA) is sensitive to skewed data (Hubert et al., 2009). To test for collinearity between variables, we tested for correlations between life history traits using a threshold of 0.7 for Spearman's rank (Dormann et al., 2013; Figure S15). Because PCA requires a dataset without missing values, we imputed life history traits which could not be calculated due to missing demographic data using the *mice* function of the *mice* R package (Van Buuren & Groothuis-Oudshoorn, 2011), taking the mean of 10 repeated imputations. To control for phylogenetic inertia in life history, we obtained a plant phylogeny for 498 out of 509 species from the Open Tree of Life via the *ROTL* R package (Michonneau et al., 2016). We then performed a phylogenetically controlled PCA for the 501 species (including *V. album*, *T. subsucculentum* and *P. furbishiae*) of four life history traits: T, η_e, L_α, $L_{\alpha\text{-}\omega}$.

3 | RESULTS

3.1 | Vital rate regressions

Overall, size and position were good predictors of mistletoe growth and fruiting, but not of survival (Figure 1). For the entire mistletoe population, survival was not significantly predicted by size ($\beta = 0.060$, $p = 0.353$) nor position ($\beta = -0.025$, $p = 0.202$) in our binomial GLMMs ($n = 2258$, Figure 1a,b). This result does not support our hypothesis (H1a) that survival would decrease with increasing size after establishment. Survival was independent of infection intensity ($\beta = 0.179$, $p = 0.078$, $n = 2258$, Figure S6a).

Our mixed effect models showed that the inherent growth rate (IGR) of individual mistletoes was best modelled as a decreasing function of parasite size ($\beta_{\text{linear}} = -0.199$, $p < 0.001$, $n = 1897$, Figure 1c). IGR decreased for larger individuals, supporting hypothesis H1b. Inclusion of a (positive) quadratic term significantly improved model fit ($\beta_{\text{quadratic}} = 0.0163$, $\Delta AIC = 112$, Table S1, Figure 1c). This result implies that the rate at which IGR decreased with size was less negative at greater sizes, and thus growth decreases with size, but at a slower rate. When added to the mixed effect model, position did not have a significant effect on IGR ($\beta < 0.001$, $p = 0.417$, $n = 1897$, Figure 1d).

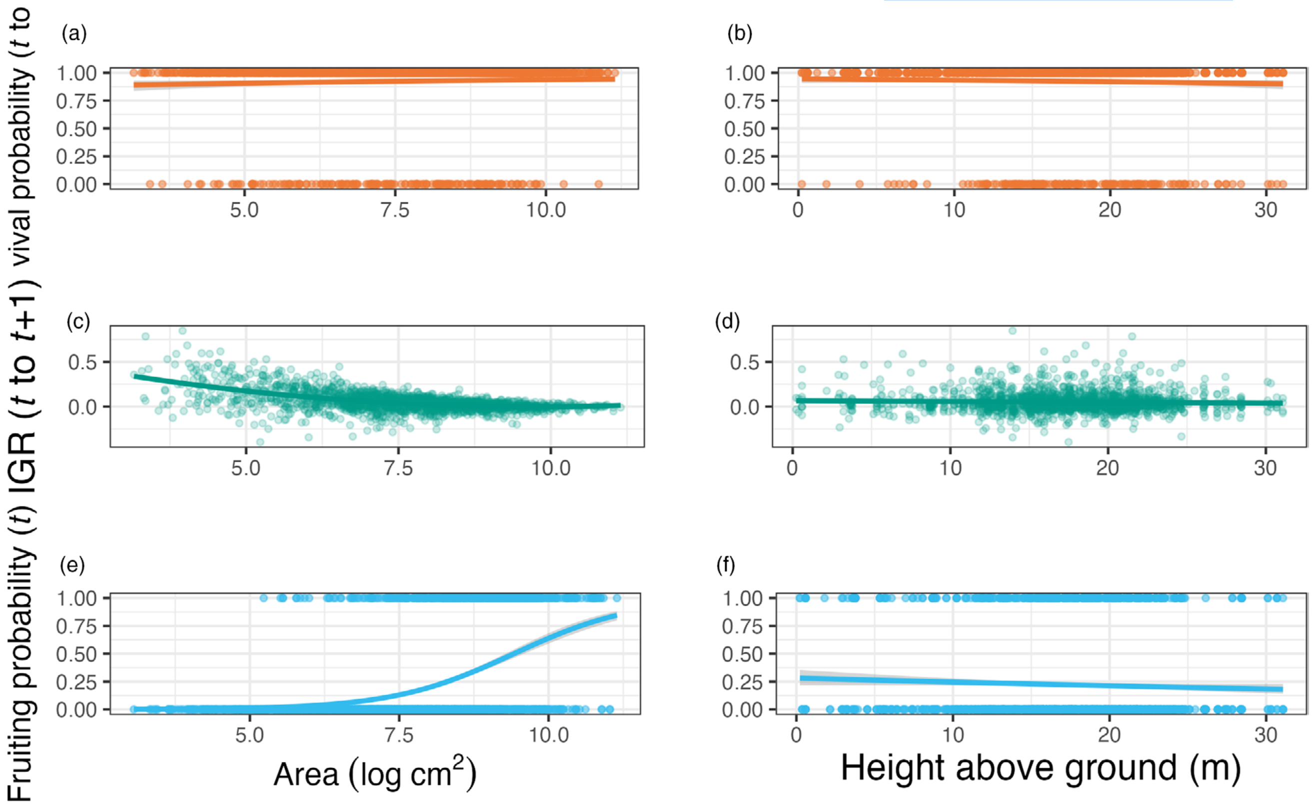

FIGURE 1 Vital rate regressions found significant effects of size on growth and size and position on fruiting probability. The plotted regressions show the effects of parasite size (log-transformed area) and position (height above-ground) on mistletoe vital rates individually (survival, growth and fruiting probability). These vital rates include: (a) survival of individuals from t to $t+1$ as a function of size; (b) survival of individuals from t to $t+1$ as a function of position; (c) relative growth rate (IGR) of individuals from t to $t+1$ as a quadratic function of size in t; (d) IGR of individuals from t to $t+1$ as a linear function of position; (e) fruiting probability as a function of size; (f) fruiting probability as a function of position. Note that fruiting probability is best explained by an additive model of size and position, not shown here. Each regression line is plotted with a 95% confidence interval.

Consequently, this result does not support our hypothesis (H1d) that growth would be greater in mistletoes that are higher in the tree crown. Growth was independent of infection intensity ($\beta=0.001$, $p=0.579$, $n=1897$, Figure S6b).

Our GLMMs showed that the probability of individuals fruiting was best modelled as an additive function of mistletoe size and position. Specifically, fruiting probability increased as a function of size ($\beta=1.175$, $p<0.001$, $n=2166$, Figure 1e), supporting hypothesis H1b. In a combined model with mistletoe size, position on the host also showed a negative relationship with fruiting probability, with parasites higher up being less likely to fruit ($\beta=-0.056$, $p=0.001$, $n=2166$, Figure 1f). This result does not support our hypothesis (H1d) that reproduction would be greater in mistletoes that are higher in the tree crown. Fruiting probability was positively related to infection intensity ($\beta=0.254$, $p=0.003$, $n=2216$, Figure S6c). Because position on the host was negatively related to infection intensity ($\beta=-0.530$, $p<0.001$, $n=2686$, Figure S6d), and both are related to host height (Figure S4), we cannot separate the effects of position and infection intensity on fruiting probability. To retain IPM simplicity, we incorporate the effects of position on the host (constant throughout the life cycle) but not infection intensity, which would require tracking individual hosts.

3.2 | Integral projection model (IPM) and life history traits

The IPM kernel at the mean mistletoe vertical position (height above-ground = 17.0 m), constructed using the vital rate regressions in Table 1 and from which life history traits were extracted, is visually represented in Figure 2. We estimated seed establishment probability as $s_0=0.0500$, which was assumed to be equal to 1- and 2-year-old individual survival (s_1 and s_2, respectively). From our IPM, we estimated a long-term population growth rate of $\lambda=1.057$, reasonably in line with evidence that European mistletoe is expanding at the northern edge of its range, including in Great Britain (Walas et al., 2022). For comparison, we also calculated population growth rate empirically as the mean change in total number of individuals observed each year, estimated similarly at $\lambda=1.083$. From our IPM, we estimated a net reproductive output, R_0, of 1.69. We estimated generation time (T) of 9.36 years, which is reasonable given a maximum longevity of 27–30 years (Zuber, 2004) and that larger individuals are the most reproductive. We estimated mean life expectancy (η_e) for a 1-year-old as 2.47 years, which is reasonable for a seedling which establishes, though this figure does not consider the high mortality of seedlings before establishment (Mellado & Zamora, 2014;

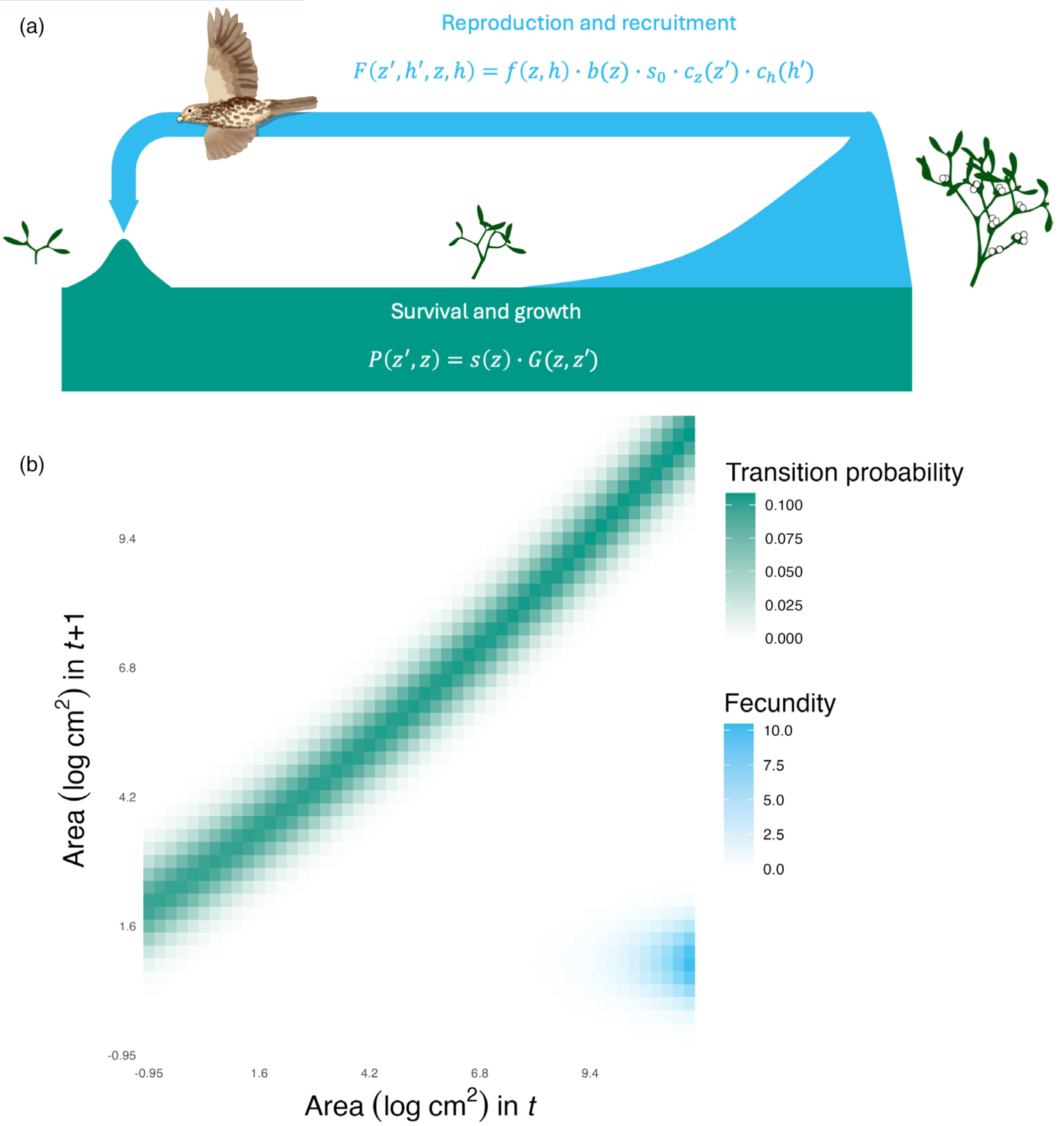

FIGURE 2 Mistletoe life history traits were extracted from our size- and position-based integral projection model (IPM). (a) simplified mistletoe life cycle, including seedling growth and survival (transitioning from smaller to larger individuals), fruiting and recruitment (mediated by birds). This life cycle is used as the basis of (b) our IPM kernel. The kernel is realised for the mean mistletoe height above-ground (17.0 m), mapping size distribution of the population in time t to the size distribution in time t+1. The IPM is plotted at different heights in Figure S9.

Zuber, 2004), estimated from our model as 92.8%. We estimated a mean age at maturity (L_α) of 4.59 years, which is also realistic given flowering is reported to begin after 3–7 years for European mistletoe (Thomas et al., 2022; Zuber, 2004). Thus, when calculated as the difference between mean life expectancy (η_e) and mean age at maturity (L_α), reproductive window ($L_{\alpha\text{-}\omega}$) was estimated as −2.13 years. This negative value is plausible as life expectancy and age at maturity distributions overlap and suggests that a mean individual dies before it reproduces. According to the stable size distribution of the IPM (Caswell, 2001), our model predicts that at equilibrium, only 14.7% of individuals are of reproductive size or larger.

Our parameter-level sensitivity analysis suggests that mistletoe life history traits are not more sensitive to perturbations to vital rates regarding reproduction and establishment (e.g. fruiting probability, establishment probability; Figure 3) than other vital rates, opposing our original expectation (H2). Population growth rate (λ), R_0, generation time, mean age at maturity and reproductive window are most sensitive to the quadratic term of our growth rate function. Only mean life expectancy was most sensitive to survival rate.

3.3 | Principal component analysis (PCA)

Our principal component analysis (PCA; Figure 4) suggests that the macroparasites for which we obtained structured population models (our own *Viscum album*, plus *Thesium subsucculentum* (Albert Gamboa et al., 2009) and *Pedicularis furbishiae* (Menges, 1990)) follow a similar demographic strategy compared to non-parasitic plants. Generation

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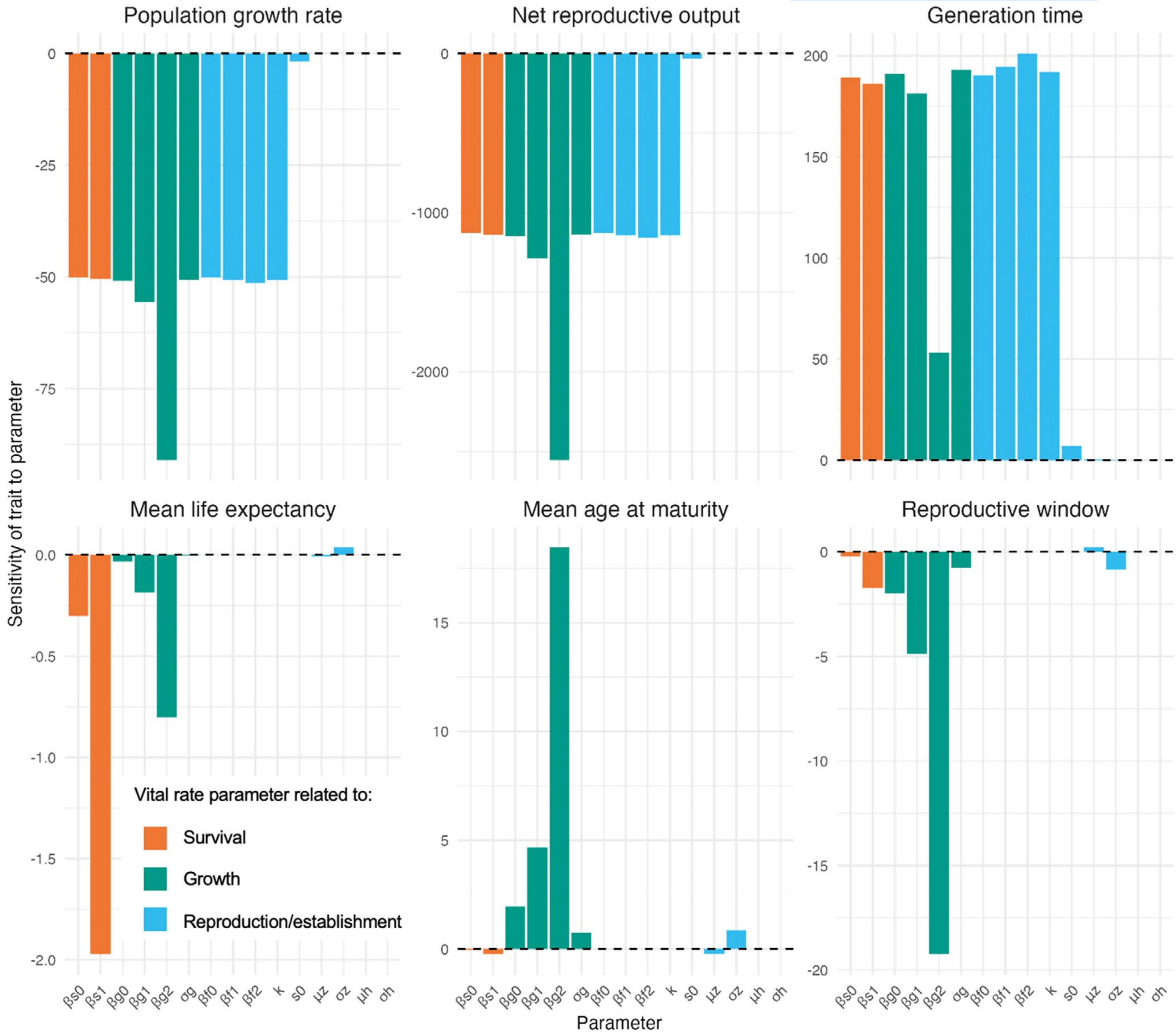

FIGURE 3 Life history traits are sensitive to a variety of IPM parameters. Brute force sensitivities of λ, R_0, generation time (T), mean life expectancy (η_e), mean age at maturity (L_α) and reproductive window ($L_{\alpha\text{-}\omega}$) to each parameter in the IPM (symbols for parameters are defined in Table 1).

time and mean age at maturity loaded strongly onto principal component 1 (PC1). As generation time provides a good proxy for a species' position on the fast–slow continuum (Gaillard et al., 2005), we refer to PC1 as the fast–slow continuum, in line with previous similar analyses (Romeijn & Smallegange, 2022; Salguero-Gómez et al., 2016). Similarly, mean life expectancy and reproductive window loaded strongly onto principal component 2 (PC2). Such life history traits describe the 'reproductive strategy' of a species (Salguero-Gómez et al., 2016), such that we refer to PC2 as the reproductive strategy axis. PC1 and PC2 explained 53.8% and 30.2% of life history trait variation, respectively. *V. album*, highlighted in Figure 4, places slightly towards the 'fast' end of the fast–slow continuum and in the centre of the reproductive strategy axis. The parasitic plants *T. subsucculentum* and *P. furbishiae* place near to *V. album* but are slightly closer to the centre of the fast–slow continuum. The placement of the three parasitic species in life history space opposes our hypothesis (H3) that parasites would exhibit a distinctive strategy compared to non-parasitic plants. While the life history strategy of European mistletoe is not as iteroparous as expected, it does exhibit an intermediate strategy on the fast–slow continuum as predicted. We detected a weak phylogenetic signal from our phylogenetic principal component analysis (Pagel's $\lambda=0.122$).

4 | DISCUSSION

Parasitic plants are distinguished from non-parasitic plants by various adaptations to their parasitic life cycles and particularly their mechanisms of resource acquisition (Queijeiro-Bolanos et al., 2017).

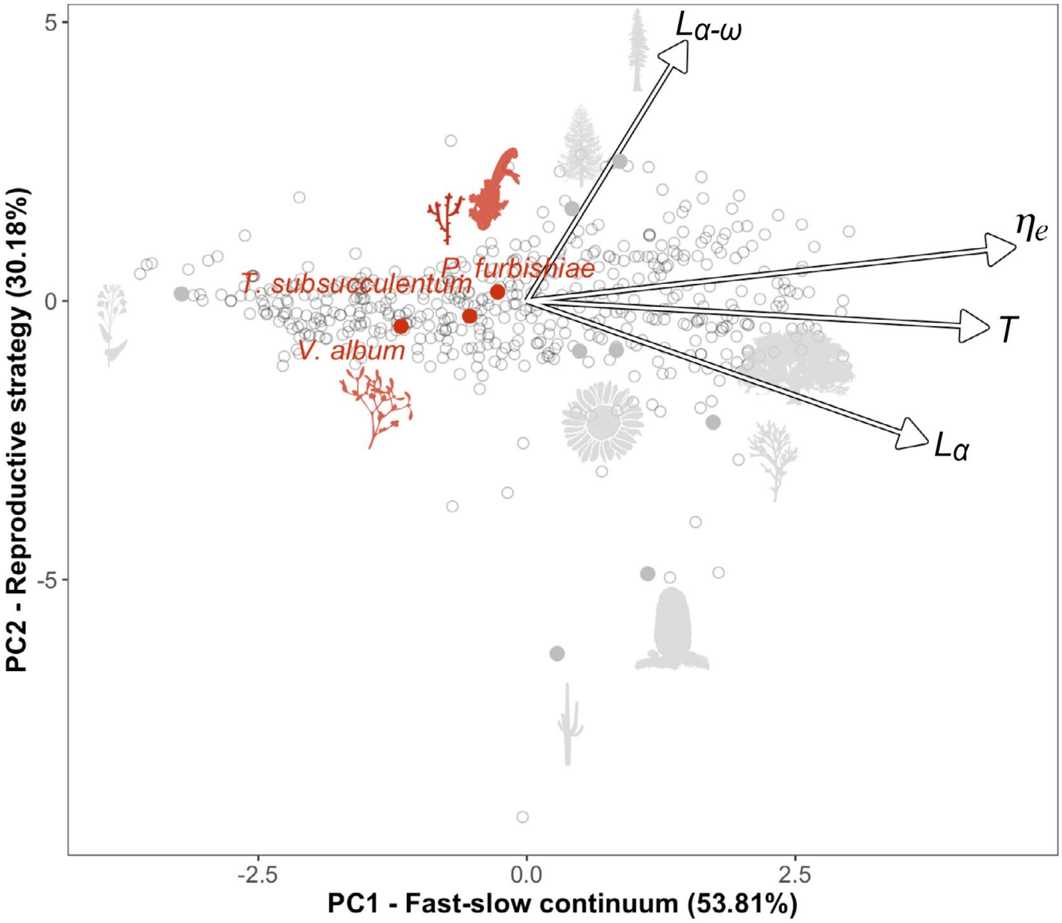

FIGURE 4 Parasitic plants do not display a significantly different life history strategy than non-parasitic plants. Phylogenetically controlled principal component analysis (pPCA) of plant life histories using life history traits derived from 500 matrix population models (MPMs) plus our integral projection model (IPM) for *Viscum album*. Principal component 1 (PC1) represents the fast–slow continuum and principal component 2 (PC2) represents reproductive strategy; variation explained by each axis is given in brackets. Contributions to each principal component are given by each of the following life history traits: Generation time (T), mean life expectancy (η_e), mean age at maturity (L_α), reproductive window ($L_{\alpha\text{-}\omega}$). The positions of *Viscum album*, derived from life history traits extracted from our IPM, and two other parasitic plants (*Thesium subsucculentum* and *Pedicularis furbishiae*) are given by the labelled red points and silhouettes. The position of eight non-parasitic plants around the PCA space is provided for reference, clockwise from the top: Hoop pine (*Araucaria cunninghamii*), coast redwood (*Sequoia sempervirens*), woodland sunflower (*Helianthus divaricatus*), Chinese incense-cedar (*Calocedrus macrolepis*), red fir (*Abies magnifica*), chiotilla (*Escontria chiotilla*), Mongolian oak (*Quercus mongolica* subsp. *crispula*) and rapeseed (*Brassica napus*).

Thus, it may be expected that parasitic plants also differ in their demographic strategies compared to non-parasitic, entirely autotrophic species. Structured population models that link individual trait heterogeneity to population dynamics, such as integral projection models (IPMs; Easterling et al., 2000), can be used to calculate life history traits that summarise a species' demographic strategy (Salguero-Gómez et al., 2016). IPMs are being applied increasingly to host–macroparasite systems (Metcalf et al., 2016), and mistletoes in particular are ideal for demographic study on account of their trackability (Aukema, 2003). Nonetheless, structured population models of parasitic plants remain rare (Römer et al., 2023). Our vital rate regressions of European mistletoe show that parasite traits, specifically size and position on the host, are related to parasite vital rates of growth and reproduction, but not survival. Once we combined our vital rate regressions into an IPM that reflects the mistletoe life cycle, we extracted life history traits that summarise European mistletoe's demographic strategy. Our principal component analysis of these traits along with two other parasitic plants and 490 non-parasitic plants suggests that the parasites and non-parasitic species follow a similar demographic strategy, contrary to our expectations.

Viscum album size, a proxy for age (Zuber, 2004), is a significant predictor of all vital rates, except survival, while vertical position on the host (height above-ground) is also a significant predictor of fruiting. Our results do not support our hypothesis (H1a) that survival would decrease with size, but rather survival rates remain roughly constant following establishment. Size-independent survival rates may be explained by opposing causes of mortality throughout the European mistletoe life cycle. For instance, smaller, younger mistletoes may be at greater risk of being out-shaded, as light access is important for young mistletoe survival as a photosynthetically active hemiparasite (Becker, 1986; Thomas et al., 2022). Simultaneously, larger, older mistletoes may exert greater hydraulic and mechanical stress on their hosts and risk inadvertently causing their own death via embolism or branch snapping, respectively (Griebel et al., 2022). We also found that survival is not significantly predicted by position on the host tree, also opposing our hypothesis (H1c) that survival would decrease with position on the host. Perhaps increased light access at the top of the host canopy for this hemiparasite compensates for increased risk of embolism (Gebauer et al., 2019; Tyree & Zimmermann, 2013) and greater exposure to high winds. In other mistletoe species, survival has been positively related to host height, but not mistletoe position, such as in *Phragmanthera dschallensis* (Loranthaceae) on *Acacia sieberiana* hosts (Roxburgh & Nicolson, 2008). However, such effects are likely due to increased mortality from grazers and fire, which are not applicable to our system.

Here, we show that increased parasite size (and thus age) is associated with a diminishing investment in its own growth and an increase in reproduction in European mistletoe, supporting hypothesis H1b. This result suggests that mistletoes increase investment in reproduction as they grow larger, at the expense of growth, an established trend observed in plants (Reekie & Avila-Sakar, 2005). Position on the host does not have a significant effect on growth but is weakly linked to a reduced probability of fruiting, opposing hypothesis H1d. Lower fruiting probability for individuals located higher on the host may be due to differential resource access, for example, if mistletoes on lower (and possibly older) branches gain priority access to nutrients being transported from the host roots. Alternatively, this unexpected result could be due to detection probability, for example, berries that are higher in the tree crown may be more difficult to detect. However, white *V. album* fruits are easily detectable in high light intensity, as is typically the case higher in the tree. Moreover, because position on the host and mistletoe size are uncorrelated, younger branches with younger, less reproductive mistletoes higher in the tree crown are insufficient to explain lowered fruiting higher up. Fruit set is independent of position in other mistletoe species, such as *Peraxilla tetrapetala* (Loranthaceae) (Robertson et al., 2008). The effects of parasite location on parasite vital rates are likely to be system-specific, as the spatial distribution of resources and/or host defences depends on the system. Indeed, a given site within a host may change in its suitability over time, as observed in *Trichuris* infecting mice (Panesar & Croll, 1980).

We also found that mistletoes were more likely to fruit when growing in trees that were more infested and that mistletoes tend to be lower down in more infested trees. Trees with greater mistletoe intensities are likely to have been infected for longer (Roxburgh & Nicolson, 2008), have a greater number of fruiting individuals which may be found lower in the crown due to 'seed rain' from above (Zamora & Mellado, 2019). Due to this alternative explanation, we cannot interpret the positive relationship between intensity and fruiting as positive density-dependence. We encourage further examination of density-dependent effects on *Viscum album* reproduction, and density-dependent demographic models, including IPMs, would be ideal for this (Ellner & Rees, 2006).

The life history traits derived from our model are sensitive to various parts of the life cycle, including survival rate and quadratic term of growth rate, opposing our hypothesis (H2). Mean life expectancy, age at maturity and reproductive window are calculated only from growth and survival rates, while population growth rate (λ), net reproductive output (R_0) and generation time (T) rely on processes throughout the whole life cycle. We expected the latter life history traits to be the most sensitive to reproduction and establishment rates because of the many filters vector-borne macroparasites must go through to transmit to a new, suitable host (Aukema, 2003; Viney & Cable, 2011). Nonetheless, most outputs were more sensitive to changes in the term describing the quadratic relationship between inherent growth rate and mistletoe size, which greatly influences the parasite size distribution. For example, increases in the quadratic relationship between size and growth may generate more large and highly reproductive individuals, which are analogous to superspreaders in that they disproportionately drive transmission dynamics (Lloyd-Smith et al., 2005). This result underscores the importance of non-uniform parasite size distributions in shaping population dynamics through heterogeneity in reproduction, as observed in trematodes (Saldanha et al., 2009).

The parasitic plants we studied here do not show distinctive demographic strategies compared to the examined 490 non-parasitic plant species as quantified by our time-based life history traits, contrary to our prediction (H3). Rather, *V. album* and the other two parasitic plants for which demographic data are available (*Thesium subsucculentum* and *Pedicularis furbishiae*) place near the centre of life history space described by our PCA. Our findings suggest that these parasitic plants likely experience similar life history constraints to those of non-parasitic plants. Indeed, despite differences in resource acquisition at the individual level, a previous study on competition also found that mistletoes exhibit similar dynamics at the population-level compared to non-parasitic species (Queijeiro-Bolanos et al., 2017). Explicit quantification of mistletoe resource allocation trade-offs could suggest mechanisms underpinning the similar demographic strategies among parasitic and non-parasitic plants. Individual-based models (IBMs; Uchmański & Grimm, 1996) offer an opportunity to link individual heterogeneity in resource acquisition and allocation (Van Noordwijk & De Jong, 1986) to population-level processes in mistletoe and other parasites.

European mistletoe exhibited a slightly more fast-paced demographic strategy than most species, which may imply a disproportionate investment in reproduction at the expense of survival (Stearns, 1998). Such a strategy may be an adaptation to overcome high seedling mortality (Mellado & Zamora, 2014; Zuber, 2004) and the specific requirements of seeds to be produced and dispersed to a suitable host branch before the host dies. Indeed, the expected probability of transmission has been suggested as the most important selection pressure in the evolution of parasite reproductive strategies (Poulin, 1995).

T. subsucculentum and *P. furbishiae* placed closely to *V. album* in our PCA, but with slower life histories, reflecting a greater investment in survival versus reproduction. As root hemiparasites (Macior, 1980; Rodríguez-Rodríguez et al., 2022), *T. subsucculentum* and *P. furbishiae* may face fewer barriers to establishment relative to *V. album*, which requires transmission to a suitable host tree via a bird vector. As such, *V. album* may invest proportionally more in reproduction to counteract high seedling mortality. All three parasites examined in our study are hemiparasites, which obtain carbon from both their host and their own photosynthesis. Future studies should examine the demographic strategies of holoparasites, which may be less constrained in their strategy as resource acquisition is mediated solely by the host (Tesitel, 2016). For example, structured population models of *Cuscuta* (Furuhashi et al., 2011) could yield insightful pairwise comparisons, as demographic data for closely related Convolvulaceae are available (Keeler, 1991).

A limitation of our study is the quantification of European mistletoe reproduction. Due to the high fecundity of some mistletoes and the practical difficulty associated with counting fruits from ground level, our estimate for berry production is based on an allometric relationship (Figure S7). Future studies linking empirical counts of berry production to mistletoe size may offer insights, considering that size~reproduction functional forms vary greatly across the plant kingdom (Bonser & Aarssen, 2009; Klinkhamer et al., 1992). Here, we show that only generation time is sensitive to this assumption (Figures S12 and S13). Moreover, it is difficult to estimate seedling establishment as *Viscum album* is not externally visible (Zuber, 2004), and inoculation experiments to measure survival empirically exhibit high seedling mortality (Kim & Yi, 2013), requiring unrealistic sample sizes. While our estimates of annual survival from seeds to 3-year-olds are uncertain, we believe our approach is optimal given the difficulty in tracking *Viscum* seeds. Our IPM yielded realistic life history traits when using both methods to quantify seedling survival, implying our conclusions are robust to this uncertainty. Also, our estimated establishment seed rate is similar to that estimated previously for *Viscum album* subsp. *austriacum* growing on its preferred host *Pinus nigra* (Mellado & Zamora, 2014). The marked difference between survival across these first 3 years (5%) compared to afterwards (>90%) implies a high level of mortality during establishment, in line with its 'faster' demographic strategy.

Viscum album is dioecious, with separate male and female individuals, which adds further complexity to modelling its life cycle. Males and females only differ in their inconspicuous flowers (~0.5 mm), which emerge in the spring when host leaves are present, such that it is difficult to reliably distinguish non-fruiting females and males in winter. Therefore, and to retain model simplicity, we ignored individual mistletoe sex, though we note that IPMs can readily accommodate sex differences (Schindler et al., 2013). Parasite sex is an intriguing trait that could impact parasite vital rates (Burns, 2021; Morand & Hugot, 2008) and applying sex-based structured population models for macroparasites is an intriguing avenue for further research. Furthermore, our study assumed recruitment was entirely due to sexual reproduction, though asexual vegetative reproduction also occurs in *Viscum album* (Thoday, 1951) to an unknown extent. Because mistletoe clones grow from cortical strands that reach around 4–6 cm per year (Zuber, 2004), clones are probably too close together to be measured as separate individuals from the ground. Consequently, though we underestimated mistletoe intensities, almost all 'individuals' as classified here were generated through sexual reproduction, so ignoring clonal reproduction had minimal effect on model construction. Nonetheless, future studies should investigate the prevalence of clonal reproduction in *Viscum album* and its contribution to population dynamics and can do so through population genetics studies (Yule et al., 2016).

Our study links the traits of parasites to their demographic strategy. However, mistletoe dynamics are also expected to depend on host factors (Fenton et al., 2015; Lemaitre et al., 2012) and avian vectors (Medel et al., 2004; Sasal et al., 2021), which can produce interesting feedback loops (Aukema, 2004; Martínez del Rio et al., 1996). *Viscum album* grows on a wide variety of host tree species (Barney et al., 1998), yet is found much more commonly on particular host species, especially within the Rosaceae (Briggs, 2021). Host factors such as wood biochemical composition (Skrypnik et al., 2021), crown architecture (Sayad et al., 2017) and immune defences (Muche et al., 2022) likely influence mistletoe vital rates. Host lifespan also limits the maximum longevity of a parasite (Nidelet et al., 2009), though mistletoe hosts can typically live over an order of magnitude longer, for example, centuries for *Tilia* (Pigott, 1991), than *Viscum album*, which lives up to around 30 years. Moreover, mistletoe berries are spread by several bird species (Zuber, 2004), which could affect mistletoe vital rates by depositing seeds disproportionately on certain hosts and with variable efficiency. Further research should quantify the relative importance of host, parasite, vector and environmental traits, as well as their interactions, to create a more holistic picture of mistletoe dynamics.

By modelling the vital rates of a plant macroparasite as a function of its size and position on its host, we summarised the demographic strategy of mistletoe and placed it within life history continua. Our results suggest that the demographic strategies of parasitic plants do not appear dissimilar from non-parasitic species. The life history strategies of animal parasites are diverse and are no longer expected to evolve down the same parasitism-associated path (Poulin, 1995) as they previously were (Noble & Noble, 1971). The strategies of parasitic plants in our study also appear unexceptional when compared to those of their non-parasitic counterparts, in line with other studies that have found little difference in population-level behaviour (Queijeiro-Bolanos et al., 2017). Though the demographic strategies of a diversity of parasitic plants remain ripe for study, our results support the view that there is a scarcity of generalisable rules that govern parasite ecology and evolution (Poulin, 2007).

AUTHOR CONTRIBUTIONS

Oliver G. Spacey, Roberto Salguero-Gómez, Owen R. Jones and Sydne Record conceived the ideas and designed methodology; Roberto Salguero-Gómez, Owen R. Jones, Sydne Record, Sharon D. Janssen and Oliver G. Spacey collected the data; Oliver G. Spacey, Wenyi Liu, Roberto Salguero-Gómez, Owen R. Jones, Sydne Record, Sharon D. Janssen, Alice Rosen and Arya Ying Yue analysed the data; Oliver G. Spacey and Roberto Salguero-Gómez led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and code supporting these results have been archived in the Zenodo repository (Spacey et al., 2026), accessible at: https://doi.org/10.5281/zenodo.18744324.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Longitudinal observation summary for the 740 individual mistletoes examined during 10 years in this study, showing in which years individuals were measured.

Figure S2. Distributions of mistletoe size (log area) and position (height above ground) are symmetrical and unimodal.

Figure S3. Our two state variables, mistletoe size (log area) and mistletoe position (height on the host), are independent of one another.

Figure S4. Host height, mistletoe position (height on the host), host species and mistletoe intensity are all related to one another.

Table S1. Vital rate regression models imply that: (i) neither mistletoe size (log(area)) nor position (height) predict survival, (ii) growth is best modelled as a quadratic function of size, and (iii) fruiting is best modelled as a function of size and position.

Table S2. Removal of mistletoes that were not measured in at least 1 year does not impact vital rate regression model selection.

Figure S5. Residual distributions for chosen vital rate regressions.

Figure S6. Relationships of mistletoe (a) survival, (b) inherent growth rate (IGR), (c) fruiting probability and (d) position (height above ground) with infection intensity.

Figure S7. Assumed exponential allometric relationship between log-transformed mistletoe area and number of berries produced, parameterised using Mellado and Zamora (2014).

Figure S8. We assumed normal distributions of 1-year-old size and position, based off roughly normal distributions observed (Figure S2).

Figure S9. IPM kernel plotted at various vertical positions, showing that only the F sub-kernel changes.

Figure S10. Life history traits emerging from the mistletoe integral projection model (IPM) are largely insensitive to the number of meshpoints at high meshpoint values.

Figure S11. IPM outputs are insensitive to the choice of population growth rate (λ) when parameterising our integral projection model (IPM) via the alternative method. Bar charts show the values of the following parameter and IPM outputs to the choice of λ (1.05, 1.10, 1.15): (a) establishment probability, s_0, (b) generation time T, (c) mean life expectancy, η_e, (d) mean age at maturity, L_α, (e) reproductive window, $L_{\alpha\text{-}\omega}$.

Figure S12. Alternative logistic allometric relationship between log-transformed mistletoe area and number of berries produced.

Figure S13. IPM outputs are not very sensitive to the berry functional form used.

Figure S14. After transformation, generation time, age at maturity and reproductive window are unimodal, and mean life expectancy is zero-inflated.

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