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Climate Change Impacts Pair-Bond Dynamics in a Long-Lived Monogamous Species

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ABSTRACT

Climate change can influence populations of monogamous species by affecting pair-bond dynamics. This study examined the impact of climate on widowhood and divorce, and the subsequent effects on individual vital rates and life-history outcomes over 54 years in a snow petrel (*Pagodroma nivea*) population. We found that environmental conditions can affect pair-bond dynamics both directly and indirectly. Divorce was adaptive, occurring more frequently after breeding failure and leading to improved breeding success. Divorce probabilities also increased under severe climatic conditions, regardless of prior breeding success, supporting the 'Habitat-mediated' mechanisms. Overall, pair-bond disruptions reduced subsequent vital rates and life-time outcomes. Climate forecasts from an Atmosphere–Ocean General Circulation Model projected increased male widowhood rates due to decreased sea ice negatively affecting female survival, despite considerable uncertainty. These findings highlight the importance of environmentally induced changes in demographic and pair-bond disruption rates as crucial factors shaping demographic responses to climate change.

1 | Introduction

Climate change is currently one of the major drivers of global biodiversity loss (Bellard et al. 2012; Malcolm et al. 2006; Thomas et al. 2004). Understanding its impact on population dynamics is crucial for accurate population forecasting and effective conservation. Numerous studies have shown that environmental conditions affect life history traits and population dynamics, but fewer have examined how these factors influence mating processes that impact demographic rates and

consequences (Hutchings and Myers 1994; Rowe et al. 1994). In monogamous species with long-term partnerships, environmental conditions can affect pair-bond dynamics by influencing both widowhood and divorce, subsequently impacting demographic processes (Sun et al. 2022a). Pair-bond disruption can also affect reproduction and life history outcomes (Black 2001; Leach et al. 2020; Sun et al. 2022a). Therefore, pair-bond disruption caused by environmental changes can act as a pathway through which climate change affects population growth and extinction risks.

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Both widowhood and divorce can disrupt pair-bonds in monogamous species, though they stem from fundamentally different causes. Widowhood, caused by the death of a partner, is regarded as a nonadaptive process, whilst divorce happens when both partners are still alive but at least one mates with a new partner. Divorce can be adaptive, following a 'win-stay/lose-switch' strategy, where individuals separate after unsuccessful reproduction and breed with new mates to improve breeding success (Bried and Jouventin 2001; Choudhury 1995). Divorce may also be non-adaptive with no clear benefit, such as interference by an intruder who outcompetes the original partner, referred to as the 'forced divorce' hypothesis (Choudhury 1995; Sun et al. 2022b). Both divorce and widowhood are influenced by environmental factors. Environmental factors can affect survival rates, leading to sex-biased widowhood if one sex is more impacted than the other. Environmental variability can also impact breeding success, indirectly increasing divorce rates (Blondel, Perret, and Galan 2000; Ventura et al. 2021), which we termed the 'Indirect Effect' Hypothesis [H1] (Figure 1, blue arrow).

Environmental conditions may also directly affect pair-bond dynamics regardless of previous breeding success, termed the 'Direct Effect' Hypothesis [H2] (Figure 1, orange arrows) (Blondel, Perret, and Galan 2000; Heg, Bruinzeel, and Ens 2003). Two scenarios, the 'Habitat-Mediated Effect' [H2.1] and the 'Discounting Effect' [H2.2], have been proposed to

describe the direct response of divorce to environmental conditions. According to the habitat-mediated effect, adverse environmental conditions could increase divorce rates, whereas the discounting effect posits that unfavourable conditions might result in reduced divorce rates.

Several mechanisms may explain the higher divorce rate under the habitat-mediated effects [H2.1]. Harsh environmental conditions can disrupt individual decision-making processes (Blondel, Perret, and Galan 2000; Culina, Radersma, and Sheldon 2015; Robert et al. 2014). Limited resources may lead individuals to associate the higher reproductive costs with the quality of their partners (Ventura et al. 2021). Harsh environmental conditions can also affect mate quality assessment, making some cues difficult to evaluate (Candolin 2019). Additionally, mate fidelity may be linked to site fidelity. Poor habitat quality can increase the likelihood of abandoning the nest site and mate, leading to more divorces during unfavourable conditions (Black 1996). Alternatively, the discounting effect [H2.2] suggests that under unfavourable conditions, individuals attribute poor breeding performance to environmental factors rather than their partners, resulting in lower divorce probabilities. This hypothesis is supported by evidence that mate and nest fidelity increases under harsh conditions in Robert et al. (2014).

Pair-bond disruptions, whether due to widowhood or divorce, entail various costs affecting individual vital rates and life-history

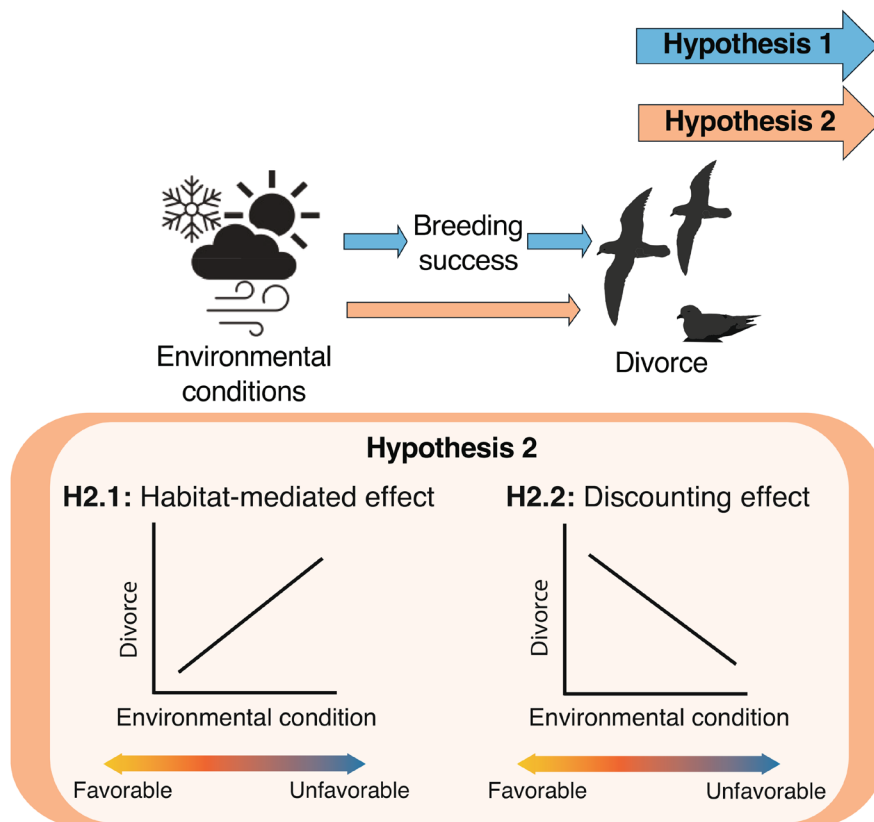


FIGURE 1 | Environmental conditions can impact divorce probability both indirectly and directly. (i) Environmental factors can affect divorce by influencing breeding success (Hypothesis 1 [H1] – indirect effect, blue arrows). (ii) Divorce probabilities, independent of previous breeding success (Hypothesis 2 [H2] – direct effect, orange arrows), can be influenced by environmental conditions through the 'habitat-mediated effect' [H2.1] or 'discounting effect' [H2.2]. If driven by the habitat-mediated effect, divorce probability is higher in unfavourable conditions, whilst the discounting effect predicts that divorce probability is lower in adverse environmental conditions.

outcomes. Seeking a new partner can increase mortality risks due to mate search costs and territorial competition (Culina, Radersma, and Sheldon 2015; Nicolai et al. 2012). After bonding with a new mate, there may be an initial reduction in breeding success due to inefficiencies in fine-tuning parental care behaviours (Harrison et al. 2009; McCully et al. 2022), termed ‘the syndrome of the first-year bond’ hypothesis (Naves, Cam, and Monnat 2007). Moreover, in many long-lived monogamous species, reestablishing functional pair-bonds after widowhood or divorce can take years, leading to skipped breeding seasons and reduced lifetime reproductive success (Jouventin, Lequette, and Dobson 1999; Sun et al. 2022a).

Utilising a 54-year capture-mark-recapture dataset and employing advanced modelling approaches that account for both divorce and widowhood, we investigated how environmental conditions influence pair-bond dynamics and demographic outcomes in the snow petrel (*Pagodroma nivea*), a long-lived monogamous seabird. Previous research has shown that winter sea ice influences adult survival (Barbraud et al. 2000), whilst air temperature, sea ice concentration and snowfall affect breeding success (Jenouvrier, Barbraud, and Weimerskirch 2005; Sauser, Delord, and Barbraud 2018, 2021b). Based on these findings, environmental conditions may affect widowhood by affecting survival. We also hypothesized that environmental conditions affect divorce indirectly by affecting breeding success [H1], and directly by altering divorce probabilities [H2] (Figure 1). The direct impact of environmental conditions on divorce probability [H2] was examined after accounting for breeding success. We expected an increased divorce probability under severe environmental conditions if influenced by the ‘Habitat-mediated Effect’ [H2.1], and a decreased divorce probability under adverse conditions if influenced by the ‘Discounting Effect’ [H2.2] (Figure 1). We anticipated that pair-bond disruptions have negative impacts on individual vital rates and life-history outcomes.

Additionally, we evaluated changes in divorce and widowhood probabilities due to climate change using projections derived from the Community Earth System Model version 2 large ensemble (CESM2-LE) (Danabasoglu et al. 2020; Maher, Milinski, and Ludwig 2021), considering uncertainties from climate variability and demographic processes (Jenouvrier et al. 2020). Natural climate uncertainties are rarely included in ecological forecasts, leading to incomplete assessments of ecosystem responses to future climate conditions, which highlights the need to integrate such variability into ecological modelling.

2 | Material and Methods

We relied on Bayesian multi-state capture-mark-recapture models (MSCMR) and absorbing Markov chains (AMCs) for our analysis. Bayesian MSCMR allowed us to estimate vital rates, divorce and widowhood probabilities, and analyse the effects of prior breeding success on divorce probabilities and climate variables on vital rates. We quantified life-history outcomes using the AMC framework. Both Bayesian MSCMR and AMC depend on the life cycle of snow petrels described in Section 2.2.

2.1 | Study Species

The snow petrel is a monogamous Antarctic species with a circumpolar distribution (Croxford et al. 1995). It forages exclusively within the marginal ice zone (Ridoux and Offredo 1989). Breeding occurs in austral summer, with arrivals at colonies in late October, copulation and egg laying by females in late November/early December. Both parents share care, alternating foraging trips during the 44-day incubation. They feed the chick until fledging, which occurs 47 days after hatching (Barbraud et al. 1999). Adults leave the colony in early March, dispersing at sea and staying in the sea ice zone during the non-breeding period (Delord et al. 2016).

The studied colony of snow petrel was located at Ile des Pétrels, Pointe Géologie Archipelago (66°40' S, 140°01' E), Terre Adélie, Antarctica. Since 1963, an annual long-term monitoring study has leg-banded adults and chicks with stainless-steel bands, determining adult sex by vocalisation and relative size (Barbraud, Lormée, and LeNévé 2000). Nest surveys during incubation and fledging periods determined breeding success and pair identities (Chastel, Weimerskirch, and Jouventin 1993). We used life histories of adults identified from 1963 to 2016, totaling 543 females and 522 males.

2.2 | Life Cycle

We structured the snow petrel population into six living states depending on pair-bond and breeding status (Figure 2). Breeders may remain with the same partner (SB), find a new partner after widowhood (NW) or after divorce (ND). Non-breeders may skip breeding whilst maintaining their pair-bond (NB), or become unmated individuals due to divorce (D) or widowhood (W). Transitions between living states from state i to state j from year $t-1$ to t depend on individual vital rates (survival- s and breeding- b probabilities) and pair-bond disruption probabilities (divorce- d and widowhood- w). Transition probabilities vary based on individual states (Figure 2, Appendix Section S1.1).

2.3 | Bayesian Framework to Estimate Vital Rates and Pair-Bond Disruption Rates

We used a Bayesian MSCMR model based on the snow petrel life cycle to estimate demographic parameters, including pair-bond disruption rates (widowhood and divorce), and demographic rates (survival, breeding and breeding success) with temporal variations. We accounted for imperfect detection by linking individual life histories to detection by estimating detection probability depending on individual states (Appendix Section S1.2). Individual life histories were modelled using Bernoulli distributions (Appendix Table S1). Directly estimated parameters included $s_{i,t}$, $w_{i,t}$, $d_{i,t}$, $b_{i,t}$ – apparent survival, widowhood, divorce and breeding probabilities in year t of individuals in state i in year $t-1$ (Figure 2) – and $r_{i,t}$ and $o_{i,t}$ – apparent breeding success and detection probabilities in year t of individuals in state i in year t . We examined how breeding success influences divorce probabilities by considering the pair's prior breeding attempt (Appendix Section S1.2). Divorce, identified when at least one

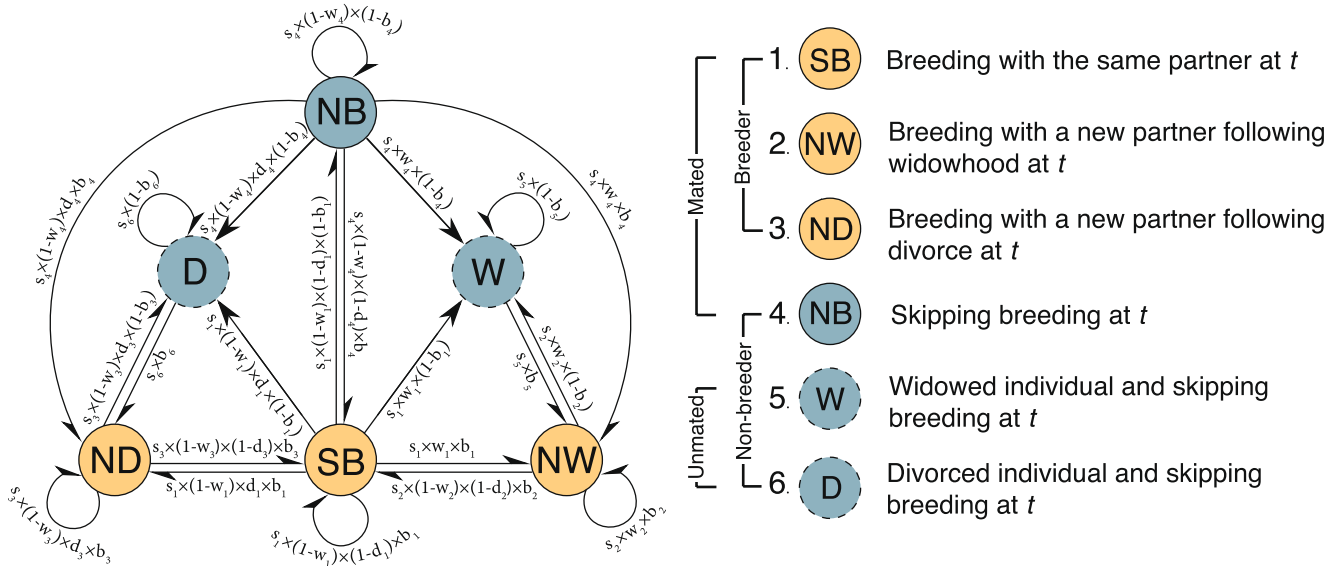


FIGURE 2 | Life cycle graph for snow petrels along with individual state definitions, which shows annual state transitions of individuals from year $t-1$ to year t between pair status defined on the right. Solid circles indicate mated individuals within a pair-bond relationship (SB, NW, ND and NB), and dashed circles represent unmated individuals that are single and not in any pair-bond relationships (D and W). Breeders and nonbreeders in year t are denoted as yellow and blue, respectively. Individuals can skip breeding at the season t , so their previous partner is defined as the partner at their last breeding season, $t-k$. Transitions between pair-bond states (shown as one-way arrows) from year $t-1$ to year t are conditional on state-specific survival (s), widowhood (w), divorce (d) and breeding (b) probabilities shown as equations on the arrows. The state-specific parameters are shown as subscripts corresponding to the number of pair states defined at right. 'Death' was not included as a state because our life-cycle graph only depicts transitions of living individuals.

partner mated with a new partner, could occur years after the last breeding attempt and subsequent non-breeding years. Thus, we included these skipped breeding years and tracked individuals' previous breeding success.

Parameter estimation in Bayesian MSCMR relied on Markov chain Monte Carlo (MCMC) methods for posterior sampling, using JAGS (Plummer 2003) via R package jagsUI (Kellner and Meredith 2021) (Appendix Section S1.2). Since mate fates are dependent – divorce affects both partners, and widowhood results from a partner's death – we applied the Bayesian MSCMR framework separately to males and females, following Culina et al. (2013).

The posterior probability of an effect was calculated as the proportion of the posterior distribution that shared the same sign as the posterior mean (Jeffreys 1998; Ly, Verhagen, and Wagenmakers 2016), which we referred to as the 'F' value onwards (Fay et al. 2022; Van de Walle et al. 2024). An F -value near 100% signifies strong evidence of an effect, whereas values around 50% indicate no clear evidence. We categorised the likelihood of an effect as follows: 80%–100% as likely, 95%–100% as very likely and 99%–100% as extremely likely (Appendix Section S1.2).

2.4 | Effects of Environmental Conditions on Pair-Bond Disruption

We investigated indirect effects (H1, Figure 1) and direct effects (H2, Figure 1) of environmental conditions on pair-bond disruption. We considered local snowfalls, air temperature and sea ice area, known to affect snow petrel life history (Barbraud et al. 2021; Jenouvrier, Barbraud, and Weimerskirch 2005;

Sausser, Delord, and Barbraud 2021a; Weathers, Gerhart, and Hodum 2000) (Appendix Section S1.4). For breeding success, we used the number of snow days, the mean maximum daily air temperature (noted as mean temperature hereafter) and the average sea ice area during incubation and the early chick-rearing period (December to February) as environmental covariates. Sea ice area was extracted from the Japanese 55-year Reanalysis (JRA-55) for adult foraging grounds (66.2°S–64.2°S, 116°E–133.2°E) (Delord et al. 2016; Kobayashi et al. 2015). Snow and air temperature were obtained from the Météo France station in Dumont d'Urville, situated about 450 m from studied colony. The winter sea ice area was shown to affect adult survival (Barbraud et al. 2000; Sausser, Delord, and Barbraud 2021a). To investigate how environmental conditions affected adult survival and thus widowhood probabilities, we used sea ice area averaged between April and September from adult non-breeding foraging grounds (64.0°S–58.4°S, 45.3°E–126.1°E, from Delord et al. (2016)) extracted from JRA-55.

We tested how environmental conditions directly affect divorce (H2, Figure 1) by investigating the relationships between environmental conditions during the previous breeding attempt and divorce. We considered previously successful and failed individuals separately controlling for effects of previous breeding success (Appendix Section S1.2).

2.5 | Life-History Outcomes

We examined how pair-bond disruptions affect life expectancy, lifetime reproductive success, breeding intervals and the

expected duration of being unmated (due to divorce or widowhood). These analyses used an absorbing finite-state Markov chain with death as the absorbing state, defined by the snow petrel life cycle (Caswell 2009) and parameterized using estimates from our Bayesian MSCMR models (Section 2.3).

The expected duration an individual remains unmated was determined by adding the time spent in divorced (D) and widowed (W) states (Caswell 2009, 2011; Roth and Caswell 2018). We computed the expected time for an individual to initiate its next breeding attempt (state SB and FB) based on its current state and transition probabilities (Roth and Caswell 2018). Lifetime reproductive success was assessed by considering reproductive outcome as a cumulative reward each time an individual enters a breeding state, following methods in van Daalen and Caswell (2017) (see also Gimenez and Gaillard (2018) for methods accounting for imperfect detection). Further details on life-history outcomes and occupancy time calculations are provided in Appendix Section S1.3.

2.6 | Projection of Pair-Bond Disruption Rates

The CESM2 Large Ensemble (CESM2-LE) ran climate projections from 1850 to 2099 with multiple simulations, varying initial conditions but keeping model parameters and external forcing constant, to provide a range of potential future climate outcomes and understand projection uncertainty (Danabasoglu et al. 2020; Rodgers et al. 2021). Projections of snow days, mean maximum daily air temperature and sea ice area during both breeding and non-breeding seasons were obtained from CESM2-LE for the region around Pointe Géologie (Appendix Section S1.5). We used 50 ensemble simulations of CESM2-LE spanning 1850–2099. The population size was assumed to be constant with an equal sex ratio, making our forecasts conservative by ignoring feedback from sex-ratio changes or pair disruptions. Annual rates of divorce and widowhood were based on the proportion of divorced and widowed individuals in the population.

3 | Results

3.1 | Pair-Bond Disruption Probability and Its Impacts on Individual Fitness

Widowhood and divorce had annual probabilities lower than 0.08. Males were likely (F -value [F]=91.9%) to have higher widowhood probabilities (0.055 ± 0.003 (mean $\pm$ standard deviation)) than females (0.049 ± 0.003 , Figure 3a), reflecting sex-specific survival probabilities. Divorce probabilities were extremely likely to increase after a breeding failure for both sexes (male: $F = 100\%$; female: $F = 99.3\%$, Figure 3b). Average divorce probabilities were 0.055 ± 0.004 for previously successful and 0.071 ± 0.005 for previously failed females. For males, estimates were 0.051 ± 0.004 for previously successful and 0.080 ± 0.005 for previously failed individuals.

Breeders with the same partner (SB) had higher survival probabilities than those that bred with a new partner after widowhood (NW, female $F = 91.8\%$, male $F = 86.7\%$) or divorce (ND, female $F = 99.5\%$, male $F = 99.6\%$, Figure 3c, Appendix

Table S2). Widowed individuals (W) had higher survival (female $F = 98.1\%$, male $F = 93.9\%$) than divorced individuals (D) (Figure 3c, Appendix Table S2). Non-breeding individuals (NB) skipping breeding had lower survival probabilities compared to SB (female $F = 97.2\%$, male $F = 94.3\%$), W ($F = 100\%$ for both sexes) and D (female $F = 92.4\%$, male $F = 92.9\%$). Overall, females had lower mean survival than males ($F = 87.3\%$).

Mated individuals (SB, NW, ND and NB) were more likely to breed the following year than divorced and widowed individuals (Figure 3c, Appendix Table S2). For females, breeding probability was lower after breeding with a new partner after widowhood (NW) or divorce (ND) compared to the same partner (NW $F = 99.8\%$; ND $F = 99.5\%$). Males that bred with a new partner also had lower breeding probability compared to those with the same partner (SB) (NW $F = 99.4\%$; ND $F = 98.4\%$). Non-breeding individuals skipping breeding (NB) had a lower breeding probability (female $F = 100\%$; male $F = 100\%$) than individuals breeding with the same previous partner (SB) the following year. Unmated individuals (W and D) had a lower breeding probability than mated individuals (SB, NW, ND and NB) (Figure 3c, Appendix Table S2), with divorced individuals (D) having even lower breeding probability (female $F = 96.2\%$; male $F = 98.7\%$) than widowed individuals (W).

For breeding success, those with the same previous partner (SB) had higher probabilities than those with a new partner after widowhood (NW, female $F = 100\%$; male $F = 99.3\%$, Figure 3c, Appendix Table S2). Divorced individuals breeding with a new partner (ND) had higher success compared to their mean success of 0.347 (female $F = 100\%$; male $F = 100\%$) before divorce (dashed line in Figure 3c, Appendix Table S2). Individuals breeding with a new partner after widowhood (NW) had the lowest success.

Unmated divorced and widowed individuals exhibited lower Lifetime Reproductive Success (LRS) (female: 2.67 ± 0.017 ; male: 3.53 ± 0.02) than mated pairs (SB, NW, ND and NB) (female: 2.95 ± 0.016 ; male: 3.81 ± 0.018) (Figure 3d). The reduction in LRS for unmated individuals was 10.5% and 8.5% in females and males, respectively. The reduced LRS stemmed from the prolonged remating process for unmated divorced and widowed individuals (Figure 3d). On average, unmated individuals required more time to breed again (female: 3.029 ± 0.012 years; male: 3.33 ± 0.013 years) than mated individuals (female: 1.726 ± 0.002 years; male: 1.680 ± 0.002 years), and spent a higher percentage of their lifetime in the non-breeding unmated state (female: $30.7 \pm 0.086\%$; male: $45.1 \pm 0.090\%$) than mated individuals (female: $46.3 \pm 0.112\%$; male: $30.6 \pm 0.115\%$).

3.2 | Environmental Effects on Survival and Widowhood

Environmental conditions impacted survival, thereby affecting widowhood probabilities (Figure 4, Appendix Table S4). Sea ice area in the preceding non-breeding season had different effects on male and female survival, influencing widowhood probability differently. Sea ice area positively affected female survival (slope = 0.158, $F = 86.2\%$, Figure 4a), whilst its corresponding impact on male widowhood probability was negative but not statistically significant (slope = -0.043 , $F = 67.6\%$, Figure 4d). Sea ice area is likely to

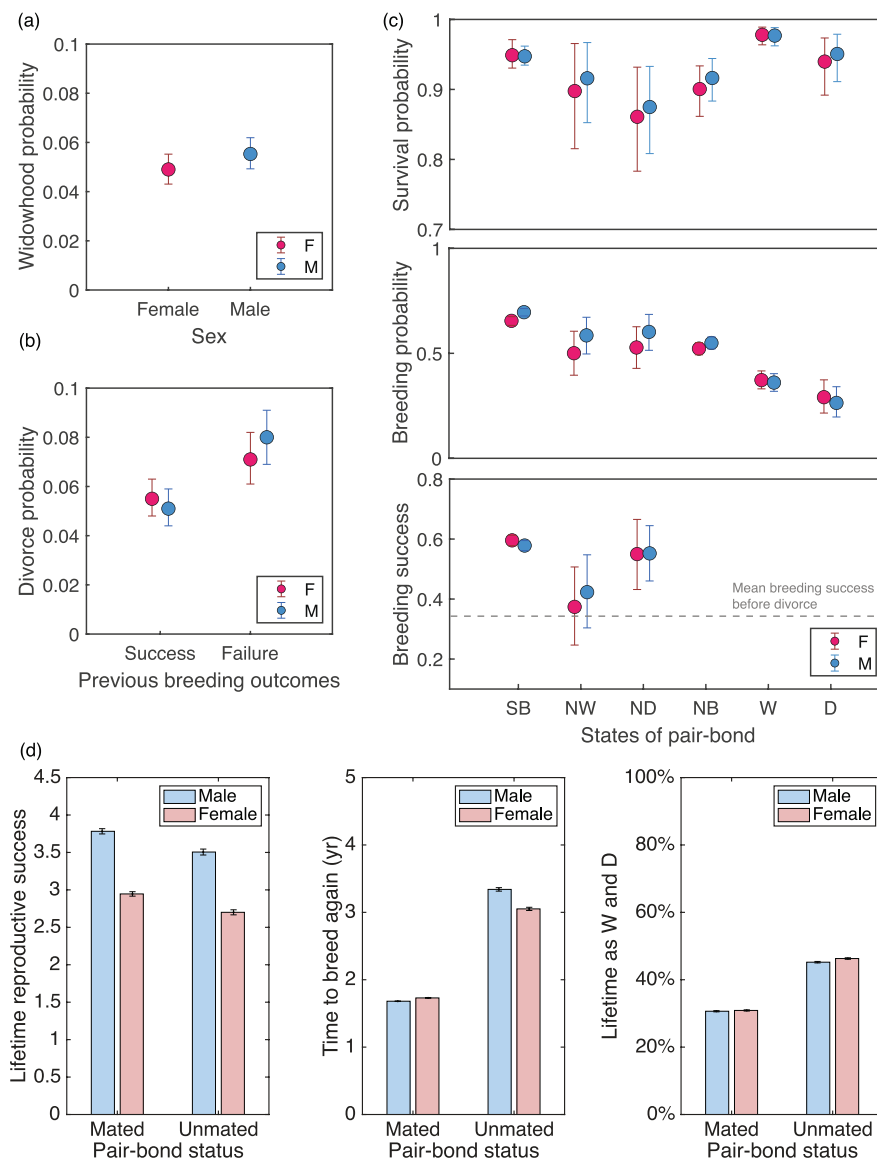


FIGURE 3 | Estimates of pair-bond disruption probabilities and the impacts of pair-bond disruption on individual vital rates and life history outcomes ($\pm 95\%$ confidence interval). (a) Probability of becoming widowed as a function of sex, (b) divorce probability as a function of sex, and the success of the previous breeding attempt and (c) sex-specific survival and breeding probabilities depending on an individual's pair state in year $t-1$ and breeding success depending on an individual's current pair state in year t . Individual pair states include breeding with the same partner (SB), breeding with a new partner after widowhood (NW) or divorce (ND), nonbreeding (NB), divorced (D) and widowed (W) states, along with a dead state. The dashed line shows the average breeding success of the last breeding attempt for pairs that divorced afterwards. (d) Sex-specific expectations of remaining lifetime reproductive success, time to reach the next breeding attempt and percentage of lifetime as divorced and widowed individuals, depending on whether an individual was mated (states SB, NW, ND and NB) or unmated (D and W).

positively affect the female widowhood probability (slope=0.099, $F=86.0\%$, Figure 4c), and had a non-significant negative impact on male survival (slope=-0.068, $F=70.1\%$, Figure 4b).

3.3 | H1: The Environment Influences Divorce by Its Effect on Breeding Success

The number of snow days is likely to negatively affect breeding success (female: slope=-0.133, $F=86.3\%$; male: slope=-0.122, $F=79.3\%$, Figure 4e). Furthermore, the mean temperature during the breeding season was very likely to positively affect male breeding success (slope=0.259, $F=95.9\%$), and likely

to positively affect female breeding success (slope=0.187, $F=93.3\%$, Figure 4f). Therefore, divorce probability increases with more snowfall and lower temperatures due to higher breeding failure probabilities, which can trigger divorce (Figure 4, Appendix Table S5).

3.4 | H2: Environmental Conditions May Still Influence Divorce Probabilities Regardless of Previous Breeding Success

After accounting for breeding success, divorce probability was higher during seasons with increased snow days (Figure 5,

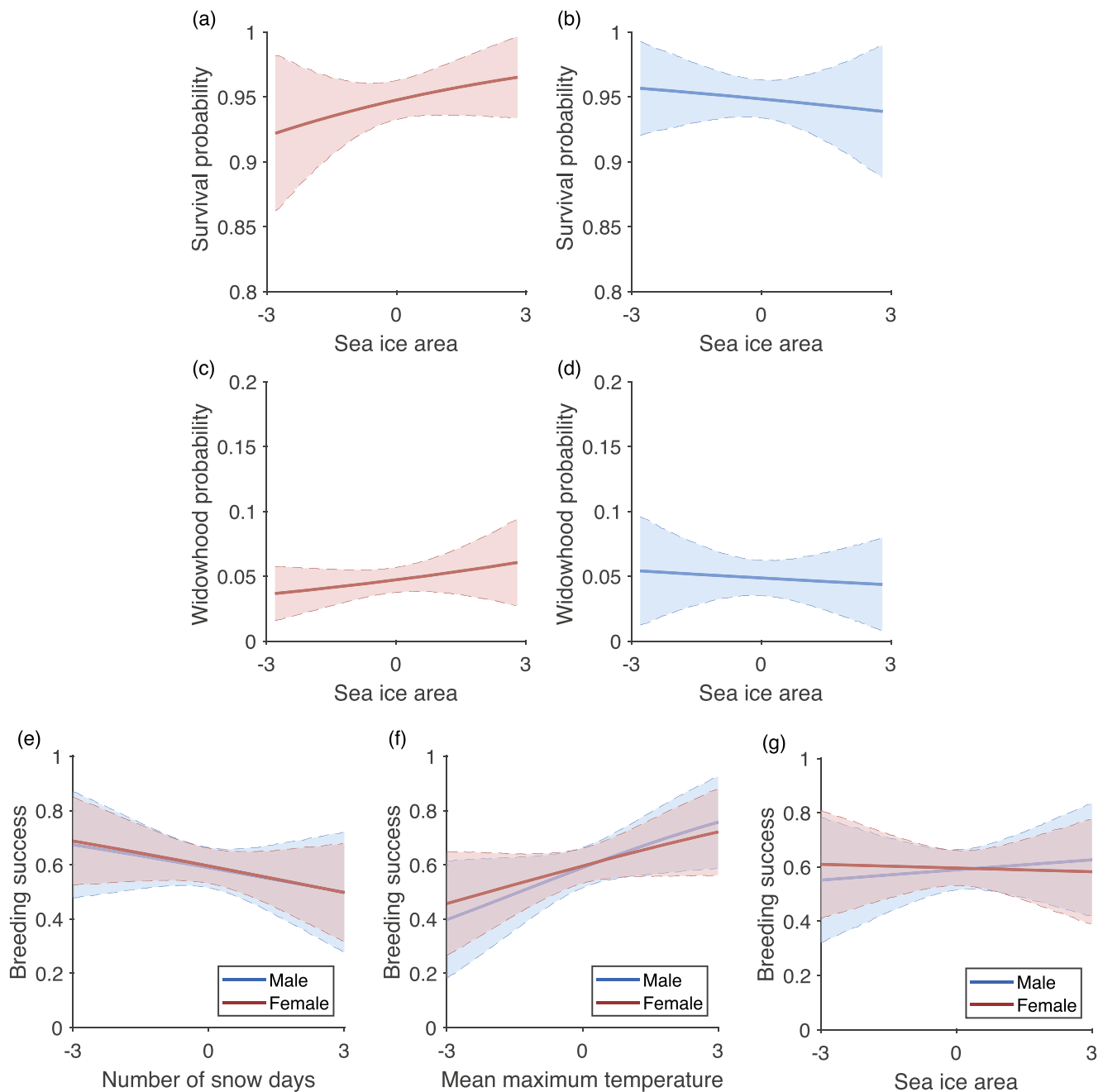


FIGURE 4 | Environmental conditions can affect pair-bond dynamics by affecting survival and widowhood probabilities. Effect of winter sea ice area (standardised) on survival (a and c) and widowhood probabilities (b and d) for female (red) and male (blue) snow petrels. Effect of the number of snow days (e), mean maximum temperature (f) and sea ice area (g) (standardised) on breeding success in snow petrels. Solid lines represent median effects, whereas the shaded area represents the 95% confidence intervals.

Appendix Table S6). Environmental conditions had varying effects on previously failed and successful breeders. In years with more snow days, divorce probability increased for previously successful individuals (males: slope=0.294, $F=99.2\%$, Figure 5b, females: slope=0.190, $F=93.0\%$, Figure 5a). For previously failed individuals, snow days had no significant effect on divorce (males: slope=0.083, $F=78.8\%$, females: slope=0.001, $F=50.3\%$, Figure 5a). Neither air temperature nor sea ice area had effects on divorce probability after controlling for breeding success (Figure 5, Appendix Table S6).

3.5 | Projection of Pair-Bond Disruption Rates

The forecasted divorce and widowhood probabilities showed significant uncertainty by the end of the 21st century (Figure 6). Declining sea ice (Appendix Figure S1) is projected to negatively impact female survival rates with all trajectories (100%) indicating a negative trend (Appendix Figure S2a), increasing male widowhood rate. All trajectories (100%) forecast a reduction in female widowhood rates and an increase in male widowhood rates (with a mean increase of 67.8%, Figure 6b,d). The increase in

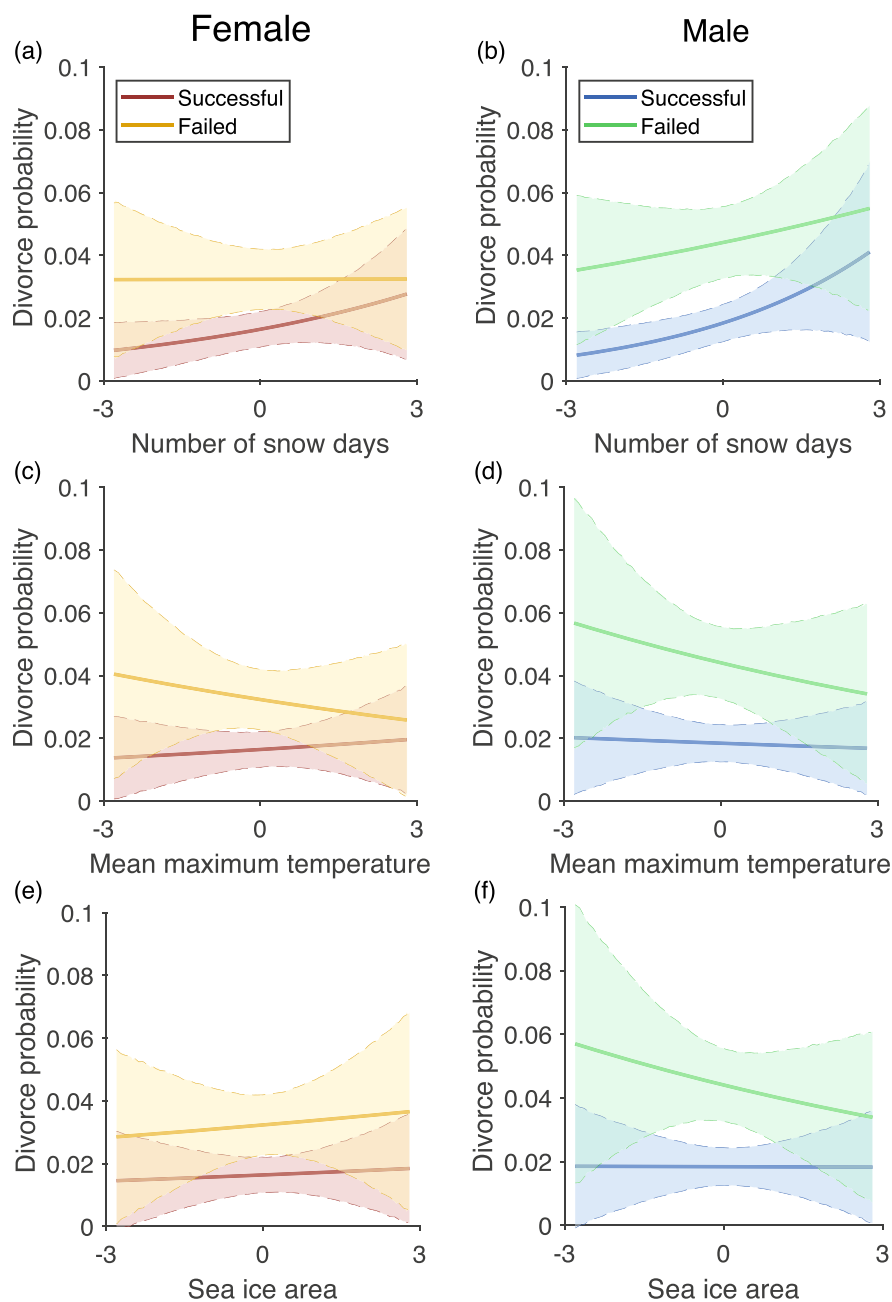


FIGURE 5 | The effects of standardised environmental conditions on divorce probability in snow petrels are presented separately for previously successful and failed individuals. The left panel (a, c, and e) displays results for females, whilst the right panel (b, d, and f) displays results for males. Solid lines represent median effects, whereas the shaded area represents the 95% confidence intervals.

male widowhood rates is associated with reduced non-breeding season sea ice (Appendix Figure S1d) and rising female mortality (Appendix Figure S2a). The female divorce rates (46% positive trends) and male divorce rates (54% positive trends) are expected to remain stable, assuming mate availability and population size remain unchanged by climate conditions (Figure 6a,c).

4 | Discussion

Our research provides new insights into how environmental factors influence pair-bond dynamics. We discovered that the

disruption of pair-bonds decreases individual survival, breeding and success rates, ultimately leading to a decline in lifetime reproductive success. The pair-bond disruption is driven by environmental variability both indirectly [H1] and directly [H2], with a higher likelihood of divorce under unfavourable conditions. Notably, widowed individuals showed higher survival and breeding probabilities compared to divorced ones, suggesting that widowed and divorced individuals may encounter different challenges when finding new mates. Despite uncertainties towards the end of the century, the anticipated rise in male widowhood rates could have significant demographic impacts.

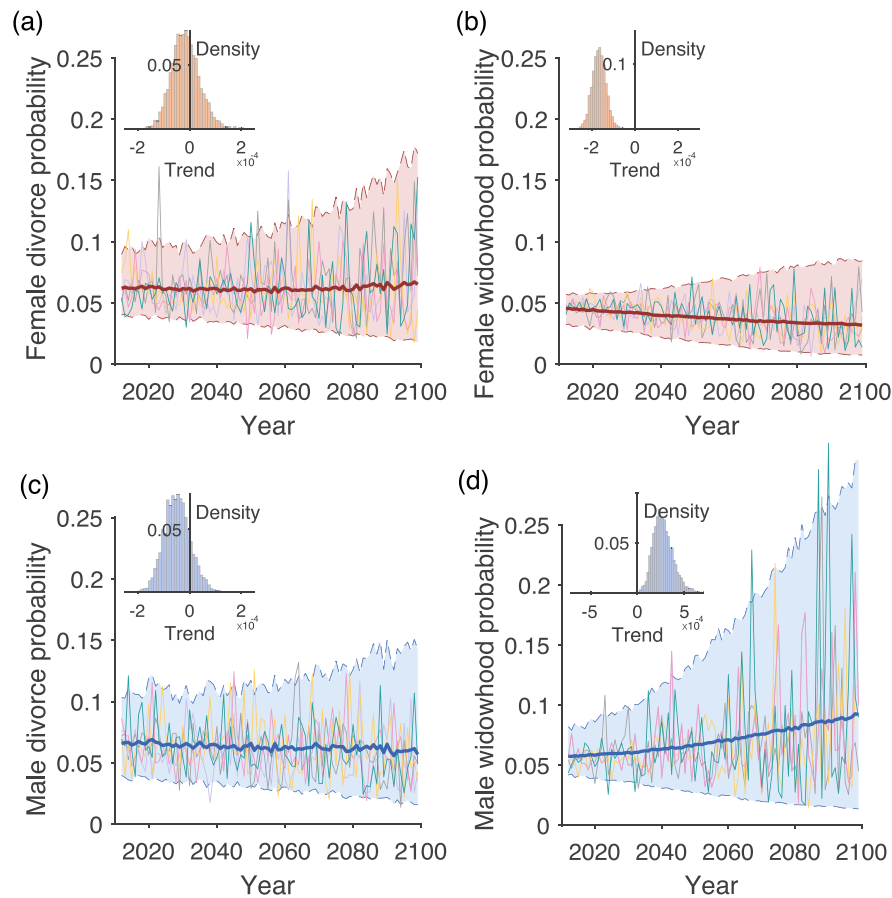


FIGURE 6 | Projections of divorce and widowhood probabilities from 2012 to 2099 using projections of environmental covariates from CESM2-LE. Panels (a) and (b) present female divorce and widowhood probability projections and panels (c) and (d) present male divorce and widowhood probability projections. The solid thick lines represent the median effects, and the shaded areas denote the 95% confidence intervals. The thin coloured lines in each panel represent five simulation trajectories randomly selected from 5000 simulations (100 stochastic simulations from each of the 50 ensembles), illustrating the variability. The density plots in each panel show the distribution of the trend values for each trajectory. The trend correlation coefficient for each trajectory was calculated using a simple linear regression with time.

4.1 | The Effect of Environmental Conditions on Pair Bond Disruption

Survival and widowhood probabilities exhibit sex-specific reactions to winter sea ice. Snow petrels are sexually dimorphic, with males being heavier and having longer and deeper bills than females (Barbraud et al. 2021). Females and males are likely to employ different foraging strategies and habitat uses, leading to varied responses to environmental conditions. The non-significant negative impact of sea ice on male survival aligns with Sauser, Delord, and Barbraud (2021a), which reported negative effects on survival only in previously breeding males. This may explain the more pronounced effects of sea ice on female widowhood probabilities since sea ice mainly affects males in pair-bonds. Whilst no prior studies have directly supported the positive effect of winter sea ice on female survival observed in our study, higher sea ice concentrations can enhance female foraging efficiency. Higher sea ice concentration was associated with increased mass gain, proportionate mass gain and improved body condition upon returning during the breeding season (Barbraud et al. 2021). If this holds true in winter, it could explain the positive correlation between female survival and winter sea ice area. The positive correlation between female

survival and sea ice area may explain the non-significant negative effects on male widowhood probability, suggesting that the impact of sea ice on female survival may vary depending on the breeding and pair-bond stage. These findings imply that sex-specific responses to environmental conditions can influence mating patterns.

Harsh environmental conditions were linked to increased divorce probabilities. In snow petrels, divorce was adaptive and triggered by breeding failure, with failed breeders exhibiting a 28.8% higher divorce probability in females (an increase of 0.016) and a 56.0% higher divorce probability in males (an increase of 0.029) compared to successful breeders. Breeding with a new partner after divorce led to increased breeding success, similar to other monogamous species such as the magellanic penguin (*Spheniscus magellanicus*, Wagner, Cappello, and Boersma (2022)) and black-browed albatross (*Thalassarche melanophris*, Ventura et al. 2021). Thus, environmental factors can influence divorce probability by affecting breeding success ([H1], Figure 4). The negative impact of snow days and the positive effect of temperature on breeding success align with previous studies (Chastel, Weimerskirch, and Jouventin 1993; Jenouvrier, Barbraud, and Weimerskirch 2005; Sauser, Delord, and Barbraud 2021a).

Incubating adults exposed to lower temperatures may consume more energy due to increased thermal loss (Kendeigh 1969), potentially leading to longer foraging trips and increased egg abandonment likelihood by the incubating partner.

Environmental conditions can also influence divorce regardless of previous breeding success, consistent with (Ventura et al. 2021). This supports the habitat-mediated hypothesis which stipulates that environmental conditions can affect the decision-making processes of divorce (H2.1 in Figure 1). Specifically, unfavourable conditions, like increased snow days, correlated with higher divorce probabilities. Physiological stress may link harsh conditions to higher divorce rates, as stressed partners might attribute poor physiological and reproductive performance to their partner's quality, leading to divorce. Studies in various species, including snow petrels, show a connection between reproductive activities and stress hormone levels (Angelier et al. 2009, 2015; Wingfield and Sapolsky 2003). Therefore, harsh environmental conditions may impede informed mate choice by hindering the reliability of mate quality assessment (Candolin 2003, 2019).

Interestingly, environmental conditions influence divorce probabilities differently for successful and failed breeders. In snow petrels, successful breeders had higher divorce probabilities in years with heavy snow, whilst heavy snow did not affect the divorce probability of failed breeders. This is because breeding failures occur mainly during the incubation and early chick rearing (Jenouvrier, Barbraud, and Weimerskirch 2005), time spent in the colony is much shorter for failed than successful breeders. Consequently, successful individuals face more stressful conditions at the nest, such as the energy expenditure for removing snow after significant snowfalls during the entire breeding season (Chastel, Weimerskirch, and Jouventin 1993; Jouventin and Bried 2001). Conversely, heavy snow may not affect failed breeders as much, as their divorce probability is primarily driven by breeding failure. These differential impacts of environmental conditions between successful and failed breeders were also found for survival and reproduction, observed in the Manx shearwater (*Puffinus puffinus*, Wood et al. (2021)) and the southern fulmar (*Fulmarus glacialis*, Jenouvrier, Péron, and Weimerskirch (2015)). Breeding states can influence the spatiotemporal environmental conditions individuals encounter through mechanisms such as time spent at the colony, microclimate variations within nests and foraging areas, thereby exposing successful and failed breeders to divergent environments.

4.2 | Demographic Consequences of Pair-Bond Disruption

Widowhood and divorce exhibited distinct impacts on vital rates. Individuals resuming breeding after divorce had greater success than those after widowhood. The lower breeding success of individuals breeding with a new partner after widowhood, compared to those breeding with the same previous partner, highlights the reproductive costs associated with non-adaptive partner changes. After divorce, individuals bred with a new partner had an immediate improvement in breeding success compared to their last breeding attempt with a previous partner. However, this partner change was also accompanied by a lower survival probability in the following breeding season compared with

individuals breeding with the same partner. This lower survival probability was also shown in individuals breeding with a new partner after widowhood. Thus, partner changes incur a survival cost, showing the trade-off between immediate breeding success and subsequent survival in long-lived species (Dobson and Jouventin 2010). The negative impact of pair-bond disruption on survival is also consistent with the previous evidence in black brant geese (*Branta bernicla nigricans*, Nicolai et al. (2012)) and great tit (*Parus major*, Culina, Lachish, and Sheldon (2015)).

In addition to immediate impacts on vital rates, widowed and divorced individuals missed several breeding seasons leading to reduced lifetime reproductive success. This may stem from challenges in securing a new mate, including the time needed to establish a functional relationship and competition for nest sites (Emlen and Oring 1977). Securing a suitable nest site is crucial for reproduction and can be challenging during unfavourable conditions (Chastel, Weimerskirch, and Jouventin 1993). Snow petrels vigorously defend their nests against intruders (C. Barbraud, personal observation), and those missing a breeding season must compete for a nest until they secure one. This is also supported by the lower breeding probability of nonbreeding individuals (NB) skipping breeding with their partners, suggesting difficulties in securing a nesting site. Thus, highly competitive individuals may face reduced fitness costs post pair-bond disruptions by quickly acquiring a new nest and mate.

Interestingly, unmated divorced individuals showed lower survival and probability of resuming breeding than widowed individuals. This aligns with Culina, Radersma, and Sheldon (2015), which found divorced individuals less likely to breed compared to widowed ones. Two possible explanations for the reduced probability of breeding for divorced individuals are (1) divorced individuals may skip breeding as an adaptive measure to conserve resources for future reproduction, whilst widowed individuals persist in seeking new partners (Coulson 1984) and (2) divorced individuals may not be the ones who initiated the divorce, therefore may tend to be of lower quality, and face greater challenges in finding a new partner (Ens, Safriel, and Harris 1993). Considering the substantial decrease in lifetime reproductive success from staying unmated, divorced individuals gained no advantage from skipping breeding. They were likely in poor condition, reducing their survival probabilities if they attempted to breed, further diminishing their reproductive success.

Widowed individuals had higher survival probabilities than divorced ones, suggesting divorced individuals might be of lower quality. In monogamous species, divorce is often adaptive following a breeding failure possibly due to a poor-quality partner. Individuals who initiate divorce are expected to trigger the separation and mate with a new partner (ND state), leaving their lower-quality partner (D state) behind (Choudhury 1995; Culina, Radersma, and Sheldon 2015; Ens, Safriel, and Harris 1993). Divorce initiators may immediately find a new partner and improve their breeding success, whereas their former partners frequently do not (Culina, Radersma, and Sheldon 2015; Culina and Brouwer 2022). Therefore, individuals unable to breed immediately after a divorce are more likely to be non-initiators of divorce, abandoned by their former partner and take longer to resume breeding compared to widowed individuals (Culina, Radersma, and Sheldon 2015; Ens, Safriel, and Harris 1993). In a

black-capped chickadee (*Parus atricapillus*) population, widowed individuals, being of higher quality, were preferred by the choosier sex and had a greater likelihood of establishing new pair-bonds (Otter and Ratcliffe 1996). The appeal of widowed individuals as potential mates to those in suboptimal pairings may contribute to higher divorce probabilities, particularly in species characterised by high mortality rates and a large proportion of widowed individuals (Coulson and Thomas 1985; Jeschke and Kokko 2008).

4.3 | Pair-Bond Dynamic Under Future Climatic Conditions and Implications on Population Dynamics

Given the complexity of forecasting population dynamics with potential temporal confounding factors (Hefley et al. 2016), we conducted a conservative forecast of widowhood and divorce probabilities, assuming a stable sex ratio and population structure. Male widowhood probabilities are anticipated to rise, whilst females see a slight decline. Divorce rates are expected to remain relatively constant. The anticipated increase in male widowhood probabilities may lead to a higher proportion of males amongst available mates, potentially intensifying intrasexual competition (Weir, Grant, and Hutchings 2011) and may, in turn, lead to higher divorce probabilities (Jeschke and Kokko 2008). The increase in widowhood probabilities may also affect the population through its impact on individual fitness. Specifically, individuals experiencing pair-bond disruption and breeding with a new partner face reductions in survival, breeding probability, breeding success and ultimately lifetime reproductive success.

Our current forecasts potentially underestimated shifts in pair-bond disruption rates. For example, the anticipated decline in female survival probabilities (Appendix Figure S2a) will result in higher rates of male widowhood and could lead to higher divorce rates. Indeed, the decline in female survival probabilities will result in skewed sex ratios, heightening competition amongst males and potentially increasing divorce rates. Additionally, this may affect the fitness of individual and population growth rate, as unmated individuals may find it more challenging to form new partnerships, likely staying unmated for extended periods and suffering further declines in lifetime reproductive success (Jenouvrier et al. 2010; Sun et al. 2022a; Tavecchia et al. 2016).

Although we showed that pair-bond disruption rates may change due to climate change, the demographic consequences of climate change through its impact on pair-bond dynamics are still unclear. To fully evaluate the demographic consequences of pair-bond disruption, we need developments of non-linear two-sex population models that integrate feedback of population structure, behavioural plasticity and evolution.

5 | Conclusion

Our study enhances our understanding of pair-bond dynamics under climate change and represents an initial effort to forecast pair-bond disruption in monogamous species. We found that widowed individuals had higher survival and breeding probabilities than divorced ones, underscoring the importance of distinguishing divorce and widowhood as distinct

mechanisms when assessing the implications of pair-bond disruption. Environmental factors can influence the likelihood of divorce and widowhood, impacting vital rates and life-history outcomes. This has significant implications for the reliability of adaptive mate choice under harsh conditions, affecting population dynamics and evolutionary trajectories. Future research is needed to better understand and project the feedback effects of environmental change on mating processes through population and evolutionary changes.

Author Contributions

Ruijiao Sun: conceptualization, investigation, interpretation, methodology, writing – original draft, writing – review and editing. **Rémi Fay:** methodology, interpretation, writing – review and editing. **Francesco Ventura:** interpretation, writing – review and editing. **Bilgecan Şen:** data curation, writing – review and editing. **Christophe Barbraud:** interpretation, funding acquisition, project administration, resources, data curation, writing – review and editing. **Karine Delord:** project administration, interpretation, resources data curation, writing – review and editing. **Kristen Krumhardt:** resources data curation, writing – review and editing. **Stéphanie Jenouvrier:** conceptualization, methodology, investigation, funding acquisition, project administration, resources, supervision, writing – review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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Ethics Statement

The Ethics Committee of IPEV and Comité de l’Environnement Polaire approved the field procedures.

Data Availability Statement

Data and code used to analyse the data are available at: <https://doi.org/10.5281/zenodo.13845663>.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.