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How the future climate may modulate the non-breeding distribution of a Vulnerable gadfly petrel

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ABSTRACT: Understanding biodiversity distribution shifts caused by climate change is one of the top conservation concerns in modern biology. In this study, we entered 8 yr of geolocation tracking data of the single-island endemic and threatened Desertas petrel *Pterodroma deserta* into a species distribution model and quantified the species–habitat relationship and how its current wintering areas could change as a result of new climatic conditions. Our model found that the species' range would increase 430.6 ± (SD) 57.8 % in future scenarios compared to its current range, as long as the species is able to reach all of the new areas identified by the models. However, the suitability of current wintering areas in the Cape Verde Islands and on the US east coast would decrease 52.8 ± 4.4 % as a consequence of the predicted windier conditions. The Desertas petrel has a small population size (160–180 pairs) and is considered 'Vulnerable' according to IUCN criteria, and individuals show high inter-annual site-fidelity to their wintering grounds. Our findings raise conservation concerns about the future of this species, which might heavily depend on the flexibility of adults and the capacity of future generations to disperse and use new wintering areas.

KEY WORDS: Desertas petrel · Ensemble species distribution modelling · Environmental changes · Representative concentration pathways · *Pterodroma deserta*

INTRODUCTION

The effects of human actions on the oceans are increasing alarmingly (Frölicher & Joos 2010, Chown et al. 2015, Halpern et al. 2015), and there is particular concern about how ocean biodiversity will respond to climate change (Burrows et al. 2011, Constable et al. 2014). Several studies on the redistribution of biodiversity in response to anthropogenic climate change have shown that organisms which are unable to meet the preferred conditions of their environmental niche are forced to shift their distribution (Ackerly et al. 2010, Doney et al. 2012, García Molinos et al. 2016) or face extinction (Thomas et al. 2004, Cheung et al. 2009, Stuart-Smith et al. 2015). Climate is the main trigger of both terrestrial and marine animal migration (Newton 2008). When environment and climate conditions at the wintering grounds change or deteriorate, migration may have adverse consequences for a population (Votier et al. 2005, Jenouvrier et al. 2009, Robinson et al. 2009, Fort et al. 2013, Middleton et al. 2013).

Individual animals can be highly consistent in their migratory schedule and wintering areas, as shown for fishes (Brodersen et al. 2012, Thorsteinsson et al. 2012), sea turtles (Schofield et al. 2010) and seabirds (Dias et al. 2011, Satterthwaite et al. 2012, Yamamoto et al. 2014, Ramírez et al. 2016, Vardanis et al. 2016), or they may be flexible and adjust their wintering areas according to environmental conditions (Quill-

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feldt et al. 2010, Dias et al. 2011, McFarlane Tranquilla et al. 2014). For instance, in some seabird species, like Cory's shearwater *Calonectris borealis* or Barau's petrel *Pterodroma baraui*, a large percentage of the population uses the same wintering grounds in several successive years (Pinet et al. 2011, Raine et al. 2013, Ramírez et al. 2016). Thus, the consequences of subtle shifts in the climate conditions within those wintering areas may have a profound effect on populations of spatially and/or temporally consistent species.

Empirical and theoretical studies on seabird species' responses to climate change suggest that they will move poleward as sea surface temperatures rise, and either gain or lose range (Péron et al. 2010, Hazen et al. 2013, Russell et al. 2015) depending on the species' ability to deal with increased wind speeds (Weimerskirch et al. 2012, Krüger et al. 2018) or reduced productivity (Grémillet & Boulinier 2009). However, most studies aiming at predicting the effect of climate change on seabird spatial distributions have been restricted to the breeding season and conducted in temperate or polar ecosystems (i.e. Péron et al. 2012, Hazen et al. 2013, Russell et al. 2015). To date, studies projecting distribution shifts induced by climate change are largely lacking for tropical and/or trans-equatorial seabird species, especially during the non-breeding season (but see Legrand et al. 2016 and Ramos et al. 2017).

In this study, we assessed the potential wintering distribution of an endemic and Vulnerable gadfly petrel, the Desertas petrel *Pterodorma deserta*, according to future climate scenarios of the Intergovernmental Panel on Climate Change (IPCC). The Desertas petrel is a relatively recently split species (Jesus et al. 2009) and is considered one of the rarest procellariiform species in the world, with a population estimated between 160 and 180 breeding pairs (Ramírez et al. 2013). It is a medium-sized pelagic seabird endemic to a single island, breeding only on a single plateau on Bugio Island (Madeira archipelago, Portugal). Its distribution range covers both subtropical and tropical temperatures with intermediate wind speeds and oligotrophic waters and includes wintering areas identified in the southwest, central tropical and northwest Atlantic Ocean (Ramírez et al. 2013, 2016). This species shows high individual wintering site fidelity (Ramírez et al. 2016).

We compared changes in the species' distribution data considering either full dispersal or limited dispersal scenarios (where dispersal refers to the ability of the species to change its distribution in projected future climate scenarios). The limited dispersal model considers that the species can only occupy the range identified in the projected distribution, therefore complying with the idea of wintering site fidelity, in contrast to the full dispersal model, in which the species is able to disperse throughout the entire range. As one can presume, there may be no capacity for a spatially consistent species to abruptly change its wintering grounds in just a few generations' time. Given the known ecological niche of the Desertas petrel and its wintering site fidelity, we hypothesized that under future climate change scenarios, suitable wintering grounds for this species would reduce greatly. To our knowledge, no study to date has projected the wintering distribution of a trans-equatorial migrant procellariiform under future climate change scenarios, and this is the first study of this type for the Desertas petrel.

MATERIALS AND METHODS

Tracking and geographical data

Fieldwork took place at Bugio Island (35° 25′ N, 16° 29′ W) located in the Desertas Islands (Madeira Archipelago, Portugal). Twenty-six Desertas petrels were tagged over 8 yr (2007–2014) with global location sensing (GLS) tracking devices (Mk14; British Antarctic Survey, BAS) providing data on 62 annual trips (see Ramírez et al. 2013, 2016 for more details on tagging and geolocation data processing). GLS devices weighed 1.5 g and were attached to the bird's tarsus using a single cable-tie and a thin bed of silicone sealant to a metal ring (Ramírez et al. 2013). The logger plus attachment represented 2–2.6% of the adult mass (below the threshold proposed by Phillips et al. 2003). Previous studies showed no effect of tagging on body condition or breeding success (Ramírez et al. 2013, 2016).

Geographical positions from November to May of each year (corresponding to the non-breeding period, Ramírez et al. 2013, 2016) were used to generate kernel utilization distributions (KUDs). Individual home ranges (95% KUD) and core foraging areas (50% KUD) were calculated from the geolocation data using the R package *adehabitatHR* (Tancell et al. 2013, Calenge 2015, Paiva et al. 2015). The smoothing parameter (*h*) was set to 1°, due to the average error of geolocation data being as large as 180 km (Wilson et al. 1992, Phillips et al. 2004, Nielsen & Sibert 2007). Individual KUDs were averaged to provide an unbiased KUD estimate at the population level (Fig. 1).

Oceanographic predictors and data processing

We used 4 oceanographic variables (Fig. 1) to characterize the oceanic conditions and to model the distribution of non-breeding Desertas petrels. Dynamic variables were extracted as monthly (November to May) composites of: chlorophyll *a* (chl *a*) concentration (AquaMODIS product, 0.04° spatial resolution, mg m^{-3}), sea surface temperature (SST, AquaMODIS, 0.04° spatial resolution, °C) and ocean surface wind speed (WS, QuickSCAT, 0.25° spatial resolution, m s^{-1}). Chl *a* and SST satellite images were downloaded from Oceancolor Browser (https://oceancolor.gsfc.nasa.gov/) and WS from the SeaWinds database (winds.jpl.nasa.gov). In addition, static bathymetric data (sea bed depth [SBD], blended ETOPO1 product, 0.01° spatial resolution, m) were downloaded from www.ngdc.noaa.gov/mgg/global/. These variables are important proxies for seabird foraging activity (Pinaud & Weimerskirch 2007, Wakefield et al. 2009, Pinet et al. 2011) and have been used in other modelling studies with gadfly petrels (Krüger et al. 2016, Legrand et al. 2016).

Median values were taken from all monthly composites in order to produce a single raster of each environmental feature to enter as an independent variable into the model calibration process. All environmental predictors were resampled to a 1° cell size using a nearest-neighbour interpolation procedure (Childs 2004).

Ensemble species distribution models

We applied ensemble species distribution models (ESDMs) over the oceanographic variables using the R package *BIOMOD2* (Thuiller 2003, Thuiller et al. 2009, 2014) implemented in software R 3.4 (R Core Team 2016) to model the current distribution and project the potential distribution onto future scenarios of climate change. In this study, the 'current distribution' refers to the occurrence probability estimated by the models given the observed environmental variables, while the 'potential distribution' refers to the models applied over the hypothetical future scenarios of climate change and dispersal. The results of ESDMs are measured as an estimated probability of occurrence, which can also be interpreted as a measure of habitat suitability (Ottaviani et al. 2004, Guisan & Thuiller 2005).

ESDMs are considered a better approach than a single algorithm when modelling distribution (Araújo & New 2007, Marmion et al. 2009, Thuiller et al. 2009). The ESDMs are a forecast ensemble of the best predictive features of each modelling technique (Araújo & New 2007). ESDMs contribute to improve the robustness of the forecast models by maximizing the accuracy of species distributions (Araújo & New 2007, Marmion et al. 2009, Thuiller et al. 2009). Despite criticisms about the use of SDMs as being simply statistical and ignoring the processes behind the species distribution, ESDMs are useful in order to predict species responses towards environmental conditions when more complex process-based models are not available (Morin & Thuiller 2009, Lozier et al. 2009, Dormann et al. 2012). In our study, to explain why and how an individual bird chooses and repeatedly uses a wintering area would require several years of tracking immature individuals until they reach maturity. At present, such data are nonexistent for this species; therefore, the SDMs can be a useful and informative tool. We used 10 modelling techniques. Of these, 5 techniques have a machine-learning process to select the better fit between environmental variables and species occurrence: random forest (RF), generalized boosted model (GBM), artificial neural network (ANN), maximum entropy (MaxEnt) and classification tree analysis (CTA); 4 are straightforward correlative-based methods: generalized linear model (GLM), generalized additive model (GAM), multiple adaptive regression splines (MARS) and flexible discriminant analysis (FDA); and the last technique, species range envelope (SRE), uses the median and quartiles of variables in geographical points to estimate the probability of occurrence (Elith et al. 2006, Rougier et al. 2015).

We used the geolocation points that fell within the core areas (50% KUD) as 'presences' in our modelling procedure following Legrand et al. (2016). SDMs require the generation of pseudo-absences (PAs) in order to calculate probabilities of occurrence. It is recommended that the number of PAs matches or approximates the number of presences (n = 8793); therefore, we generated 10 000 random PAs on 20 repetitions (VanDerWal et al. 2009, Barbet-Massin et al. 2012) across the whole Atlantic Ocean between 50° N and 50° S. Each model was set with 10-fold cross-validation, with data split at 80% for model calibration (training) and 20% for testing. We used the 'ggpairs' function of the 'GGally' R package (Schloerke et al. 2017) to test the correlation between explanatory variables of the training dataset for both the presences and randomly generated PAs. The level of correlation was not enough to hinder the analysis (Fig. 2).

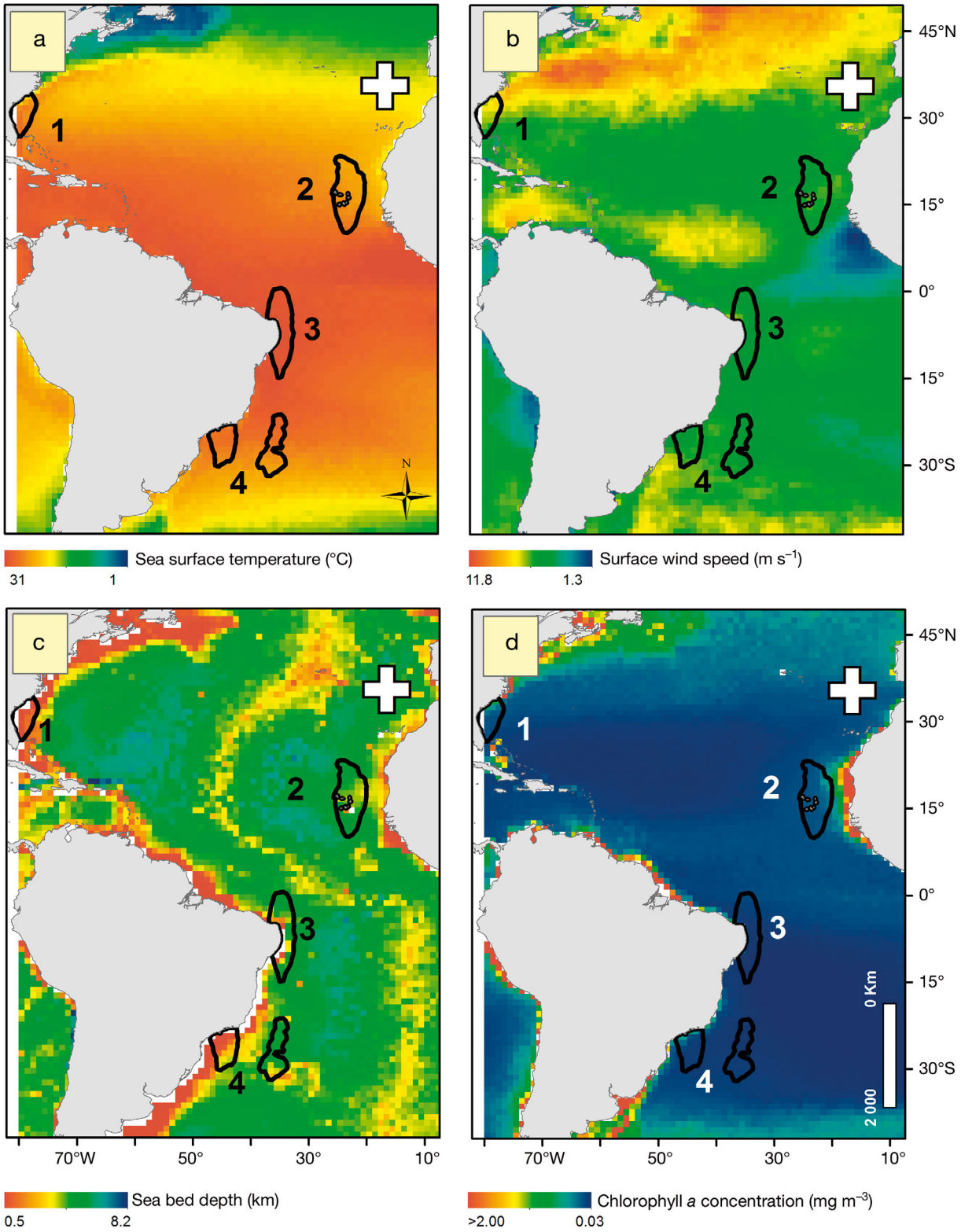

Fig. 1. Wintering core areas (50% kernel utilization distribution) of Desertas petrel *Pterodroma deserta* calculated from the tracking data overlaid onto the environmental variables used for modelling: (a) sea surface temperature, (b) surface wind speed, (c) sea bed depth and (d) chlorophyll *a* concentration. Numbers refer to the wintering area designations: (1) US east coast, (2) Cape Verde Islands, (3) northern Brazil and (4) southern Brazil. The white cross marks the position of the breeding colony at Desertas Islands (Madeira archipelago)

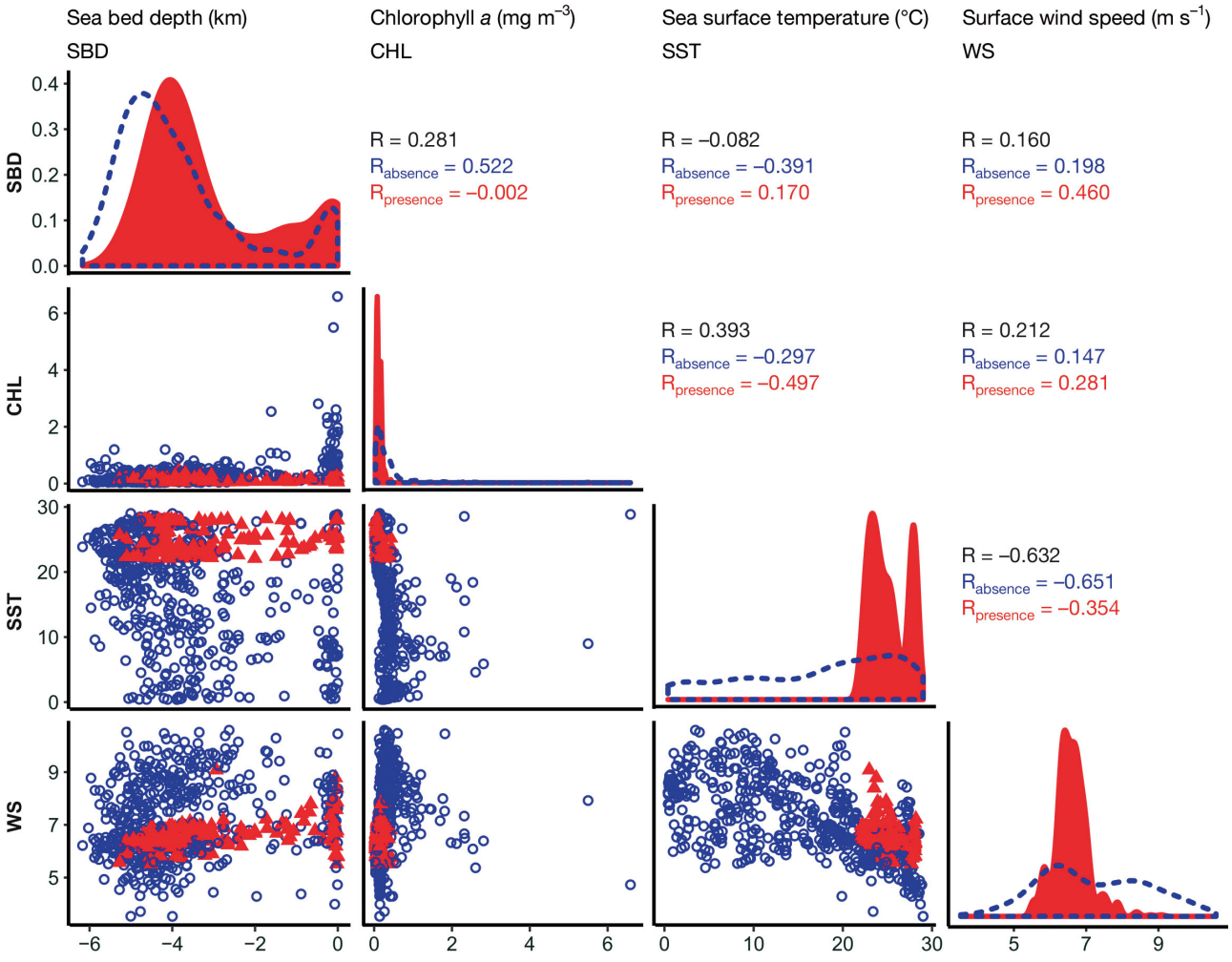

Fig. 2. Histogram and correlation (R) scatterplots for the distribution of the environmental variables used in the training steps of Desertas petrel *Pterodroma deserta* modelling values for both presences (red triangles, red solid shapes) and pseudo-absences (blue circles and blue dashed shapes): sea bed depth (SBD), chlorophyll *a* concentration (CHL), sea surface temperature (SST) and surface wind speed (WS)

The accuracy of the models was assessed using the area under the curve (AUC) of the receiver operating characteristics (ROC) and true skill statistics (TSS) (Pearson et al. 2006, Allouche et al. 2006). These accuracy measures are considered suitable for assessing the performance of the models, as they assess the models' ability to predict presences and absences (Lobo et al. 2008). We used repetitions with AUC and TSS ≥0.8, as this value is generally accepted as an indicator of very good discriminatory ability of the model (Engler et al. 2004). *BIOMOD2* then joins all models by an accuracy-weighted averaging approach, whereby more accurate models have a greater influence on the final distribution (Thuiller et al. 2009). Variable importance was calculated as the proportion of change in AUC by excluding 1 variable in turn and retaining the others.

IPCC future scenario projections

We used the 4 scenarios of climate change of the IPCC that assume different concentration pathways of greenhouse gases and their radiative forcing, termed the representative concentration pathways (RCPs; IPCC 2014). These scenarios assume the following: (1) low emissions reverting to pre-industrial conditions (RCP 2.6); (2) the emissions remain constant in relation to the current levels of emissions (RCP 4.5); (3) emission levels slowly increase in relation to current levels (RCP 6.0); and (4) emission levels quickly increase in relation to current levels (RCP 8.5). We used the climate projections of the Coupled Climate-Carbon Earth System Models (ESM2M) (Dunne et al. 2012, 2013) from the NOAA CMIP5 data portal (http://nomads.gfdl.noaa.gov) for

SST, chl *a* and WS. Bathymetry was treated as a fixed variable in future projections. All variables in the future projections were resampled to a 1° cell size using a nearest-neighbour interpolation procedure (Childs 2004).

The ESDMs used to predict species distributions were then extrapolated to future conditions of SST, chl *a* and WS using projections for 2050 and 2100 under RCP scenarios 4.5, 6.0 and 8.5. The same temporal resolution from the oceanographic variables was used to resample the variables in future scenarios (median from Desertas petrel wintering months). *BIOMOD2* calculates the threshold of probability of occurrence that maximizes sensitivity and specificity, meaning that it calculates the best value to correctly classify the continuous probability in binary (1 and 0). Hence, we created polygons from the mean distribution of the ensemble projections, using the models' mean threshold probability of 64.76% (Jiménez-Valverde & Lobo 2007, Barbet-Massin et al. 2012).

Distribution change

Distribution change was calculated using the species range change (SRC) tool in the *BIOMOD2* package (Thuiller 2003, Thuiller et al. 2009). SRC is measured as the percentage of suitable habitat change for each scenario compared to the current distribution. *BIOMOD2* allows us to calculate SRC considering full dispersal (whereby the species is able to reach all of the new suitable habitat predicted by the model) or limited dispersal (the species is limited by its current distribution, therefore complying with the idea of wintering site fidelity; Ramírez et al. 2016).

Taking into account the limited dispersal scenario, we calculated the change in suitability within each estimated wintering ground by subtracting the potential probability of occurrence by the current prediction. We classified negative values as 'Decrease'=1 in suitability in the potential distribution, and positive values as 'Increase'=0 in suitability in the potential distribution. We then applied a binomial generalized linear mixed model with the R package *lmerTest* to test differences in suitability change among wintering areas. Grid cells were repeated through years and different scenarios; therefore, positions of the grid cells were used as random terms [glmer (Suitability Decrease Probability ~ Current Suitability × Wintering Area+ (1|Grid ID), family= 'binomial'].

RESULTS

Current wintering areas and distribution

The current wintering areas (50% KUDs) used by the Desertas petrel were located over the US east coast, Cape Verde Islands, and northern and southern Brazil (Fig. 1). All SDMs were accurate, but 5 out of 10 models performed better: CTA, GAM, GBM, MAXENT and RF (Table 1). SST ranked as the most important variable in all models, followed by WS in 7 out of the 10 models (Table 1).

Table 1. Mean ± SD model accuracy measured as the area under the receiver operating characteristics curve (AUC) and true skill statistic (TSS) and environmental variable importance calculated as the percentage of change in AUC by excluding 1 variable in turn and retaining the others. ANN: artificial neural network, CTA: classification tree analysis, FDA: flexible discriminant analysis, GAM: generalized additive model, GBM: generalized boosting model, GLM: generalized linear model, MARS: multiple adaptive regression splines, MAX: maximum entropy model, RF: Breiman and Cutlers random forest for classification and regression, SRE: surface range envelopes. **Highest percentage value in each model, *second highest percentage value

Model	AUC	TSS	Sea bed depth	Chlorophyll *a* concentration	Sea surface temperature	Sea surface wind speed
ANN	0.935 ± 0.028	0.800 ± 0.069	24.5 ± 8.2	12.0 ± 5.9	64.1 ± 15.8**	36.6 ± 10.6*
CTA	0.989 ± 0.003	0.963 ± 0.006	17.5 ± 1.6	3.9 ± 3.4	73.5 ± 2.8**	21.7 ± 2.2*
FDA	0.964 ± 0.004	0.813 ± 0.012	7.6 ± 0.3	4.7 ± 0.4	90.3 ± 0.2**	11.3 ± 0.5*
GAM	0.976 ± 0.003	0.891 ± 0.009	13.3 ± 0.3	10.0 ± 0.6	58.9 ± 0.7**	25.7 ± 0.2*
GBM	0.991 ± 0.002	0.937 ± 0.007	10.0 ± 0.3	11.7 ± 0.7*	77.6 ± 1.1**	9.8 ± 0.3
GLM	0.936 ± 0.004	0.789 ± 0.010	15.1 ± 0.3	13.5 ± 0.4	50.4 ± 0.4**	31.3 ± 0.2*
MARS	0.967 ± 0.004	0.836 ± 0.013	8.7 ± 0.5	4.5 ± 0.3	74.3 ± 2.2**	22.0 ± 0.6*
MAX	0.970 ± 0.005	0.859 ± 0.012	13.6 ± 1.1	19.8 ± 2.2*	48.7 ± 1.8**	17.4 ± 1.7
RF	0.999 ± 0.001	0.995 ± 0.002	17.8 ± 0.3	37.4 ± 0.7*	62.9 ± 0.5**	21.9 ± 0.4
SRE	0.857 ± 0.007	0.713 ± 0.014	20.3 ± 0.5	23.1 ± 0.2	46.1 ± 0.1**	28.9 ± 0.2*

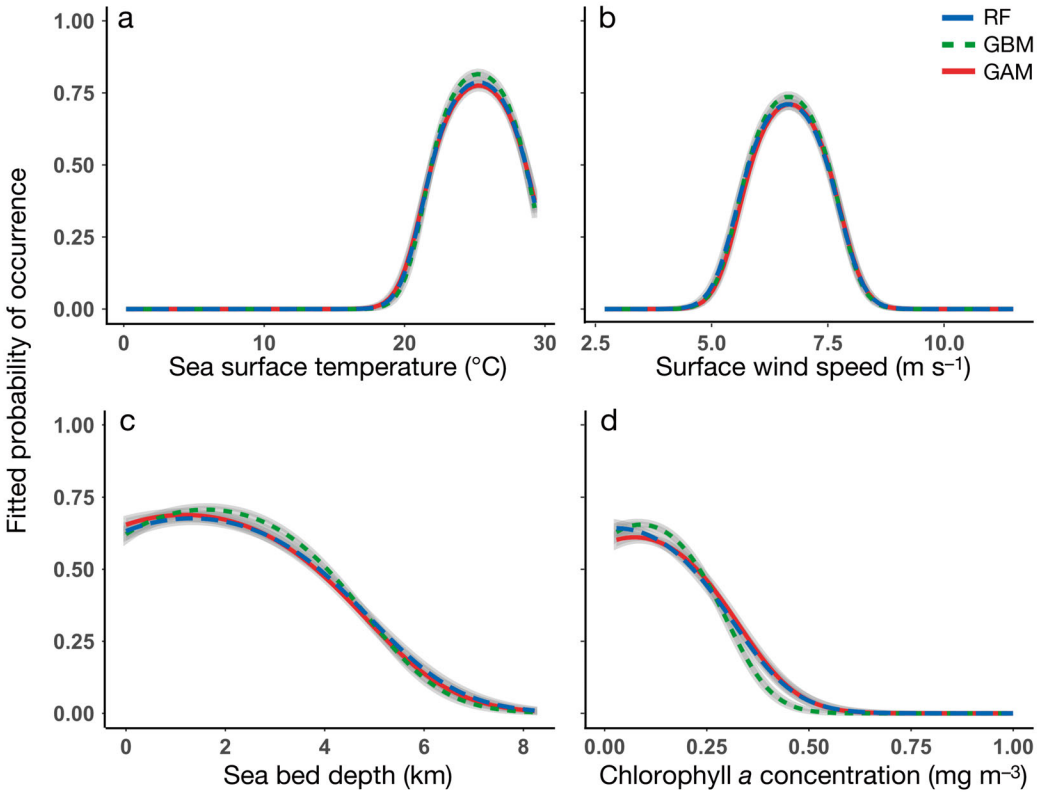

Fig. 3. Probability of occurrence of Desertas petrel *Pterodroma deserta* in response to environmental variables fitted by the 2 most accurate machine-learning models (RF: random forest, GBM: generalized boosted model) and the most accurate correlative model (GAM: generalized additive model): (a) sea surface temperature, (b) surface wind speed, (c) sea bed depth and (d) chlorophyll *a* concentration. Binomial trend line ± SD (grey area)

Models produced similar outputs and very consistent environmental response curves for fitted predicted occurrence in relation to SST, WS, SBD and chl *a* (Fig. 3). They indicated that the main suitable habitats were those with the following characteristics: 20–30°C SST and 5–8 m s^{-1} WS from shallow to deep and oligotrophic waters (Fig. 3). Such habitats were reflected in the areas of higher predicted probability of occurrence and matched the 50% KUD except in 2 cases: (1) 2 pelagic areas in the central area of both the North and South Atlantic Ocean, and (2) 1 area in the extreme north of South America that extends towards Central America. These 2 predicted areas showed apparently suitable areas not currently used by the sampled birds (Fig. 4).

Potential distribution under different climate change scenarios

The full dispersal potential distribution compared to the actual distribution indicated that the amount of suitable area for this species increased in all scenarios (Table 2, and see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m599p253_supp.pdf). The limited dispersal approach indicated that 47.9–58.8% of suitable area remains for all scenarios (Table 2). SST (Fig. S2) and WS (Fig. S3) seemed to be the key factors limiting suitable habitats when plotting the potential distribution against the climate variables in 2050 and 2100. SST marked the northern and southern limits of the species' distribution, which expanded polewards in future projections; this meant that the core winter distribution is defined by areas of intermediate WS and low to intermediate productivity (Fig. 5).

Change in suitable habitat within current wintering grounds

The mean suitability change was negative for all wintering grounds (Cape Verde Islands: −57.1 ± (SD) 1.9%; northern Brazil: −19.7 ± 1.7%; southern Brazil: −11.1 ± 1.21%, US east coast: −33.0 ± 3.12%). This means that under a limited dispersal approach, the

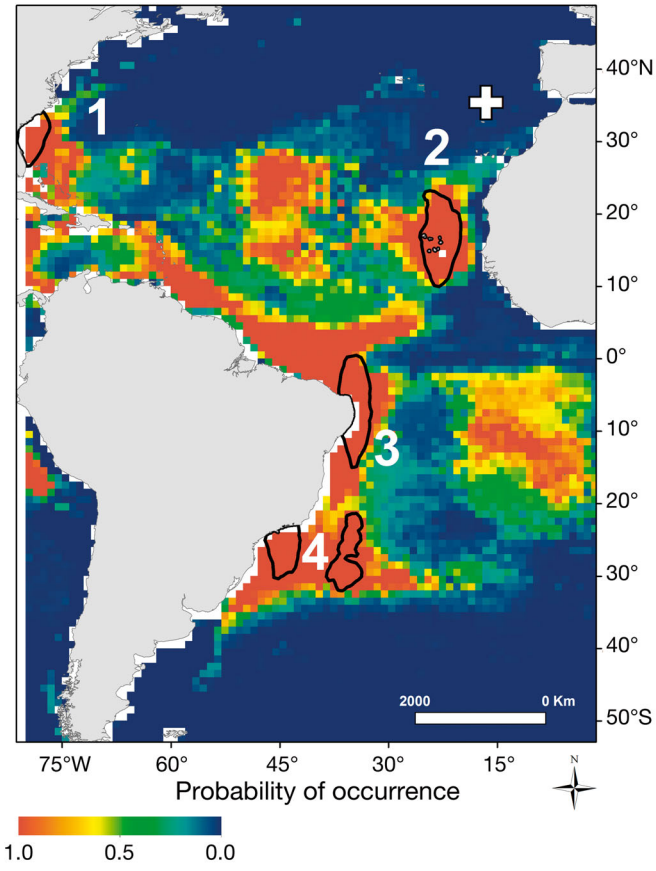

Fig. 4. Ensemble modelled probability of occurrence (actual distribution) of wintering areas of Desertas petrel *Pterodroma deserta* indicating the 4 main wintering areas, and showing the winter core areas from 50% kernel utilization distributions (black lines): (1) US east coast, (2) Cape Verde Islands, (3) northern Brazil, (4) southern Brazil. The white cross marks the position of the breeding colony at Desertas Islands (Madeira archipelago)

predicted wintering areas would be smaller than those observed at present. Areas of currently higher suitability (high probability of occurrence) within wintering grounds had a lower suitability in the future, which was true for all wintering grounds separately (Table 3, Fig. 6). The Cape Verde Islands had the lowest probability of suitability increase, and the reverse trend was observed for the US east coast wintering grounds (Fig. 6). Trends were consistent among scenarios and years (Fig. 6).

DISCUSSION

We found that the Desertas petrels were associated with subtropical to tropical temperatures in oceanic shallow to deep oligotrophic waters with intermediate WS. Our models indicate that the area characterized by these variables will increase in future projections. On one hand, increased temperatures will facilitate the expansion of northern and southern limits of the species' potential distribution, and the increase in WS contributes to a reduction in chl *a* concentrations, allowing for a longitudinal expansion of the Desertas petrel wintering grounds. On the other hand, our models indicated that the suitable habitat observed within the current wintering grounds would deteriorate, leading to a loss of approximately 50% of the current suitable wintering habitat of this species.

Table 2. Species range change measured as the percentage of the future range in relation to the current range of Desertas petrel *Pterodroma deserta*, considering limited and full dispersal over different representative concentration pathway (RCP) future climate change scenarios for 2050 and 2100. Details of RCPs are given in the 'Materials and methods'

RCP	Year	Future range size (% of current range)	
		Limited dispersal	Full dispersal
4.5	2050	47.9	386.8
	2100	52.4	382.1
6.0	2050	47.9	381.8
	2100	53.5	490.9
8.5	2050	56.2	431.2
	2100	58.8	510.6

The poleward shift in the range of this species caused by an increase in SST has previously been verified in modelling studies (Péron et al. 2012, Russell et al. 2015, Krüger et al. 2018), and suggests that several species could change their distribution according to this expectation (Péron et al. 2010, Weimerskirch et al. 2012, Poloczanska et al. 2016). The same logic is expected in our study, with the Desertas petrel's range increasing polewards due to climate change. On the other hand, the increased WS at higher latitudes may become a barrier for latitudinal dispersal in the future (Weimerskirch et al. 2012, Cornioley et al. 2016, Tarroux et al. 2016, Krüger et al. 2018). Increased wind speeds at intermediate latitudes and the expansion of less-productive areas would allow the Desertas petrel to expand its longitudinal distribution in future scenarios, but may also deteriorate the habitats within its current wintering grounds (this study). These current wintering areas are used by several seabird species throughout the year (Grecian et al. 2016, Ramos et al. 2017) as both breeding and non-breeding areas, including gadfly petrels (Krüger et al. 2016, Ramos et al. 2017) and shearwaters (González-Solís et al. 2009, Dias et al. 2011, Hedd et al. 2012, Freeman et al. 2013, Missagia

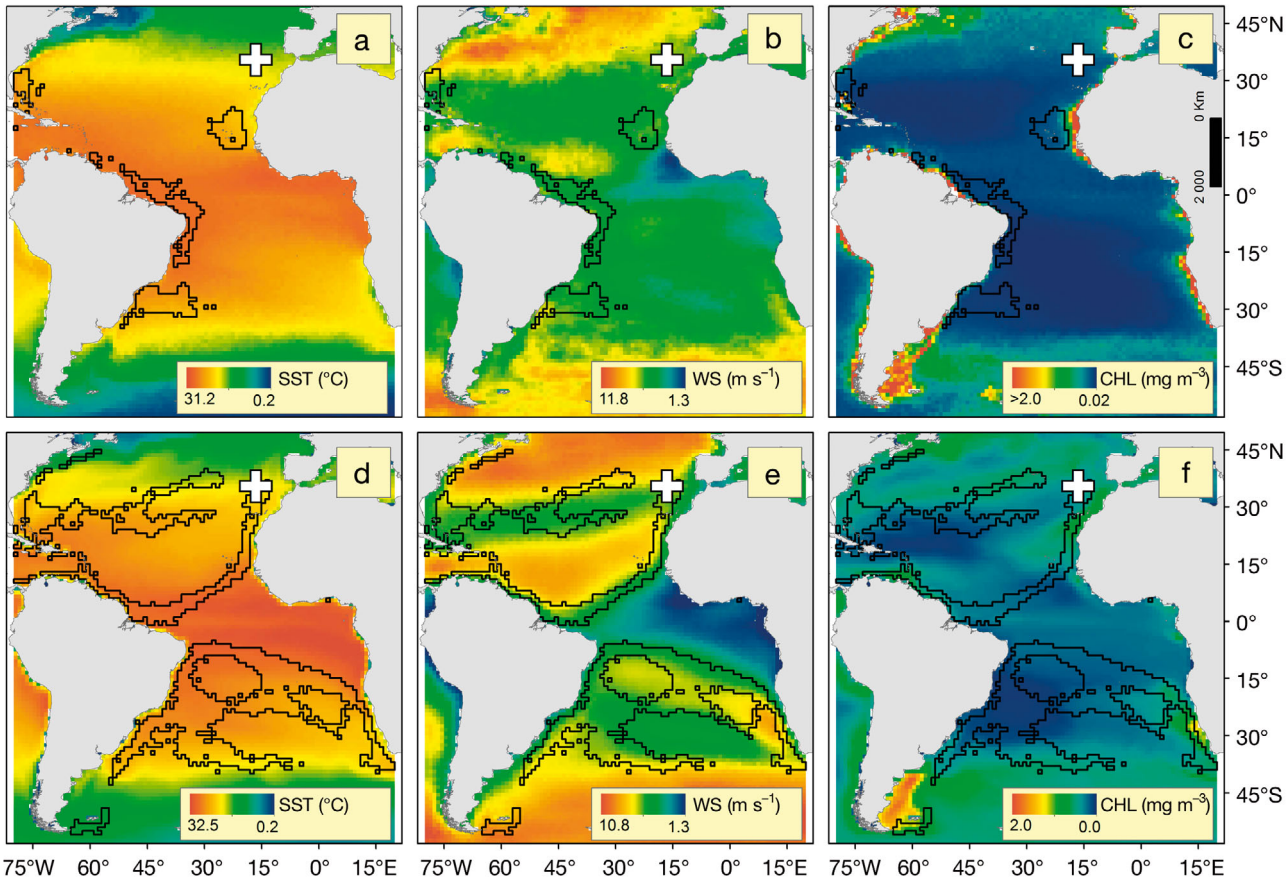

Fig. 5. Current wintering areas of Desertas petrel *Pterodroma deserta* (black lines) plotted with the current (a) sea surface temperature (SST), (b) surface wind speed (WS) and (c) chlorophyll *a* concentration (CHL), and potential wintering areas of Desertas petrel (black lines) shown with the projected (d) SST, (e) WS and (f) CHL in future scenarios of climate change. Potential wintering areas (full dispersal scenario) and projected environmental variables are presented as medians from the 3 representative concentration pathways (RCPs 4.5, 6.0 and 8.5) for 2050 and 2100. The white cross is the position of the breeding colony at Desertas Islands (Madeira archipelago)

et al. 2015). Typically, the wintering grounds are close to year-round upwellings (Gregg et al. 2005, Behrenfeld et al. 2006), ocean gyres (McClain et al. 2004, Gregg et al. 2005) and/or seamounts (Kitchingman et al. 2008, Wessel et al. 2010), making them spatially and temporally predictable. The productivity in these areas is highly dependent upon wind currents and local circulation trends (Young et al. 2011, Lluch-Cota et al. 2013, Sydeman et al. 2014). Changes in WS may have large impacts on local and

Table 3. Binomial generalized linear mixed model results testing the probability of decreased suitability conditions in wintering areas of the Desertas petrel *Pterodroma deserta* based on the current predicted suitability from the ensemble species distribution modelling output

Explanatory variable	$F_{7,1978}$	Reference area	Compared to	Estimate	SE	z	p(>|z|)
Prediction	24.783			8.05	1.77	4.56	<0.0001
Wintering area	5.497	South Brazil	Cape Verde Islands	4.19	4.62	0.91	0.3647
			US east coast	–35.94	8.48	–4.24	<0.0001
			North Brazil	5.74	2.90	1.98	0.0479
Prediction × Wintering	8.014	South Brazil	Cape Verde Islands	0.46	5.53	0.08	0.9331
			US east coast	45.37	10.69	4.24	<0.0001
			Northern Brazil	–7.69	3.43	–2.24	0.0250

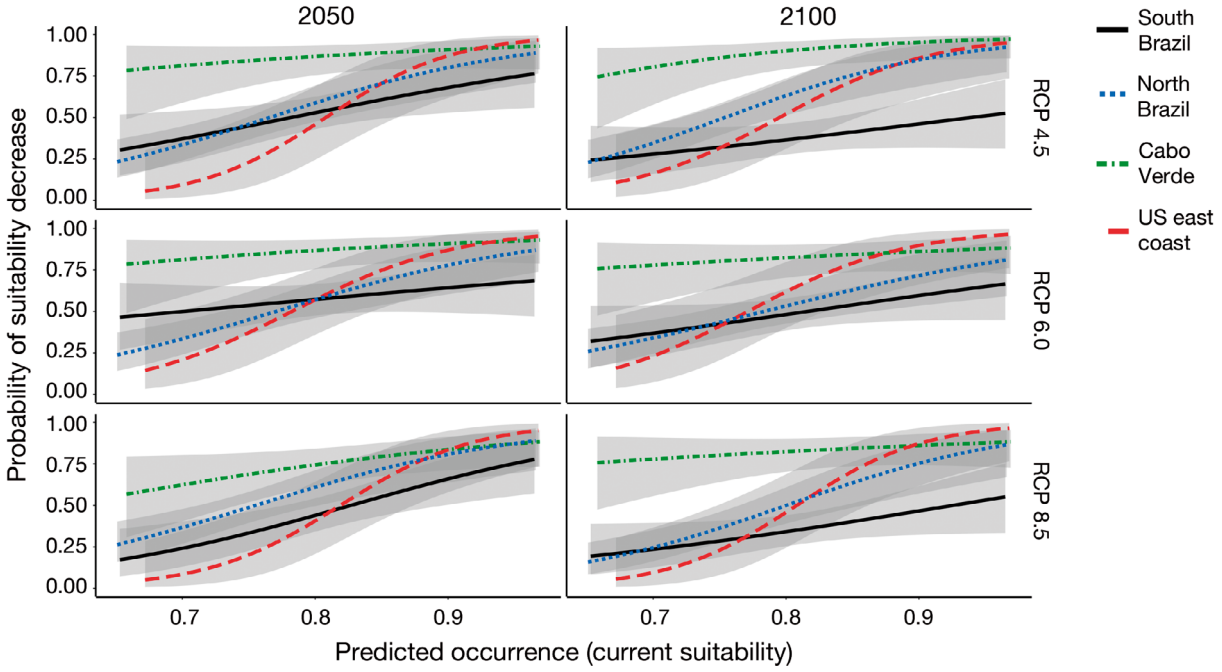

Fig. 6. Probability of habitat suitability decrease over future climate conditions within the current wintering grounds (current suitability above 0.647) of the Desertas petrel *Pterodroma deserta*. RCP: representative concentration pathway (see 'Materials and methods' for details of the scenarios)

global marine productivity (Young et al. 2011, Lluch-Cota et al. 2013, Sydeman et al. 2014), with varying consequences for top predators. The increasing evidence that wind trends have been shifting in the last decades (Young et al. 2011, England et al. 2014, Sydeman et al. 2014), added to the increase of low productivity zones in the open ocean (Gregg et al. 2005, Behrenfeld et al. 2006, Polovina et al. 2008), raises concerns about how the habitats within those areas may shift and what the consequences for marine biodiversity will be (Grémillet & Boulinier 2009, Raymond et al. 2010).

The potential wintering distribution of Desertas petrel will drastically change according to the future IPCC scenarios under both the limited and full dispersal scenarios. Under the limited dispersal hypothesis, which is a reasonable hypothesis considering the high wintering site fidelity of gadfly petrels (Pinet et al. 2011, Ramírez et al. 2016), Desertas petrels may suffer considerable losses of their wintering habitat availability within an individual's lifetime. However, no long-term data are available to quantify what it takes for a site-faithful seabird to move. Previous studies suggest that some seabirds may insist on a chosen area even under unfavourable conditions (i.e. Danchin et al. 1998, Bried & Jouventin 2002, Hamer et al. 2002, Naves et al. 2006), while other species may be more flexible (Dias et al. 2011), and therefore more adaptable, i.e. more likely to change their wintering areas after several 'bad years' (i.e. Clausen et al. 2018). Based on existing scientific data, site consistency could represent a maladaptive behaviour under climate change scenarios, as the areas selected by the birds could act as an ecological trap reducing the species' productivity (Fletcher et al. 2012, Sih 2013, Hale et al. 2016). Different levels of wintering consistency may be found for different trans-equatorial migrating seabird species (Dias et al. 2011, Raine et al. 2013, Müller et al. 2014, Ramírez et al. 2016), and one can advocate that the amount of risk imposed by changing climate conditions may vary as a function of an individual's ability to shift its wintering area, and the ability of new generations to select new wintering areas. The process by which immature seabirds select their wintering areas remains unknown. Understanding how birds choose their wintering grounds would inevitably require tracking of juveniles for several years, plus several years of tracking the same individuals to check their probability of changing wintering grounds and testing the influence of climate. Nonetheless, social information theory predicts that less experienced animals may follow more experienced ones in order to try to find suitable conditions (Péron & Grémillet 2013). In this case, the ability of a species to cope with deteriorated climate conditions may depend on the ability/flexi-

bility of the next generation(s) to explore and find new wintering grounds independently of the social information made available by experienced individuals. In the case of seabirds who can live longer than 40 yr, such as petrels, such changes will be felt within a few generations. This means there may not be enough time for a species with such a reduced population size to realize evolutionary solutions to deal with changing conditions in their wintering habitat.

It is crucial for birds to be able to cope with unsuitable conditions, as the wintering season has negative effects on adult survival and recruitment of new breeders (i.e. Sandvik et al. 2007, Sandvik & Erikstad 2008, Barbraud et al. 2012). Under a full dispersal scenario, climate change may substantially increase the suitable habitat available for Desertas petrels, but if the species shows long-term fidelity to sites, and if the influence of adults on immature birds in terms of their choice of wintering areas is strong, then the species may experience losses of suitable wintering habitat at alarming rates. This perspective is disturbing considering the vulnerability of this species to stochasticity due to its small population size. We suggest continued monitoring of the population via tracking of adults and immatures, as well as recording demographic data, since this will enable us to ascertain whether our projections are correct. Furthermore, and as stated before, the wintering areas used by the Desertas petrel are also used by several other seabird species. Deteriorating conditions in these particular areas may represent a potential threat for most of the other co-occurring species. We envisage similar studies should be applied to those species as well.

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