

LETTER

A wolf in fox's clothing? Using stable isotopes to quantify ecological replacement

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Abstract

Ecological replacement as a conservation tool presupposes that nonnative taxa can restore degraded ecosystems by performing the ecological functions of extinct taxa. This assumption is rarely tested however, largely because it is difficult to quantify the functions of species extirpated long ago. Here, we test whether feral South American grey foxes (SAGF), introduced to the Falkland Islands ~90 years ago, act as unintended ecological replacements for endemic Falkland Islands wolves (FIW), extirpated during the 19th century. Using hair stable isotope ratios as proxies for diet, we show that the isotopic niche space of modern SAGFs almost completely encompasses that of archaic FIWs. However, the former's niche is larger so while SAGFs may play similar ecological roles to FIWs, they probably perform additional functions, which may or may not be desirable. In so doing, we illustrate a generalized framework for using comparative isotopic niche analysis to test for ecological replacement objectively.

KEYWORDS

Bayesian niche overlap, ecological analogue, proxy species, stable isotope analysis, taxon substitution, warrah

1 | INTRODUCTION

During the Anthropocene, human-induced extinctions, especially of predators and large herbivores, have resulted in widespread ecosystem changes (Malhi et al., 2016).

Moreover, unintentionally or deliberately introduced species have replaced many native species, especially on islands (Wardle, Bardgett, Callaway, & van der Putten, 2011). Although nonnative taxa are conventionally considered detrimental, some now suggest that they can

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be beneficial if they fill the ecological roles of extirpated natives, thereby restoring ecosystems towards their pre-Anthropocene states (Lundgren et al., 2020; Schlaepfer, Sax, & Olden, 2011). Indeed, the deliberate introduction of such *ecological replacements* has been advocated as a conservation tool (Donlan et al., 2006; Falcón & Hansen 2018; Griffiths, Hansen, Jones, Zuë, & Harris, 2011; Seddon, Griffiths, Soorae, & Armstrong, 2014). However, many assumptions underlying this approach remain untested. This is in part because most animal extinctions caused directly or indirectly by humans occurred in prehistory (Barnosky, 2008), meaning that the former ecological functions of those species can be inferred only indirectly, for example by comparing their locations in trait space with extant taxa (Lundgren et al., 2020). However, the ecological effects of nonnatives (positive or negative), are notoriously difficult to predict (Vitule, Freire, Vazquez, Nuñez, & Simberloff, 2012). As rewilding and other forms of ecological restoration become more common, there is an urgent need to quantify the likely or realized effects of ecological replacement (Seddon et al., 2014; Vitule et al., 2012). Given that many species, especially predators, impact ecosystems through their diet, we suggest that one way of doing this is to compare the volume and overlap of dietary niches of extinct taxa and their potential ecological replacements. Stable isotope ratios in the tissues of consumers predictably reflect those in their food (Phillips et al., 2014) so one indirect but tractable way of doing this is to quantify isotopic niche volume and overlap using modern and historical tissue samples (Chamberlain et al., 2005; Fox-Dobbs, Nelson, Koch, & Leonard, 2012; Newsome et al., 2010).

To exemplify this approach, we consider whether non-native South American grey foxes (*Lycalopex griseus*, hereafter SAGF) act as de facto ecological replacements for extinct Falkland Island wolves (*Dusicyon australis*, hereafter FIW; Figure S1, Table S3). FIWs likely reached the Falklands from mainland South America naturally at least 16,000 years ago (Austin et al., 2013). Prior to their extirpation by man around 1876, they were the archipelago's only endemic land mammal and large terrestrial predator. Historical accounts (notably by Charles Darwin) are limited but indirect evidence suggest that FIWs were hypercarnivorous (Meloro et al., 2017). SAGFs were introduced to at least eight islands in the Falklands between 1923 and 1933 for fur farming but rapidly became feral (Bernhardson, 1988). In their native Patagonia, SAGFs are mesocarnivores, consuming berries, invertebrates, small birds/mammals, farm animals, and carrion (del Solar & Rau 2004). In the Falklands, they also predate/scavenge penguins and other marine organisms (Vick, 2019). Due to their impact on native birds and

sheep, SAGFs have recently been eradicated from three islands, with complete eradication suggested (Mischler, 2009; Poncet et al., 2011). However, if SAGFs act functionally like FIWs, the Falklands ecosystem could be closer to its pre-Anthropocene state with them than without. Stable isotope (SI) analysis has been used to assess the diets of both modern and archaic canids (Darimont & Reimchen 2002; Fox-Dobbs, Bump, Peterson, Fox, & Koch, 2007; Krajcarz, Krajcarz, & Bocherens, 2018). Here we use this technique to test whether feral SAGFs in the Falkland Islands occupy the former isotopic niche of the FIW.

2 | METHODS

SI ratios in food sources available to canids in the Falklands vary along two axes relevant to our study (Figure 1A): The ratio $^{13}\text{C}:^{12}\text{C}$ (hereafter $\delta^{13}\text{C}$) increases from terrestrial to marine sources, while $^{15}\text{N}:^{14}\text{N}$ (hereafter $\delta^{15}\text{N}$) increases stepwise with trophic level (Phillips et al., 2014). We measured these ratios in modern SAGF and historical FIW tail guard hairs collected on Weddell Island, Falklands (November–December 2018) and East and West Falkland (~1837–1877), respectively (Supporting Information Methods, Table S1, Figure S2). Canids have one annual molt in spring, with new tail guard hairs grown from mid-summer to autumn, so we assume that tail hair SI ratios reflect diet during that period (Darimont & Reimchen 2002; Maurel, Coutant, Boissin-Agasse, & Boissin, 1986). Where sufficient tissue was available, we cut hairs in two, and analyzed the proximal and distal halves separately to check for seasonal shifts in diet (Supporting Information). To characterize the isotopic signatures of food sources known or suspected to be consumed by the two canid species, we analyzed tissues collected on Weddell Island and collated SI data from the literature, together encompassing berries, terrestrial invertebrates (camel crickets), higher marine predators (penguins, sea lions, seabirds), marine herbivores (limpets and geese), and terrestrial herbivores (geese, sheep) (Supporting Information, Table S2). We prepared samples and measured SI ratios via mass spectroscopy using standard methods (Supporting Information).

To estimate the diet of modern SAGFs, we fitted Bayesian mixing models to the consumer and source SI data described above (Supporting Information). We specified priors on SAGF diet based on the percentage volume of each prey type found in the feces collected on Weddell Island (Vick, 2019). We determined the isotopic niche region (N_R) of each canid species using Bayesian estimation. Here, we define N_R as the minimum ellipse in

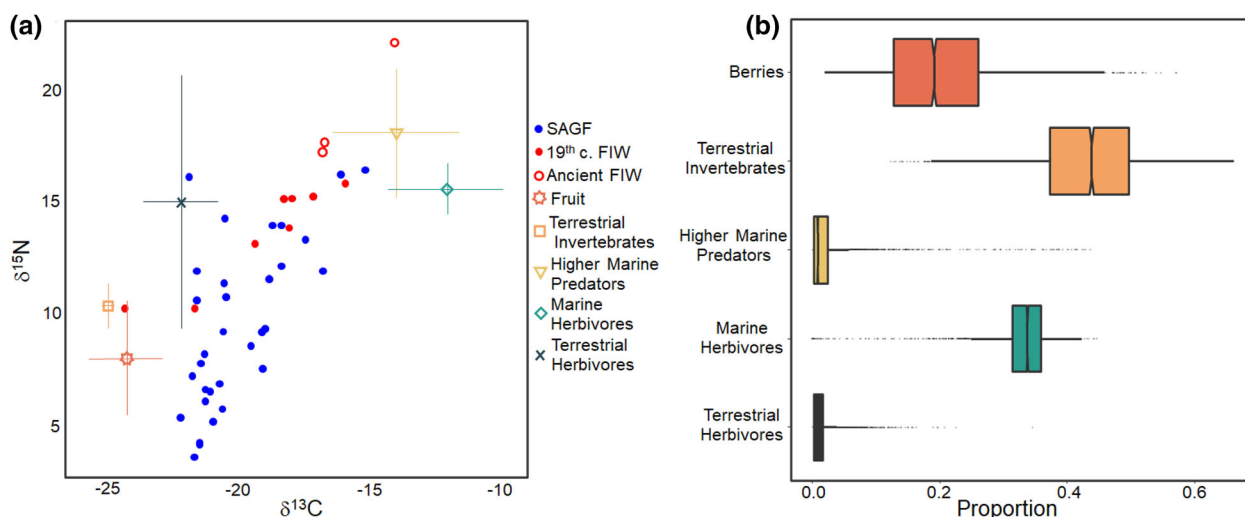


FIGURE 1 (A) Stable isotope signatures of modern South American grey foxes (SAGF, $n = 32$) and extinct Falkland Islands wolves (FIW, $n = 11$) in the Falkland Islands and average ($\pm 1\text{SD}$) signatures of their potential food sources, plus (B) estimated proportion of those food sources in the diet of modern SAGFs. Nineteenth century FIW samples were analyzed during the present study and ancient FIW samples (calibrated age ranges: tooth (top right point), 2212–2108 BCE; pelvic bone, 1162–1221 CE; shoulder blade, 1148–1214 CE) by Hamley et al. (2021)

$\delta^{13}\text{C}$, $\delta^{15}\text{N}$ space within which an individual has a 95% probability of being found (Swanson et al., 2015). To quantify niche overlap, we used Monte Carlo sampling (Swanson et al., 2015) with 10,000 draws to estimate the probability that a randomly drawn SAGF would occur in $N_R(\text{FIW})$ and vice versa. We also compared N_R volume between the two species, assuming this to be a proxy for their functional diversity (Lundgren et al., 2020). To control for potentially confounding changes in background $\delta^{13}\text{C}$ (e.g., due to the Suess effect), we corrected FIW $\delta^{13}\text{C}$ values empirically by measuring the difference in $\delta^{13}\text{C}$ in herbivorous geese (*Chloephaga spp.*) sampled contemporaneously with both the FIWs and SAGFs (Tables S1 and S2). To check whether small sample sizes of FIWs relative to SAGFs biased the likelihood of overlap, we randomly drew $n = 5, 10, 15, 20, 25$, and 32 SAGFs and recalculated niche overlap as before, repeating this procedure 100 times without replacement.

3 | RESULTS

We were able to obtain hair samples from eight of the nine extant FIW skins held in museum collections (Table S1) and from 32 SAGF on Weddell Island. There was no significant evidence of systematic seasonal shifts in diet among SAGF ($\delta^{15}\text{N}$: paired t -test $t_{31} = 0.39$, $p = .692$; $\delta^{13}\text{C}$: $t_{31} = 0.71$, $p = .478$) or FIW ($\delta^{15}\text{N}$: $t_7 = 0.24$, $p = .817$; $\delta^{13}\text{C}$: $t_7 = 0.01$, $p = .989$) (Figure S3). Locations of SAGF in isospace indicate a relatively terrestrial, mid to low trophic diet (Figures 1, 2, and Figure S4). Bayesian mixing models predict that terrestrial invertebrates ($x = 43.8\%$ of

diet; 95% CI = 23.7–58.2%), marine herbivores ($x = 33.8\%$; 21.4–39.6%), and berries ($x = 19.1\%$; 5.1–41.6%) dominate, with relatively little consumption of higher marine predators ($x = 9.0\%$; 0.01–14.8%) and terrestrial herbivores ($x = 7.0\%$; 0.01–7.7%; Figure 1B). FIW SI signatures were similar but their locations in isospace suggested a relatively more marine, higher trophic level diet than SAGFs (Figure 1). Moreover, the FIW N_R volume was less than that of SAGFs (Welch's two-sample t -test: $t_{183} = 27.69$, $p < .001$). The probability of a FIW occurring in the SAGF niche region was 0.79 (95% CI 0.52–0.97) but that of a SAGF occurring in $N_R(\text{FIW})$ was 0.23 (95% CI 0.12–0.55; Figure S5). The probability of FIW occurring in the SAGF N_R reached an asymptote around 15–20 SAGF SI samples, indicating that our conclusions were unlikely to be affected by sample size (Figure S6).

4 | DISCUSSION

Previous studies have compared past to present day isotopic niches of members of the same or similar species (Chamberlain et al., 2005; Fox-Dobbs et al., 2012; Newsome et al., 2010) but as far as we are aware, this is the first study to explicitly compare isotopic niches between an extinct species and a potential ecological replacement. Given the burgeoning interest in ecological replacement as a conservation tool (Falcón & Hansen 2018; Griffiths et al., 2011; Seddon et al., 2014), we foresee that similar studies will become more common. In particular, there are two scenarios where the methods we demonstrate may find wider applicability: Firstly, in instances such as

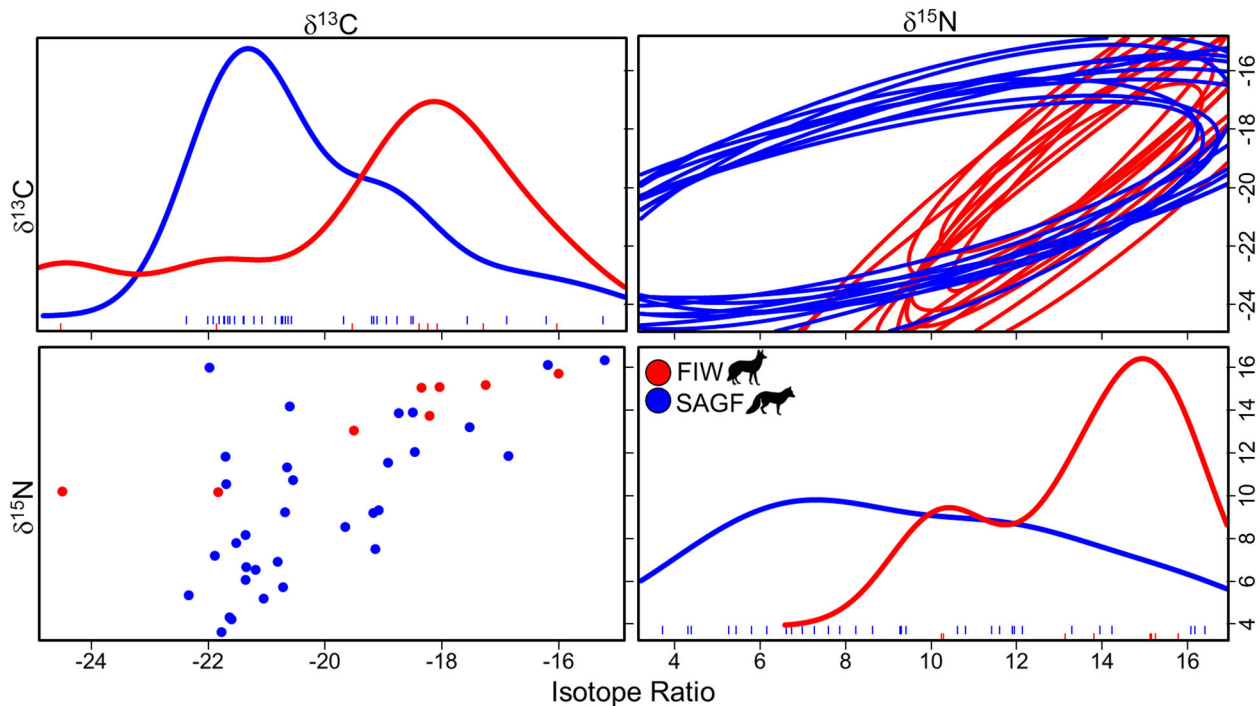


FIGURE 2 Isotopic niches of modern South American grey foxes (SAGF, $n = 32$) and historical Falkland Islands wolves (FIW, $n = 8$) in the Falkland Islands. Top left and bottom right panels show the probability density for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Ellipses top right show ten random realizations of each species' probable niche region (N_R), defined as the ellipse containing 95% of that species' niche volume, estimated from the stable isotope signatures of individuals, bottom left

ours, where nonnative species have already been introduced, accidentally or intentionally, and may now act as a de facto ecological replacement. For example, Lundgren et al. (2020) identify instances globally of introduced taxa that potentially act as ecological replacements for extinct terrestrial herbivores. Secondly, as deliberate introductions are increasingly being advocated and used to restore ecosystems (Donlan et al., 2006; Falcón & Hansen 2018; Griffiths et al., 2011; Seddon et al., 2014), trial introductions in limited, experimental areas are likely to be prescribed by regulatory authorities before wider reintroductions are permitted (Aslan, Aslan, Croll, Tershy, & Zavaleta, 2014). For example, this approach was used when nonnative giant tortoises were introduced in the Mascarene Islands (Griffiths & Harris 2010; Griffiths et al., 2011). Currently however, it is unclear how to test whether the candidate species acts functionally in an acceptably equivalent manner to the missing species. Our study illustrates how stable isotope analysis can provide one objective means of doing so. For example, a testable prediction about a candidate proxy might be that once the system has reached equilibrium, its isotopic niche overlaps that of the missing species by some threshold percentage (e.g., 90%).

To illustrate how isotopic niche overlap and volume might be interpreted in this context, we place our results in a generalized conceptual framework in which we envis-

age five scenarios implying markedly different degrees of functional congruence between the missing species and its potential replacement (Figure 3). In the first and second scenario, niche volume is similar but isotopic overlap is zero or slight (Figures 3A and B). This implies that not only does the replacement species fail to fulfill the functions of the missing species, it also performs novel functions, potentially perturbing the ecosystem in unexpected ways. In the third, the replacement species' niche overlaps that of the original entirely but its volume is greater (Figure 3C). Hence, although the replacement should perform all the functions of the original species, it may perform additional functions, perhaps with unintended consequences. The fourth scenario (Figure 3D) is the reverse of latter—that is, while the replacement species fulfills only some of the functional roles of the missing species, there is less risk of novel functions occurring. In the final scenario, niche volume is similar and overlap is perfect or nearly so (Figure 3E). Based on stable isotope data alone, this would suggest that the replacement species largely replicates the functions of the extirpated species.

Before applying this framework, careful consideration should be given to whether it is tractable for the system in question. In general, this means meeting the same criteria required of isotopic diet studies (Phillips et al., 2014;

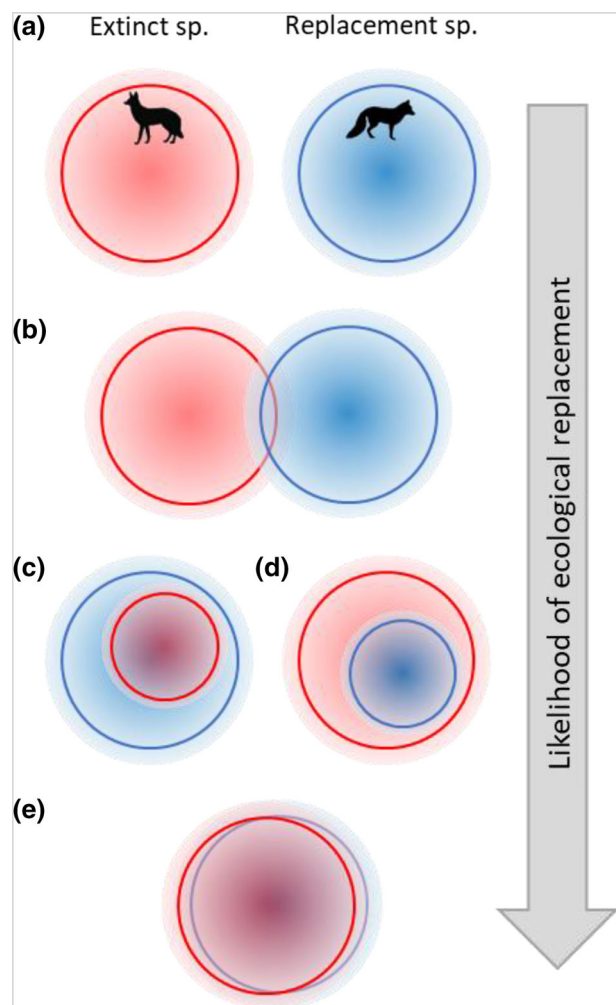


FIGURE 3 Idealized isotopic niche overlap scenarios arranged in increasing order of the likelihood that the replacement species (S_R) matches the functional role of the extirpated species (S_E). Shaded areas show each species' utilization of a two-dimensional isotopic niche space and solid lines their corresponding niche regions, N_R , defined as in Figure 2. (A) No overlap, (B) small overlap, (C) S_R completely overlaps S_E but S_E only partially overlaps S_R , (D) S_E completely overlaps S_R but S_R only partially overlaps S_E , (E) perfect or near-perfect overlap

Shipley & Matich 2020). Firstly, there should be sufficient isotopic variation along ecologically meaningful axes to discriminate between functionally relevant groups of food sources. This is more likely in island ecosystems, such as ours, which have simple trophic dynamics ($\delta^{15}\text{N}$) and marked marine-terrestrial gradients ($\delta^{13}\text{C}$), than in more diverse, purely terrestrial ecosystems. Secondly, isotopic ratios in food sources should vary little within the geographical range of the taxa being compared. This criterion is most likely to be met by organisms with small ranges and when the extirpated and replacement species inhabit the same geographical area. Thirdly, temporal variation in baseline isotopic conditions should also be small, which

is most likely if the missing species was extirpated relatively recently, although it is possible to control for background isotopic variation (e.g., due to the Suess effect) by measuring stable isotopes in lower trophic level organisms, spatiotemporally matched to the taxa of interest (see Section 2). Similarly, because diet can vary seasonally and with age, care should be taken to compare isotopic values in tissues that integrate equivalent periods (Bocherens, Anglade, & Hobson, 2014). In addition to these caveats, it is also important to consider what functional differences might be indistinguishable using isotopic techniques alone. For example, scavengers may have identical isotopic signature to predators but fill quite different ecological roles (Kane, Healy, Guillaume, Ruxton, & Jackson, 2017). Ideally, additional techniques, such as paleontology (Pobiner, 2008; Rawlence, Wood, Bocherens, & Rogers, 2016) and comparative trait analysis (Lundgren et al., 2020; Meloro et al., 2017), should be used to assess the functional congruity of extinct and potential replacement species. Notwithstanding these caveats, stable isotope analysis remains one of the few tools available to assess ecological replacements for the many species extirpated before the modern scientific era.

Here, we found that although feral SAGFs in the Falkland Islands now occupy much of the former isotopic niche of the extinct FIW, the pattern of overlap was most similar to scenario 3 described above (cf. Figures 2 and 3)—that is, SAGFs occupied a larger isotopic niche than FIWs. FIWs were sampled on East and West Falkland, and SAGFs were sampled on nearby Weddell Island (Figure S2), but we cannot rule out the possibility that spatial variation in baseline SIs affected our results. However, climate and vegetation are very similar across all three islands (Strange, 1992), and no systematic differences were apparent in FIW SI signatures between East and West Falkland (Figure S7). Assuming that spatial effects were insignificant, our results are consistent with SAGFs having a broader diet and therefore performing ecological functions not formerly expressed by FIWs. They also indicate that FIWs may have consumed a greater proportion of seabirds and/or marine mammals than SAGFs. This is possibly because FIWs were larger than SAGFs (respective body masses 12–14 kg vs. 2.5–5 kg; Table S3), and therefore better able to predate or scavenge large prey. Feeding mode cannot be resolved using stable isotopes, but comparative dentition and cranial morphology suggest that while both *Dusicyon* and *Lycalopex* species have generalist traits, the former were better adapted to scavenging (Meloro et al., 2017; Prevosti & Martin 2013; Prevosti et al., 2015). Alternatively, the isotopic differences between FIWs and SAGFs may have resulted from a shift in food availability over the past two centuries. Increased human colonization of the Falklands in the early 19th century led to an expansion of pastoralism, an increase in

sheep numbers, a 75% reduction in tussac grass (*Poa flabelata*) cover and associated loss of breeding birds (especially seabirds), and large decreases in populations of pinnipeds and penguins, which were hunted for oil (Strange, 1992). Indeed, consistent with a shift towards a lower trophic level, more terrestrial diet by the mid-19th century, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in FIW hair was lower than in prehuman era FIW bone and tooth remains from West Falkland (Figure 1) (Hamley et al. 2021). However, the growth period for hair is several months and for collagen, several years (Guiry, 2012; McLaren, Crawshaw, & Patterson, 2015), so these differences could also reflect seasonal shifts in FIW diet.

Given that the SAGF isotopic niche did not exactly overlap with the FIW niche, it is pertinent to ask whether the presence of SAGFs is likely to make the Falklands ecosystem closer or further from its pre-Anthropocene state. Wild canids primarily affect communities from the top-down (Darimont & Reimchen 2002; Fox-Dobbs et al., 2007, 2012). In the 19th century, Darwin (1838) noted that upland geese (*Chloephaga picta*) bred only on small outlying islands, attributing this to the threat of predation from FIWs. Presently, upland geese breed on most of the larger Falkland Islands (Strange, 1992) but not on Weddell Island, where SAGFs are abundant (Vick, 2019). Prior to the introduction of sheep, upland geese were the primary terrestrial grazers in the Falklands, so limits on their distribution by FIWs were likely to have had cascading effects on vegetation, nutrient cycling, avian nesting habitat, and so on. (Fox-Dobbs et al., 2012). We presume that SAGFs may have similar effects on those islands where they are present but further study would be required to confirm this. Hence, while our study cannot fully resolve whether SAGFs act as ecological replacements for FIWs, it illustrates how much needed quantitative evidence can be brought to bear on such questions.

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ETHICS STATEMENT

All research activities were conducted in accordance with the University of Glasgow Research Ethics Committee (permit approval 46a/18).

DATA AVAILABILITY STATEMENT

Raw stable isotope values can be found in the Supporting Information, Tables 1 and 2. Code needed to reproduce this analysis can be found on Github (<https://doi.org/10.5281/zenodo.4415840>).

AUTHOR CONTRIBUTIONS

TJC and EDW conceived the ideas and designed methodology; TJC, BV, IM, and EDW collected samples; TJC, BV, JN, and EDW prepared samples and conducted stable isotope analysis; TJC and EDW led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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SUPPORTING INFORMATION

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

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