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RESEARCH ARTICLE

Temporal and spatial equivalence in demographic responses of emperor penguins (*Aptenodytes forsteri*) to environmental change

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Abstract

1. Population ecology and biogeography applications often necessitate the transfer of models across spatial and/or temporal dimensions to make predictions outside the bounds of the data used for model fitting. However, ecological data are often spatiotemporally unbalanced such that the spatial or the temporal dimension tends to contain more data than the other. This unbalance frequently leads model transfers to become substitutions, which are predictions to a different dimension than the predictive model was built on. Despite the prevalence of substitutions in ecology, studies validating their performance and their underlying assumptions are scarce.
2. Here, we present a case study demonstrating both space-for-time and time-for-space substitutions (TFSS) using emperor penguins (*Aptenodytes forsteri*) as the focal species. Using an abundance-based species distribution model (aSDM) of adult emperor penguins in attendance during spring across 50 colonies, we predict long-term annual fluctuations in fledgling abundance and breeding success at a single colony, Pointe Géologie. Subsequently, we construct statistical models from time series of extended counts on Pointe Géologie to predict average colony abundance distribution across 50 colonies.
3. Our analysis reveals that the distance to nearest open water (NOW) exhibits the strongest association with both temporal and spatial data. Space-for-time substitution performance of the aSDM, as measured by the Pearson correlation coefficient, was 0.63 and 0.56 when predicting breeding success and fledgling abundance time series, respectively. Linear regression of fledgling abundance on

NOW yields similar TFSS performance when predicting the abundance distribution of emperor penguin colonies with a correlation coefficient of 0.58.

4. We posit that such space–time equivalence arises because: (1) emperor penguin colonies conform to their existing fundamental niche; (2) there is not yet any environmental novelty when comparing the spatial versus temporal variation of distance to the nearest open water; and (3) models of more specific components of life histories, such as fledgling abundance, rather than total population abundance, are more transferable. Identifying these conditions empirically can enhance the qualitative validation of substitutions in cases where direct validation data are lacking.

KEYWORDS
Antarctica, fundamental niche, model transferability, space-for-time substitution, space–time equivalence, species distribution models, time series

1 | INTRODUCTION

Many population ecology and biogeography applications require transferring models across space and/or time to provide predictions beyond existing data bounds (sensu Sequeira et al., 2018). For example, predicting invadable areas for invasive species (e.g. Lyons et al., 2020), determining translocation sites for threatened species (e.g. Bellis et al., 2020), and predicting how a disease will spread from its point of origin (e.g. Williams et al., 2008) are all examples of spatial transfers. Similarly, forecasts of species distributions and trends under climate change are examples of temporal transfers (e.g. Fordham et al., 2013; Jenouvrier et al., 2014; Keith et al., 2008). However, this fundamental application in ecology is also one of its biggest challenges (Yates et al., 2018). One important aspect of this challenge is that ecological data are usually spatiotemporally unbalanced such that the spatial or the temporal dimension tends to contain more data than the other. For example, in countries with no consistent ecological monitoring programs and in geographic regions that are difficult to travel to, high-quality ecological data (population counts, mark-recapture, etc.), which are available as relatively long time series, are usually confined to a limited number of sites, and spatially widespread data rarely contain long-term temporal information (e.g. occurrence). So, model transfers frequently need substitutions (Lovell et al., 2023), which are predictions to a different dimension than the predictive model was built on.

In this context, space-for-time substitutions (SFTS) are one of the most common forms of model transfers for projecting species ranges and distributional shifts under climate change (Lovell et al., 2023). Time-for-space substitutions (TFSS), on the other hand, are rarely conducted explicitly, but are usually implicit in applications like population viability analysis and matrix population models where data come from a single or a few populations (e.g. Jenouvrier et al., 2014; Şen et al., 2023). Even though substitutions are prevalent in ecology, studies that validate them and their assumptions are rare. The small number of studies that do so generally demonstrate mixed results, where successful transfers and substitutions are highly context dependent (e.g. Adler & Levine, 2007; Banet & Trexler, 2013; Blois, Zarnetske, et al., 2013; Bradter et al., 2022; Isaac et al., 2011). Therefore, treatments of specific cases are necessary to demonstrate the conditions under which substitutions work or fail.

Substitutions are hypothesized to work if the functional form of the relationship between the environment and an ecological response remains stationary across space and time, defined as space–time equivalence (Lovell et al., 2023). However, this equivalence can break down for several reasons. First, populations of interest may not be in equilibrium with their environment, across time and/or space. Equilibrium in this context does not refer to the dynamics of a population near carrying capacity but rather to whether the distribution of populations for a species closely conforms to its existing fundamental niche (Peterson, 2011). Dispersal ability and biotic interactions, such as competition and predation, can limit species distributions beyond the abiotic suitability of their habitats to establish nonequilibrium distributions (Anderson, 2013; Araújo & Pearson, 2005; Peterson, 2011). In these cases, for species where their realized niche is smaller than its fundamental niche, models built with only environmental variables may not transfer and substitute well, as any environmental relationship detected in one dimension might not suffice to make predictions in the same or another dimension to new locations and time periods. For example, species distribution models (SDMs) built with data from non-equilibrium distributions will not be able to estimate the full abiotic niche of the species, hampering its transferability in the process (Peterson, 2011).

Second, space–time equivalence might not continue to hold true in novel environmental conditions. When models require mathematical extrapolation to predict spatial and/or temporal population responses to novel environments, their predictive performance will likely be hindered (e.g. Fitzpatrick et al., 2018; Williams et al., 2013; Williams & Jackson, 2007). Although there are some methodological approaches for model extrapolation (e.g. Anderson, 2013), there is not yet a widely accepted solution for this issue.

Lastly, some ecological responses can be more transferable than others, making them more likely to demonstrate space–time equivalence. For example, abundance data have been shown to increase the predictive performance of species distribution models that only use occurrence data (Howard et al., 2014). However, models of abundance themselves can suffer from low transferability, especially when multiple sources of stochasticity are involved at various stages of a species' life history (e.g. Talis et al., 2022). We are not aware of studies that have explicitly investigated the transferability or substitution of population responses other than occurrence and abundance.

A detailed understanding of demographic responses is especially crucial in regions where harsher environmental events occur more frequently. The Antarctic polar region, amid the rapid acceleration of global change, emerged as a critical indicator for climate-induced alterations, and the pronounced melting of sea ice and the retreat of glaciers have been linked to responses at both the individual and population levels (e.g. Clark et al., 2024). In the Southern Ocean, sea ice serves as an integral but extremely dynamic component of the landscape, and changes in its extent and timing are poised to disrupt ecological dynamics across trophic levels from primary producers to apex predators (Rogers et al., 2020). This scenario underscores the imperative for methods that anticipate the broad-scale ecological ramifications of climate change with data that may be patchy in either space or time.

Here, we demonstrate an example of both SFTS and TFSS using data from multiple emperor penguin (*Aptenodytes forsteri*) colonies as a case study for model substitution and transferability in unique environments. We use an index of pan-Antarctic emperor penguin population abundance from a multi-level model that combines satellite data, aerial counts, and ground counts to build an abundance-based species distribution model (aSDM; LaRue et al., 2024). We then use this aSDM to predict the long-term time series of colony abundance at a single colony, Pointe Géologie, and compare these predictions to time series of fledgling abundance (counted number of live chicks) and breeding success (fledgling abundance divided by the number of breeding pairs) at this colony (Figure 1). Finally, we build statistical models with these long-term counts at Pointe Géologie and predict fledgling abundance across all colonies, allowing us to compare the predictive capacity of environmental variability across spatial and temporal gradients conditional on our model set (Figure 1). We discuss these results in the context of space–time equivalence, conformance to fundamental niche, transferability of different ecological responses, and environmental novelty to showcase the conditions that lead to successful substitutions across time and space.

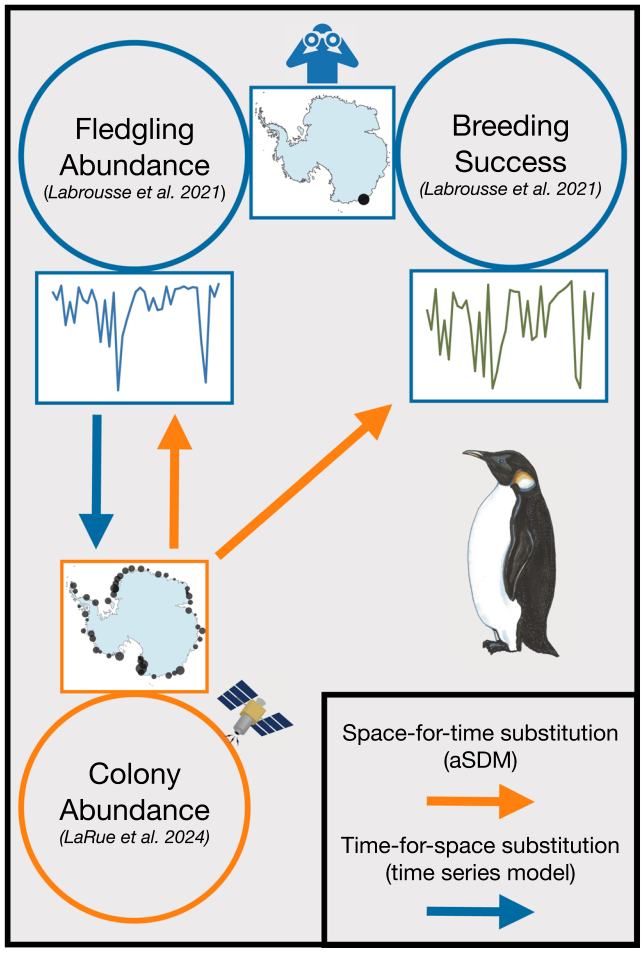

FIGURE 1 Overview of the workflow of substitution analysis where aSDM stands for abundance-based species distribution model. The satellite symbol shows that the main penguin counting method was via remote sensing, and the person holding binoculars shows ground counts. Maps show the location of penguin counts for their respective counting methods. Colony abundance was pan-Antarctic, while fledgling abundance and breeding abundance were on a single colony (Point Géologie) with their respective time series shown as separate plots.

2 | MATERIALS AND METHODS

2.1 | Estimating pan-Antarctic abundance of the emperor penguin

We used the published indices of adult abundance at attendance at breeding colonies during spring (hereafter colony-abundance) for 50 emperor penguin colonies (LaRue et al., 2024). LaRue et al. (2024)'s model (hereafter colony-abundance model) uses satellite observations of colony area and aerial counts of colonies from 2009 to 2018. Fifty colonies included in the colony-abundance model were known to exist prior to 2015 and therefore had >5 years of data available for analysis. LaRue et al. (2024) initially estimated the global population during a 10-year period for the 46 colonies documented in the first global census of the species (Fretwell et al., 2012). Recent discoveries of four additional colonies bring the total number of colonies considered to 50.

The satellite imagery captures adult emperor penguins at breeding colonies during spring, which is primarily comprised of breeders but also contains an unknown number of failed breeders, pre-breeders, and non-breeders. The daily count of adult penguins at a colony can fluctuate substantially throughout the spring survey period due to several factors, including the synchronization of breeding activities, variations in the timing of adult foraging trips,

the presence or absence of non-breeding adults, emigration, breeding failures, and shifts in parental behaviour, such as crèching. Generally, the number of breeding adults tends to decrease over the spring survey period as individuals leave the colony following reproductive failures (Winterl et al., 2023). It is likely that non-breeding penguins also depart gradually over time. Therefore, these estimates reflect only the individuals present in late spring and are likely indicative of the breeders who have successfully raised chicks.

2.2 | Abundance-based SDMs

Using the time series of colony abundances estimated with the colony-abundance model, we computed the average colony abundance on log scale between 2009 and 2018 for each colony j. This averaging process made sure that only spatial information was used when building the aSDM. We obtained Y_j^{μ}, the posterior mean, and Y_j^{σ}, the posterior variance of the average abundance of colony j, from the LaRue et al. (2024) population model. Then, we associated Y_j^{μ} and Y_j^{σ} with environmental variables in a separate state–space model where Y_j^{μ} is treated as the observation and Y_j^{σ} as the observation error:

$$Y_j^{\mu} \sim \mathrm{N}\left(z_j, Y_j^{\sigma}\right),$$

$$z \sim \mathrm{N}\left(\alpha + X\beta, \sigma^2\right),$$

where z is the vector of latent average colony abundances, z_j is the abundance of colony j, α is the global colony abundance average, β is the vector of slopes for the matrix of variables $\mathbf{X}$ and σ^2 is the process error.

This framework is a straightforward aSDM where average colony abundance is a linear function of each environmental covariate (Waldock et al., 2022). We found that quadratic functions and non-linear methods, such as random forests, do not lead to better model fit (refer to Appendix S1), so we retained a simple linear relationship between covariates and log(abundance). We used eight environmental variables in this aSDM: sea ice concentration (SIC) in four seasons, including nonbreeding (January to March), laying (April and May), incubation (June and July), and rearing (August to December); fast ice area (FIA), fast ice emergence date (TOE) and breakout date (TOB); and distance from the colony to nearest open water (NOW). We calculated average SIC within a 750-km polygon for the nonbreeding season and a 500-km polygon for the breeding seasons using sea ice data observed with passive microwave radiation at a 25 × 25 km resolution (DiGirolamo et al., 2022) and rescaled to a 1° resolution. We selected these polygon sizes so that SIC values were strongly correlated with the SIC of the much larger spatial field (~2000 km) used in Jenouvrier et al. (2012) but still small enough to distinguish regional differences among colonies. We used a larger polygon for the nonbreeding season because the foraging distance increases compared with the breeding season (Zimmer et al., 2007). We first calculated seasonal averages for SIC, then averaged them between 2009 and 2018.

We calculated FIA, TOB and TOE within a 100 km buffer (smaller buffers do not have enough annual variability to reliably calculate a decadal average) of each colony using a 1 km × 1 km resolution map of landfast sea ice (Fraser et al., 2020). We calculated NOW using the same landfast sea ice data. These data are available at 15-day intervals (Fraser et al., 2020), so we calculated seasonal averages of each variable for each year (except for TOE and TOB). We only used the rearing period for FIA and NOW as it has already been demonstrated that this is the most important season for fast ice-related environmental factors for emperor penguins (Labrousse, Fraser, et al., 2021), but we also note that fast ice products are highly correlated across seasons in our case (>0.8). We averaged fast ice variables between 2009 and 2017 (we did not have access to data from 2018).

We determined variables that have strong associations with average colony abundance using regularized horseshoe priors, which is a Bayesian sparse modelling approach (Şen et al., 2023; Vehtari et al., 2017). In sparse modelling, the slopes of variables with weak effects are 'pulled' towards 0, while slopes of stronger effects can escape this 'pull' and move further away from 0, making it easier to distinguish important variables (refer to Appendix S1 for information about regularized horseshoe priors).

2.3 | Pointe Géologie models

We modelled previously published time series of Pointe Géologie, spanning 1979 to 2018, of fledgling abundance and breeding success (number fledged chicks per egg; Labrousse, Fraser, et al., 2021; Labrousse, Iles, et al., 2021). We used these ecological responses because, as explained above, abundances estimated with colony-abundance models are more likely due to successful breeders and thus are closely indexed to adult presence during spring. Using linear regression, we associated annual counts of fledgling abundance and breeding success in Pointe Géologie with annual measurements of five variables also used in the aSDM: SIC for four breeding seasons and NOW. We did not have access to the remaining three variables (FIA, TOB and TOE) for years before 2000. As opposed to the aSDM, which was built along a spatial gradient, these models only employed temporal gradients as they were built with data only from a single colony. We applied regularized horseshoe priors to determine variables with the strongest associations as above. Labrousse, Fraser, et al. (2021) and Labrousse, Iles, et al. (2021) have already demonstrated the effect of NOW on breeding success. Our analysis extended this work to include SIC variables as covariates and fledgling abundance as an additional response. All models were fit with Stan using the R package rstan (Stan Development Team, 2024).

2.4 | Validating substitutions in time and space

To validate our space-for-time substitution, we used aSDM to predict time series of colony abundances for Pointe Géologie from 1979 to 2018 (Figure 1) using only the covariates that had strong associations in the aSDM and the Pointe Géologie models (Figure 2). When there

were multiple variables that had strong associations with average colony abundance, but some of these were weakly associated with Pointe Géologie time series, we built an aSDM with only the shared variables and predicted the time series using only the slopes of the variables that are shared between the aSDM and time series models. Finally, we compared the posterior mean of this predicted time series with the observed time series at Pointe Géologie (breeding success, fledgling abundance) and assessed their correlation with the Pearson correlation coefficient.

To validate time-for-space substitution, we used the linear regression of fledgling abundance of Pointe Géologie and predicted the distribution of fledgling abundances across 50 colonies (Figure 1) using averages of variables between 2009 and 2018 and with variables that were selected in both aSDM and Pointe Géologie models (Figure 2). We compared the posterior mean of predicted fledgling abundance with the posterior mean of average colony abundance (Y_j^{μ}) from colony abundance model and report their correlation with Pearson correlation coefficient.

3 | RESULTS

Nearest open water was the variable with the strongest slope when modelled with regularized horseshoe priors in aSDM and both Pointe Géologie models (Figure 2). Sea ice concentration (SIC) slopes were pulled to 0 for Pointe Géologie models, but SIC in the laying period had a slope strong enough to be close second to NOW in aSDM (Figure 2). The aSDM built with SIC (laying) and NOW explained 42% of the variation of average colony abundances, and Pointe Géologie models of breeding success and fledgling abundance explained 40% and 32% of the variation, respectively. NOW had a negative effect on all three responses (colony abundance $\beta = -0.68(\mp 13)$, breeding success $\beta = -0.0055(\mp 0.0009)$, fledgling abundance $\beta = -0.018(\mp 0.003)$, Figure 3), whereas SIC (laying) had a positive effect on average colony abundance ($\beta = 0.39\,(\mp 0.15)$, Figure S1).

We used only the slope of NOW from the aSDM to predict colony abundance time series of Pointe Géologie, as NOW was the only variable among all three models with a strong slope estimate (Figure 2). The correlation between these colony abundance predictions of Pointe Géologie and breeding success, and fledgling abundance time series were 0.63 and 0.56, respectively (Figure 4). Similarly, we used average NOW (between 2009 and 2018) of each of the 50 colonies to predict the fledgling abundance of each colony using the fledgling abundance model of Pointe Géologie, and the correlation between these predictions and average colony abundance estimates was 0.58 (Figure 5).

4 | DISCUSSION

We demonstrated ecological responses related to the breeding ecology of emperor penguins, namely, breeding success, fledgling abundance, and the index of abundance of adult birds in attendance during spring can be substituted across both time and space, suggesting space–time equivalence (Figures 4 and 5). It is particularly important to validate the conditions hypothesized to create this space–time equivalence because

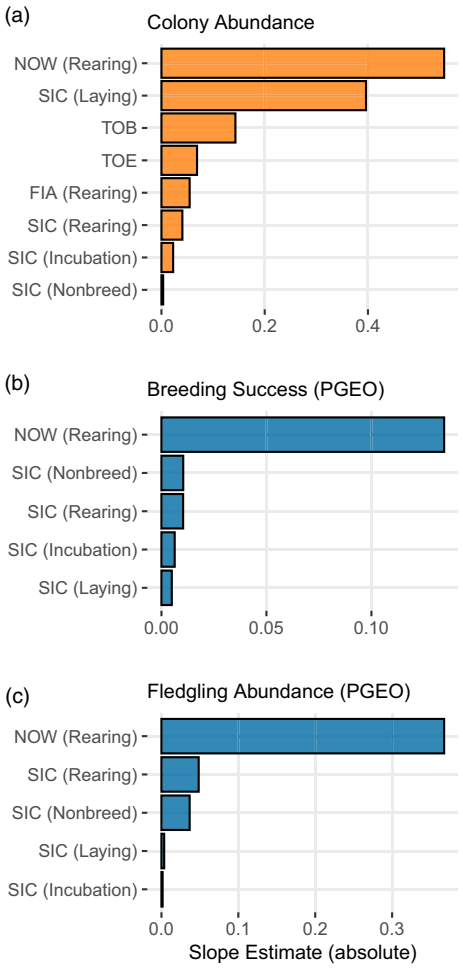

FIGURE 2 Posterior averages of slopes of regularized horseshoe regression with three different sets of data. Index of adult abundance at attendance during spring (Colony abundance) (a) in the pan-Antarctic, and breeding success (b) and fledgling abundance (c) time series at Pointe Géologie (PGEO). Higher slopes indicate larger effect sizes and more important variables. Environmental variables include Sea ice concentration (SIC) in four seasons, nonbreeding (January to March), laying (April and May), incubation (June and July), and rearing (August to December); fast ice area (FIA), fast ice emergence date (TOE), and fast ice breakout date (TOB); and distance to nearest open water (NOW).

the listing of the emperor penguin under the Endangered Species Act (Jenouvrier et al., 2021) is informed by research that employs the assumption of space–time equivalence (Jenouvrier et al., 2014). In the following sections, we delve into three key conditions: the alignment of a species' population distribution with its established fundamental niche, the emergence of novel environmental conditions, and the transferability of different ecological responses.

4.1 | Conformance to fundamental niche

Emperor penguins show signs that their distribution of populations closely conforms to its scenopoetic fundamental niche (environmental variables that are not affected by the focal species) on

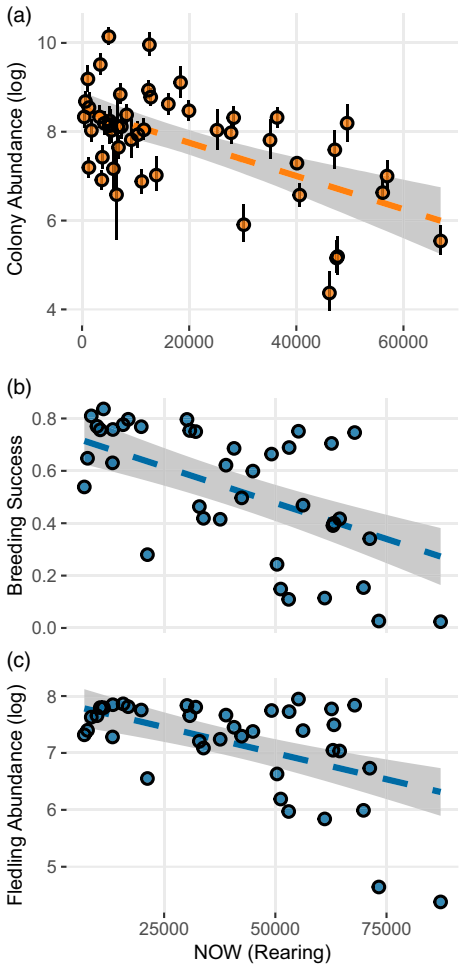

FIGURE 3 Univariate relationship between distance to nearest open water (NOW, meters) and three ecological responses. Index of adult abundance at attendance during spring (Colony abundance) (a) in the pan-Antarctic, each point represents the average abundance of a single colony between 2009 and 2018 as estimated by the colony-abundance model; vertical lines show the 95% credible interval of these estimates. Breeding success (b) and fledgling abundance (c) time series from Pointe Géologie. Each point represents count data from a single year.

a regional scale. While dispersal behaviour, biotic interactions such as predation by leopard seals (Kooyman et al., 1990), and competition for resources with other Antarctic species (LaRue et al., 2021) can potentially lead to the local absence of emperor penguins and even isolation of some of their colonies, they are widely and homogenously distributed across Antarctica (Labrousse et al., 2023; Labrousse, Iles, et al., 2021; LaRue et al., 2024; Santora et al., 2020; Trathan et al., 2020; Figure 5b). There is at least one emperor penguin colony in every region of Antarctica, even under different configurations of these regions depending on sea ice characteristics (LaRue et al., 2024). So, the global population of emperor penguins is facing the full spatio-temporal extent of the existing Antarctic environment. In our models, this environment presented itself as the distance to the NOW, which is a direct physical and physiological limit to emperor penguins. As the travel distance to open water and therefore to polynyas increases, they have to spend more energy to reach these food sources, decreasing their chick feeding frequency, which causes starvation and increased mortality, thus finally impacting fledging and breeding success (Labrousse, Fraser, et al., 2021; Labrousse, Iles, et al., 2021).

Though we used the 50 colonies reported in LaRue et al. (2024) for analysis, the inclusion of recently discovered smaller colonies could potentially disrupt both space-for-time and time-for-space substitution abilities of our models as they are more likely to show idiosyncratic dynamics (Fretwell, 2024; Fretwell & Trathan, 2021). Especially massive breeding failure and the frequent 'blinking' of some colonies, when they completely (apparently) disappear in certain years, do not appear to be caused by the annual variability in the distance to NOW. Similarly, local conditions might dominate the expected effects of fast ice on the breeding success of certain colonies and reduce the transferability of environmental relationships. For example, the number of chicks in the Taylor Glacier colony during the 1988–2010 period appears largely unrelated to the distance to NOW (Robertson et al., 2014). In this colony, however, both the distance to NOW and the number of chicks (and breeding success) vary considerably less than Pointe Géologie (refer to fig. 5 in Robertson et al. (2014)).

4.2 | Novel environmental conditions

Substitutions often fail when they are used to try and predict ecological responses in a novel environment (Sequeira et al., 2018; Yates et al., 2018). Environmental relationships detected within the bounds of the existing data do not necessarily apply in novel environmental conditions. Novelty in this context can either be defined as conditions not observed in the data (e.g. highest temperature was 2.5°C in the data but predictions were in the 3°C–4°C range) or conditions that exist now but form unique combinations in the future (e.g. rainy or hot conditions in the data but never together, hot rainy days in the future). In this case, however, the range of variability of NOW across Antarctica and across time in Pointe Géologie is very similar (Figure 3) so the extrapolation required to make substitutions (Figures 4 and 5) was minimal.

Antarctic sea ice is highly variable in time and space (Massom & Stammerjohn, 2010). Until recent years, evidence suggests that the observed trends in Antarctic sea ice were likely associated with natural variability instead of a forced anthropogenic signal (e.g. Polvani & Smith, 2013). However, the absence of novel conditions will not necessarily continue to hold true under climate change, when extreme weather conditions will start to occur with increasing frequency (Jenouvrier et al., 2022). For example, the concept of 'time of emergence' denotes the point in time at which the influence of anthropogenic climate change becomes discernible from natural climate variability, marking the potential onset of novel conditions (Jenouvrier et al., 2022). This emergence time varies across seasons and emperor penguin colonies concerning sea ice (refer to fig. S5 in Jenouvrier et al., 2022). Notably, in East Antarctica, colonies tend to experience an earlier time of emergence compared with those in the Ross, Bellingshausen, Amundsen, and Weddell Seas. For the majority

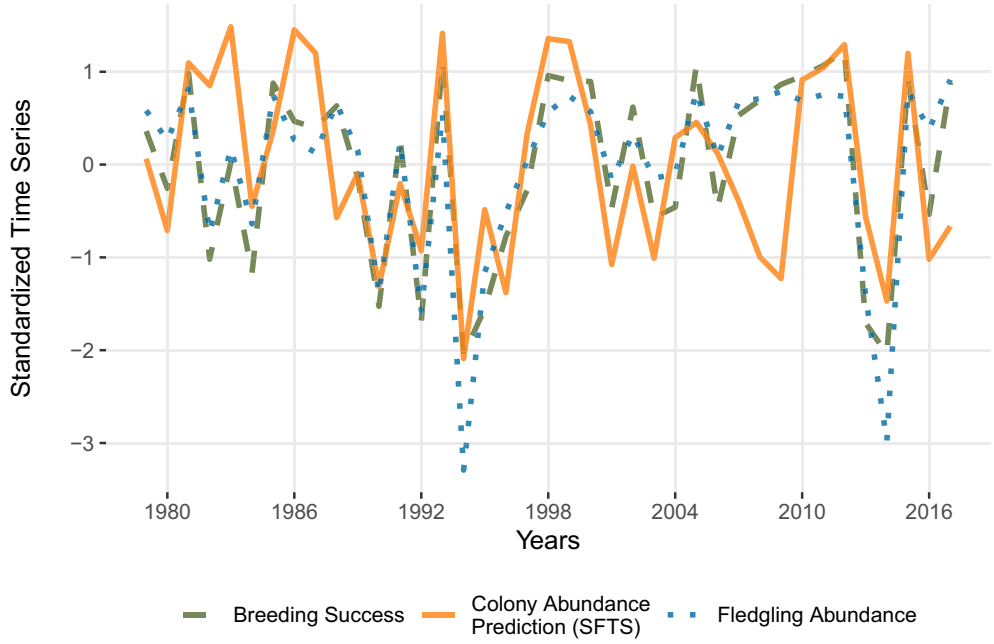

FIGURE 4 Time series of breeding success, fledgling abundance and posterior average of predictions of adult birds in attendance at colonies during spring (Colony Abundance Prediction) by the abundance-based species distribution model (aSDM) via space-for-time substitution (SFTS). These predictions constitute an example of space-for-time transfer. Each time series is standardized ($(x - \bar{x}) / \sigma$) so that they can plotted on the same scale. This standardization does not affect their comparison metric (Pearson correlation coefficient).

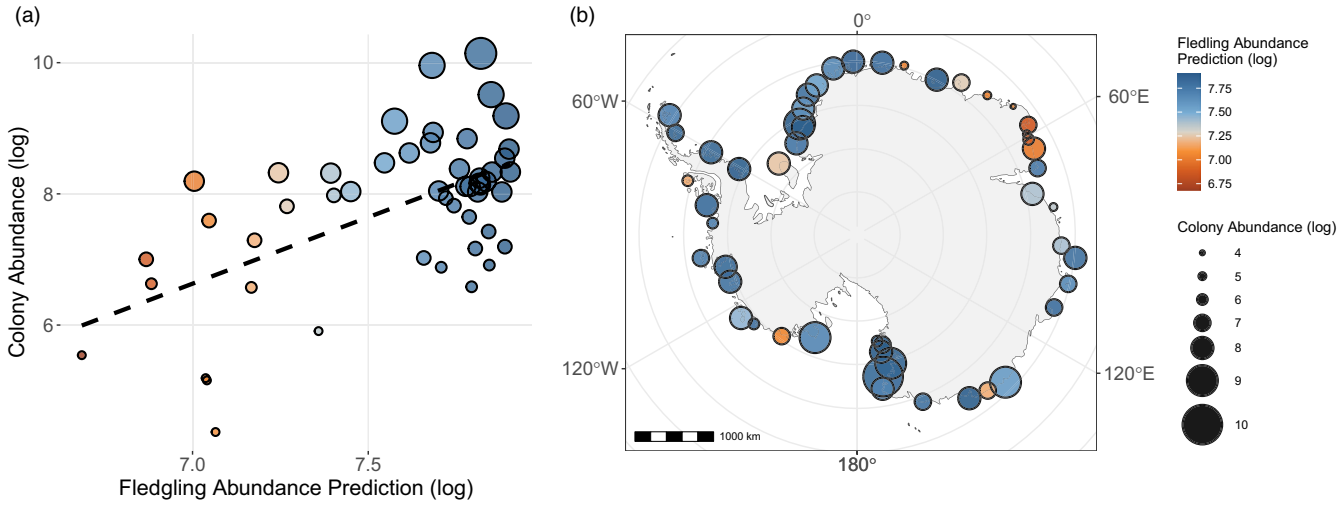

FIGURE 5 Comparison of the index of adult abundance at attendance during spring (Colony abundance) and the posterior average of fledgling abundance prediction of 50 colonies via time-for-space substitution as a scatterplot (a) and across the Antarctic distribution of the emperor penguin (b). Fledgling abundance predictions were made by their respective statistical model using data from Pointe Géologie.

of locations, the time of emergence for both emperor penguin populations and sea ice are projected to occur after the year 2040.

More recently, the effects of such events became more apparent in the breeding season of 2022 in the Bellinghausen Sea region, when early fast ice break-up possibly led to breeding failures at five colonies (Fretwell et al., 2023). Indeed, linear relationships we detected with NOW across time and space (Figure 3) will not extrapolate reliably when NOW gets close to 0, as emperor penguins will not be able to find fast ice to breed on, and may rely on nearby ice shelves or glaciers as breeding platforms (Fretwell et al., 2014). Under these conditions, where previously modelled relationships break down as a consequence of species or population-level tipping points, different extrapolation strategies will be required (e.g. Trathan et al., 2020).

4.3 | Transferability of different ecological responses

Here, we measured the space-for-time substitution ability of the index of abundance of adult birds in attendance at colonies during

spring and the time-for-space substitution ability of fledgling abundance. Usually, however, the most common ecological responses modelled and used for substitutions are species occurrences and total population abundance (e.g. Blois, Williams, et al., 2013; Bradter et al., 2022). We hypothesize that vital rates and abundance estimates that relate to a more specific component of the life history (such as the index of abundance we used) are more transferable, and therefore better at substitutions, than occurrence and total population abundance. This is because observed species distributions and abundances are usually the culmination of multiple processes such as dispersal and biotic interactions, but they can also be subject to different stochastic processes that can potentially obscure the relationship between vital rates and environmental conditions, lowering the intrinsic predictability of the ecological response being modelled (e.g. Şen et al., 2023). Moreover, because populations are subject to a multitude of demographic processes, with the environment exerting varied and sometimes opposing effects on vital rates throughout the life cycle (Jenouvrier, 2013), it may be simpler to identify a single process (e.g. reproduction or mortality) that is strongly influenced by a specific environmental variable, facilitating more efficient transferability.

For example, time series models of Adélie penguin (*Pygoscelis adeliae*) colony abundances, in general, have low spatio-temporal transferability (Şen et al., 2023). Talis et al. (2022) have demonstrated that such low transferability can be caused by the life history of Adélie penguins, in which adults can decide to skip breeding in a given year. Even if the environment is directly linked to the survival of the species, interrelated probabilistic life history events can add demographic stochasticity to the system and cause population growth and environmental conditions to appear completely unrelated, removing all environmental signals from the data (Şen et al., 2023; Talis et al., 2022). Higher-quality data, such as mark-recapture data are likely not subject to such limitations.

Widespread mark-recapture programmes, such as Monitoring Avian Productivity and Survivorship (MAPS; DeSante et al., 2015) in the US, can be used to test our argument that vital rates are indeed more transferable compared with higher-level ecological responses such as population abundances. In the absence of such high-effort long-term data across populations, however, satellite counts (for species in which such counts are appropriate; LaRue et al., 2017) can be used to predict certain demographic responses in a reliable manner, as we have shown with aSDMs (Figure 4).

5 | CONCLUSIONS

We demonstrate a high level of transferability in both space and time for the reproductive processes of emperor penguins, supporting the robustness of previous forecasts which have assumed uniform responses to sea ice changes across colonies. However, these results should be tempered with the recognition that such forecasts typically overlook the potential plasticity in life history traits, microevolutionary processes, and biotic interactions. Notably, breeding on ice shelves might emerge as a strategy in response to changing conditions. This adaptation, however, may impose higher energetic costs and expose penguins to more hazardous and windy environments, potentially undermining their sustainability. Additionally, competitors and predators of emperor penguins might have their own unique responses to climate change altering some of the direct relationships represented by sea ice conditions. Despite these challenges, advancements in satellite imagery technology have greatly enhanced our conservation efforts and understanding of these dynamics. Future research employing open capture-recapture data-driven methods could support more precise and comprehensive evaluations of whether focusing on individual demographic processes rather than complex population dynamics could improve the accuracy of transferability assessments.

AUTHOR CONTRIBUTIONS

Bilgecan Şen, Christian Che-Castaldo and Stéphanie Jenouvrier conceived the ideas and designed methodology; Michelle A. LaRue, Christophe Barbraud, Karine Delord, Heather J. Lynch, and Stéphanie Jenouvrier curated penguin data and provided guidance on its use; Kristen M. Krumhardt, Laura Landrum and Marika M. Holland curated environmental data and provided guidance on its use; Bilgecan Şen analysed the data; Bilgecan Şen, Christian Che-Castaldo, Michelle A. LaRue and Stéphanie Jenouvrier interpreted the results; Bilgecan Şen led the writing of the manuscript; Christian Che-Castaldo, Heather J. Lynch, and Stéphanie Jenouvrier acquired funding and supervised the project. 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

Code and data are available in the Zenodo repository: https://doi.org/10.5281/zenodo.14796339 (Şen et al., 2025).

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SUPPORTING INFORMATION

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

Appendix S1: Temporal and spatial equivalence in demographic responses of emperor penguins (*Aptenodytes forsteri*) to environmental change.

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