

Reproductive success of a keystone herbivore is more variable and responsive to climate in habitats with lower resource diversity

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Abstract

1. The effects of climate on wild populations are often channelled through species interactions. Population responses to climate variation can therefore differ across habitats, owing to variation in the biotic community. Theory predicts that consumer demography should be less variable and less responsive to climate in habitats with greater resource diversity.
2. We tested these predictions using a long-term study of breeding lesser snow geese along the western coast of Hudson Bay, Manitoba, Canada. Reproductive success was measured in 22 years from 114 locations, in either coastal or inland habitat types. We used Bayesian analysis to estimate the response of reproductive success to climate in each habitat type, along with residual variation not explained by climate. We then quantified gosling diet composition in each habitat type to test the prediction that reproductive success would be less variable and more responsive to climate in habitats with lower resource diversity.
3. Reproductive success responded positively to seasonal warmness, but this response was much stronger in inland habitats than in coastal habitats. Site- and year-level random effects were also three to five times more variable in inland habitats. Simultaneously, land cover diversity and gosling diet diversity were lower in inland habitats.
4. Our study illustrates that spatial variation in resource diversity (and thus, species interactions) can have important effects on consumer responses to climate. In this system, climate change is expected to disproportionately increase the reproductive success of snow geese in vast inland habitats, potentially counteracting management efforts to reduce the abundance of this keystone herbivore.

KEYWORDS

Anser caerulescens, climate change, consumer–resource, rarefaction, reproductive success, snow goose, variability

1 | INTRODUCTION

Predicting the responses of populations to ongoing climate change requires a clear understanding of the relationship between demographic rates (e.g. survival and reproduction) and environmental

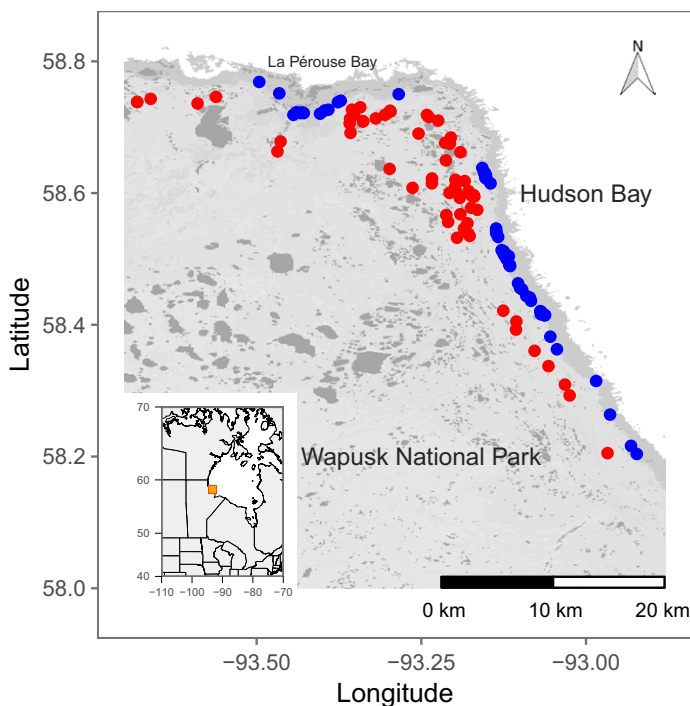
drivers (Ehrlén & Morris, 2015; Jenouvrier, 2013). In general, climate variation can influence demography directly through effects on physiological function (Pörtner & Knust, 2007) and indirectly through changes in species interactions (e.g. by altering the abundance, distribution or phenological synchrony of interacting

populations; Tylanakis, Didham, Bascompte, & Wardle, 2008; Miller-Rushing, Høye, Inouye, & Post, 2010). The indirect effects of climate change may be particularly challenging to anticipate because species often respond idiosyncratically to climate (Cleland, Chiariello, Loarie, Mooney, & Field, 2006; Parmesan, 2007; Thackeray et al., 2010). Meanwhile, the indirect effects of climate change can often be larger than direct effects on physiology, particularly for endotherms occupying higher trophic levels (Ockendon et al., 2014). Given that the biotic community can vary substantially across a species range and may respond idiosyncratically to environmental variation, accounting for species interactions remains a key challenge for predicting population responses to future climate (Araújo & Luoto, 2007; Ehrlén & Morris, 2015).

Principles from classic ecological theory may help address this challenge. Theory predicts that consumer population dynamics should be more stable in habitats with greater resource diversity (McCann, 2000). For example, if phenology varies among plant species, greater plant diversity should increase the probability that consumers are favourably “matched” with at least one resource at each point throughout the season. This, in turn, should reduce variation in herbivore demography due to trophic mismatch (Miller-Rushing et al., 2010). This prediction follows from the insurance and averaging effects of diversity (Doak et al., 1998; Naeem & Li, 1997; Yachi & Loreau, 1999). Because resource phenology (hence, resource quality and availability to consumers) is often driven by climate (e.g. Doiron, Gauthier, & Lévesque, 2015; Mulder, Iles, & Rockwell, 2016), it follows that consumer demography should be more responsive to climate covariates when resource diversity is low. Simultaneously, if unmeasured climate variables affect resource availability, lower resource diversity should increase residual demographic variation (i.e. variation not explained by measured climate covariates).

The lesser snow goose (*Anser caerulescens caerulescens*; hereafter “snow goose”) is a keystone herbivore that breeds in high-latitude ecosystems and a species for which the potential indirect effects of climate change have recently been highlighted. Goslings are highly sensitive to plant quality on the (sub-)Arctic breeding grounds, and reduced quality and availability of plant resources are associated with declines in gosling growth and survival (Aubry et al., 2013; Cooch, Lank, Rockwell, & Cooke, 1991; Dickey, Gauthier, & Cadieux, 2008; Doiron et al., 2015; Sedinger, Flint, & Lindberg, 1995). The nutritional quality of leaves typically declines throughout the breeding season (Gadallah & Jefferies, 1995), and warmer seasons cause these declines to occur more rapidly (Doiron, Gauthier, & Lévesque, 2014). Asynchrony between the date of gosling hatch and peak resource quality are therefore hypothesized to influence the early-life demography of snow geese (Aubry et al., 2013; Doiron et al., 2015). Like many herbivores, however, snow geese are capable of consuming a variety of plant species from a range of habitat types (Winiarski, McWilliams, & Rockwell, 2012), and plant species differ in their nutritional quality, phenology and responsiveness to climate (Gadallah & Jefferies, 1995; Mulder et al., 2016). Thus, the consequences of climate variation for geese are likely to depend on the diversity of habitats and plant species to which they have access.

In Wapusk National Park in western Hudson Bay, expanding populations of snow geese have recently begun using novel inland habitats for nesting and brood rearing in addition to the coastal habitats that were traditionally used for breeding (Aubry et al., 2013; Winiarski et al., 2012; Figure 1). Along the Hudson Bay coast, the transition from coastal saltwater vegetation communities into vast inland freshwater meadows produces a strong gradient in vegetation communities that potentially influences resource diversity (Riley, 2003). This system therefore provides an ideal opportunity



Habitat type

- Coastal
- Inland

FIGURE 1 Banding sites used for analysis of snow goose reproductive success between 1990 and 2015. Habitat type for each banding site was determined using ordination analysis of land cover, based on Brook and Kenkel's (2002) land cover map for Wapusk National Park. All banding sites from 1990 to 2015 were used in the land cover ordination to describe habitat composition. From this ordination, only highly coastal and highly inland sites (N = 114) were selected for analysis of gosling reproductive success (see Materials and Methods section)

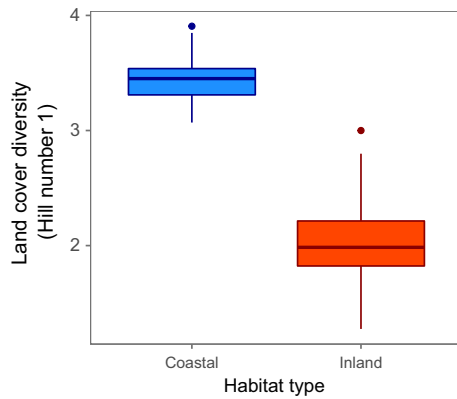


FIGURE 2 Relationship between habitat type at banding sites and land cover diversity within 2 km of banding sites. Land cover diversity was calculated as the exponent of Shannon diversity (Hill number 1), based on land cover classes from Brook and Kenkel's (2002) land cover map for our study area. Our analysis made use of 114 banding sites (57 in each habitat type)

to examine the degree to which habitat (and by extension, resource diversity) interacts with seasonal climate to influence consumer demography. For snow geese, this question is particularly of conservation relevance because management efforts have failed to curb population growth and attenuate the destructive potential of overabundant snow goose populations (Alisauskas et al., 2011; Koons, Rockwell, & Aubry, 2014). Depending on the nature of demographic responses to climate across this habitat gradient, climate change could either mitigate or exacerbate conservation concerns.

We first use a long-term dataset (1990–2015; 22 years of data and 114 sampling sites) to quantify the effects of breeding season climate on snow goose reproductive success in two distinct breeding habitat types (coastal and inland). We then test the prediction that demographic responses will be weaker in habitats with higher resource diversity by quantifying the diversity of resources available to goslings at two scales: (1) at the landscape scale by measuring the diversity of land cover types available to goslings in each habitat type, and (2) at the level of individuals by measuring the diversity of resources identified in gut contents of goslings collected from each habitat.

2 | MATERIALS AND METHODS

2.1 | Study location and data collection

Annually since 1968, large flocks of adult snow geese and attendant goslings have been banded for mark-recapture studies across the Hudson Bay Lowlands in northern Manitoba, Canada (for further details see Cooke, Rockwell, & Lank, 1995; Aubry et al., 2013; banding sites from 1990 to 2015 used for analysis are depicted in Figure 1). Historically, snow goose nesting and brood-rearing areas were confined to a small area of coastal saltmarsh at La Pérouse Bay. Saltmarsh vegetation communities consist primarily of small

graminoids including *Puccinellia phryganodes* and *Carex subspathacea*, along with a variety of perennial forbs (e.g. *Ranunculus cymbalaria*, *Argentina egedii* and *Primula egalikensis*). Inland from the coastal saltmarsh areas, the landscape transitions into expansive freshwater meadows dominated by large sedges (e.g. *Carex aquatilis* and *Scirpus cespitosus*). Following rapid population growth and concomitant degradation of saltmarsh areas resulting from destructive foraging by overabundant adult snow geese (Abraham, Jefferies, & Alisauskas, 2005; Jefferies, Jano, & Abraham, 2005), the breeding colony expanded into these inland freshwater landscapes (Aubry et al., 2013). Today, the nesting and brood-rearing areas are diffused over approximately 100 km of coastline and up to 10 km inland within Wapusk National Park (Winiarski et al., 2012; Aubry et al., 2013; Figure 1).

In this study, we only use data from 1990 onwards (after the majority of landscape degradation had occurred) to minimize the confounding effects of long-term changes in resource use by goslings during periods of ongoing habitat degradation. In total, geese were banded at 204 unique locations from 1990 to 2015 (4–14 locations per year; hereafter referred to as “banding sites”). However, for our analysis, we only use data from highly coastal and highly inland banding sites, resulting in 114 site-year combinations (Figure 1; also see further details below).

2.2 | Habitat covariates

To investigate the response of snow goose reproductive success to climate across contemporary brood-rearing habitats, we first classified habitat composition across the study area. We used Brook and Kenkel's (2002) land cover map to characterize landscape composition within 2 km of banding sites, where reproductive success was measured (see Appendix S1 for further details and assumptions of this approach). The first axis from a land cover ordination described the overall habitat at each banding site: highly negative values indicated highly coastal habitats, while highly positive values corresponded to inland habitats (Figure 1; also see Figures S1 and S2 in Appendix S1). Habitat ordination scores were bimodal, with many sites occurring in highly inland or highly coastal landscapes (Figure S2 in Appendix S1). Thus, to provide a clear test of the potential for habitat to influence demographic responses to climate, we focused our analysis on only the 30% most coastal and 30% most inland sites, thereby omitting “intermediate” sites. In total, 114 banding sites from 22 study years (1–11 banding sites per year) were included in our analysis of reproductive success. We then treated habitat type as a discrete variable with two levels: coastal and inland (also see Figure S2).

We also measured the diversity in land cover types available to goslings within 2 km of each banding site by calculating the exponent of Shannon diversity, often referred to as Hill Number 1 (Hill, 1973). This metric is influenced by both the number and relative evenness of land cover types. Goslings inhabiting highly coastal sites had access to a greater diversity of land cover types than goslings in highly inland sites (Figure 2).

We used Landsat imagery to quantify the severity of habitat degradation across the landscape (details of the analysis are described in Appendix S1). Degradation was concentrated primarily in coastal sites (Figure S4), and position along the landscape MDS1 axis (above) therefore simultaneously describes landscape composition and severity of historical degradation at each banding site. We thus calculated “residual habitat degradation” after controlling for landscape composition. The residualized effect was then included as an explanatory covariate in competing models for reproductive success (see below).

2.3 | Climate covariates

Temperature and precipitation potentially affect reproductive success through direct (physiological) and indirect pathways (e.g. via effects on goose and plant phenology; Aubry et al., 2013; Doiron et al., 2014, 2015). Based on previous work at our study site, we therefore restricted our consideration of climate variables to these few that have been previously shown to affect snow goose development or early-life demography (Aubry et al., 2013).

For each year of study, we calculated early-, mid- and late-season measures of temperature and precipitation. Temperature was calculated as cumulative growing degree days on calendar days 144, 174 and 204 (hereafter referred to as GDD144, GDD174 and GDD204). These metrics describe overall seasonal warmth until the early, mid and late periods of the breeding season, respectively. Similarly, we calculated cumulative precipitation within the 2 weeks surrounding calendar days 144, 174 and 204 (denoted precip144, precip174 and precip204).

Goslings hatch later in cold seasons (Figure S5), likely because nesting is constrained by availability of snow-free nesting sites (Newton, 1977). The time elapsed between gosling hatch and banding operations (the date at which we measured reproductive success) could influence the proportion of goslings surviving until banding, as well as gosling size and condition at banding (Flint, Sedinger, & Pollock, 1995). To account for the potentially important effects of goose phenology, and thus time elapsed/gosling age at banding beyond that which is explained by seasonal warmth, we extracted residuals from a generalized additive model that predicted the days elapsed between banding and mean gosling hatch as a function of seasonal warmth (Figure S7). We included the effect of “residual age” as a covariate in models for reproductive success.

2.4 | Analysis of snow goose reproductive success

Our primary objective was to examine the response of snow goose reproductive success to seasonal climate and to specifically test whether this response differed across habitat types. We used numbers of adults and juveniles in late-summer (pre-fledging) flocks at banding site as a measure of reproductive success (see raw observations of reproductive success in Figure S8). This measure integrates egg production by adult females, hatching success of eggs and gosling survival until banding. Yet, variation in this metric is likely to

primarily reflect variation in gosling survival following hatch; snow goose clutch size is relatively invariant and egg survival is extremely high (Cooke et al., 1995). Adult mortality and migration (of either breeders or non-breeders) during the breeding season could introduce additional variation into this metric of reproductive success. However, non-breeders and adults that lose their entire clutch during the incubation period appear to emigrate from the study area prior to banding (Abraham, 1980). Furthermore, age ratios are commonly used in the absence of long-term individual-based reproductive data for geese (e.g. Alisauskas, 2002; Dickey et al., 2008; Morrisette, B  ty, Gauthier, Reed, & Lefebvre, 2010; Ross, Alisauskas, Douglas, & Kellett, 2017).

We conducted an analysis of reproductive success in two steps. In the first step, we fit a series of generalized linear mixed models (GLMMs) using maximum likelihood and used model selection to determine the climate covariates that most strongly predicted reproductive success. In this step, we included random effects of banding site and year and fixed effects of habitat degradation and gosling age (see details of model selection in Appendix S2). In this step, GDD204 received the highest support of any temperature covariate and was therefore incorporated into more a complex Bayesian analysis in step 2 (see below). No precipitation covariates received more support than a null model, and we therefore did not include them in step 2.

In the second step of analysis, we used Bayesian methods to analyse the relationship between reproductive success, habitat and GDD204 and to specifically examine the interactive effects of habitat and climate (see extended details in Appendix S2). A Bayesian framework also allowed us to estimate different variances for the year and site error terms separately within in each habitat type. If resource diversity affects the stability (i.e. variance) of reproductive success, and resource diversity differs among habitats, we expect that the variance of year and site random effects should differ between habitats.

Thus, we estimated reproductive success as the observed number of goslings in a flock of size N , at banding site i in study year j as follows:

$$y_{ij} \sim \text{Binomial}(\theta_{ij}, N_{ij})$$

$$\begin{aligned} \text{logit}(\theta_{ij}) &= \alpha_0 + \alpha_1 \times \text{hab}_i + \alpha_2 \times \text{GDD204}_j + \alpha_3 \times \text{hab}_i \times \text{GDD204}_j \\ &+ \alpha_4 \times \text{deg}_{ij} + \alpha_5 \times \text{age}_{ij} + (\varepsilon_{\text{SITE}} | \text{hab}_i) + (\varepsilon_{\text{YEAR}} | \text{hab}_i) \end{aligned} \quad (1)$$

$$(\varepsilon_{\text{SITE}} | \text{hab}_i) \sim \text{Normal}(0, \sigma_{\text{SITE}, \text{hab}_i}^2)$$

$$(\varepsilon_{\text{YEAR}} | \text{hab}_i) \sim \text{Normal}(0, \sigma_{\text{YEAR}, \text{hab}_i}^2).$$

The proportion of goslings comprising the flock, θ_{ij} , was therefore modelled as a function of habitat type (hab, which is a discrete variable), climate (GDD204), their interaction, residualized habitat degradation (deg) and residualized gosling age (age). We included separate “site” and “year” random effect variances for coastal and inland habitat types; the terms $\varepsilon_{\text{SITE}} | \text{hab}_i$ and $\varepsilon_{\text{YEAR}} | \text{hab}_i$ denote “site” and “year” effects, respectively, conditional on the habitat type at site i . Covariate effects were fit on the logit scale, and continuous

covariates were standardized prior to analysis. This hierarchical model was fit using the *JAGSUI* package in R, adapting code from Kéry and Schaub (2012, ch. 3). We specified vague priors for all parameters and assessed model convergence using standard diagnostics. Goodness-of-fit was assessed both visually and using Bayesian posterior predictive checks (Appendix S2).

2.5 | Analysis of gosling diet diversity

To examine spatial differences in gosling diet composition, we collected goslings throughout the 2014 and 2015 seasons from representative coastal and inland brood-rearing areas. Both years were exceptionally warm; in 2014, the value of GDD204 was in the 98th percentile of warmness across the study, while in 2015, GDD204 was in the 81st percentile. Goslings were humanely euthanized according to CWS permit 11-MB-SC001 (IACUC approval number 2208). Goslings were necropsied and gut contents removed. We first sorted gut contents to the level of family. Although we were unable to identify all graminoid leaves to the level of species, we sorted unknown grasses and *Carex* specimens into small (c. 0–1 mm width), medium (c. 1–3 mm width) and large (>3 mm width) specimens. Each size category likely encompasses multiple species or genera and could thus be interpreted as a conservative estimate of species diversity. After sorting, we dried samples at room temperature and weighed them to the nearest milligram. We considered any items weighing <5 mg to be “trace” amounts of material potentially consumed incidentally, and we therefore did not include these extremely rare items in subsequent analysis of diet diversity.

We categorized each gosling as “inland” or “coastal” habitat based on land cover composition within 2 km of the location it was collected (see Appendix S1). We then used rarefaction to compare the relative diversity of diet items consumed by goslings collected in coastal and

inland habitats. We constructed separate rarefaction curves for inland and coastal habitats in each year and for diet specimens sorted to species and family levels. We constructed curves based on two diversity metrics (richness and the exponent of Shannon diversity), each of which places different weight on rare items. We used the *iNEXT* function documented in the Supplement of Chao et al. (2014) to perform sample-based rarefaction and compute unconditional 84% confidence intervals (Gotelli & Colwell, 2011).

3 | RESULTS

3.1 | Effects of breeding season climate on reproductive success across habitats

We found strong support for the hypothesis that seasonal temperature (GDD204) affected snow goose reproductive success differently across habitat types. The effect of an interaction between GDD204 and habitat (median estimate on logit scale = -1.05 , 90% CRI = -1.93 to -0.17) resulted in much stronger effects of GDD204 in inland habitats (Figure 3a; note that this figure presents model predictions after transforming responses and covariate values back to the respective real scales of each variable). Thus, in general, flocks contained higher proportions of goslings in coastal habitats, but extremely warm years resulted in similar reproductive success across the landscape.

The residual component of reproductive success (i.e. variance not explained by GDD204 or other covariates) was also more variable in inland habitats than coastal habitats, both between years and across sites (Figure 3b). The *SD* of the random year effect was approximately 2.8 times higher in inland than coastal habitat types (90% CRI for ratio = 1.5–4.3). Similarly, the *SD* of the random site effect was approximately 5.2 times higher in inland than coastal habitat types (90% CRI for ratio = 3.8–6.8).

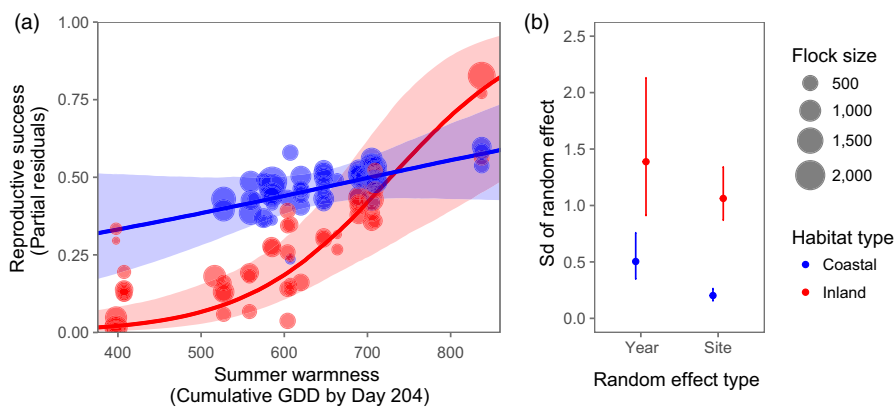


FIGURE 3 Estimated effects from Bayesian analysis of snow goose reproductive success, measured as the proportion of banded flocks comprised of goslings. Panel (a): relationship between reproductive success and seasonal warmth (GDD204) in each habitat type. Shaded ribbons depict 90% Bayesian credible intervals around predictions. Partial residuals portray raw data after removing confounding effects of residual habitat degradation, gosling age and random year effects (see raw data in Figure S8). Panel (b): standard deviation of year and site random effects, estimated separately for each habitat type. Points represent median posterior estimates; error bars indicate 90% credible intervals

Habitat degradation (i.e. the residualized effect beyond that which was accounted for by habitat composition) and gosling age (beyond which was accounted for by breeding season temperature) were not strong predictors of reproductive success; median posterior estimate of effect size was small, and 95% CRI for both effects broadly overlapped zero (Appendix S2). Results were qualitatively similar based on an analysis that only used a subset of data from years containing observations from both coastal and inland habitat types simultaneously (presented in Appendix S3).

3.2 | Gosling diet diversity across habitats

We identified plant specimens from gut contents of 99 goslings, 89 of which contained at least 5 mg of material (46 goslings in coastal habitats and 43 in inland habitats). We identified a total of 21 plant species in gosling gut contents (mean = 1.9 species per gosling, range = 1–5 species per gosling), comprising 12 plant families (mean = 1.8 plant families per gosling, range = 1–4 families per gosling). Total dry mass of contents in goslings ranged from 5 to 3,281 mg. Small and medium grass and *Carex* leaves comprised the largest proportion of most gosling diets in both coastal and inland habitats, although coastal goslings consumed larger quantities of smaller-leaved graminoids (Figure S11 in Appendix S4). Inland goslings also consumed a variety of heavier graminoid species that were generally absent from the diets of coastal goslings (e.g. *Scirpus cespitosus* and *Equisetum variegatum*). Diets of several goslings collected from inland habitats contained a large number of *Andromeda polifolia* and *Dryas integrifolia* flowers (Figure S11 in Appendix S4). The leaves of these species are not likely to be highly digestible, but consumption of numerous flowers and fruit by several individuals indicates that certain phenological stages of these plant species may provide

temporary resource pulses to goslings. Conversely, coastal gosling diets contained a variety of perennial forbs, including *Primula ega-likensis*, *Ranunculus cymbalaria* and *Argentina egedii*, although these were generally found in much smaller quantities than graminoid leaves.

Rarefaction indicated that diet diversity was greater for goslings in coastal habitats than inland habitats (Figure 4). This pattern was consistent whether plants were identified to the species or family levels (Figure 4; left and right columns, respectively) and whether diversity was calculated as richness or the exponent of Shannon diversity (Figure 4; top and bottom rows, respectively). These results were also consistent across years (e.g. in 2014 and 2015; Figure S12 in Appendix S4). Thus, goslings inhabiting inland habitats had lower diet diversity (Figure 4) and had access to a lower diversity of land cover types (Figure 2). Consequently, reproductive success was more variable and more responsive to climate in these habitats with lower resource diversity (Figure 3).

4 | DISCUSSION

Our results suggest that plant diversity modifies the effect of seasonal climate on reproductive success of this herbivore. Snow goose reproductive success responded more strongly to seasonal warmth in inland habitats that contained lower resource diversity (Figures 3a and 4). Simultaneously, residual spatial and temporal variation in reproductive success (i.e. variation not explained by seasonal warmth; Figure 3b) was much greater within inland habitats, implying stronger responses to other unmeasured environmental variables in these habitats. Other studies have also documented considerable variation in demographic responses to

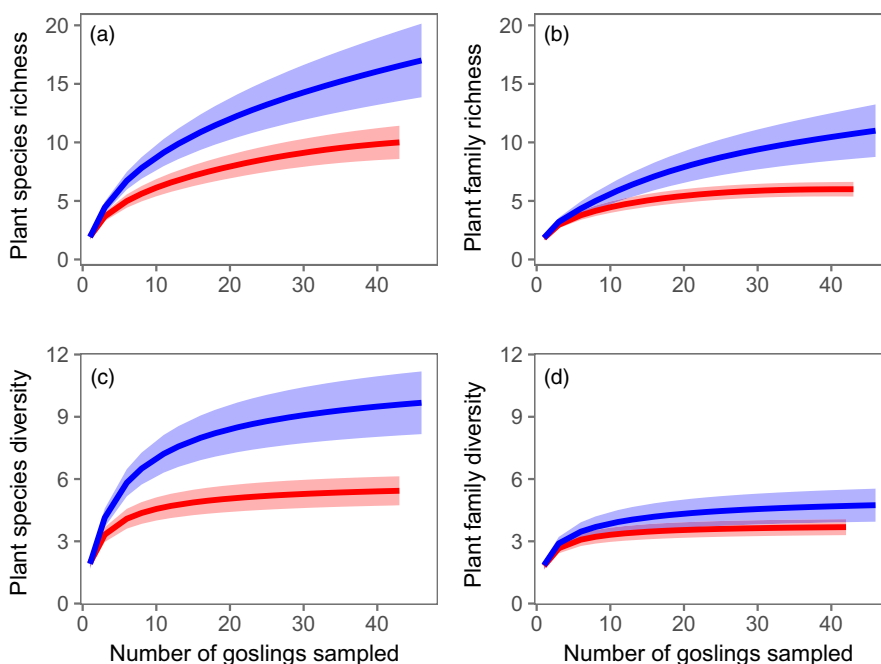


FIGURE 4 Rarefaction curves for diets of goslings collected in coastal (blue) and inland (red) habitats. Curves are calculated for diet items classified to species (left column) and family (right column). Top row depicts curves based on species/family richness (Hill number 0). Bottom row depicts curves based on species/family diversity using the exponent of Shannon diversity (Hill number 1). Data were pooled across two years of sampling (2014 and 2015); see Figure S12 in Appendix S4 for curves plotted separately for each year. Shaded ribbons represent 84% confidence intervals around rarefaction estimates, where non-overlap indicates a statistically significant difference in diversity with a type I error rate of $p < .05$ (Gotelli & Colwell, 2011)

particular environmental drivers among populations within a species (e.g. in birds: Sæther et al., 2003; van de Pol et al., 2013; in plants: Malyshev et al., 2016). Differences in these responses are often attributed to local adaptation. Our study provides evidence that such differences can also be driven by spatial variation in trophic interactions, in this case, through differences in resource diversity. In our study, these effects also occurred over relatively small spatial scales (<5 km; Figure 1) where local adaptation is unlikely to occur. This provides further evidence that species interactions are important determinants of population responses to climate (Araújo & Luoto, 2007; Ehrlén & Morris, 2015; Ockendon et al., 2014).

The demographic relationships we detected are consistent with predictions from classic diversity–stability theory. However, tests of the stabilizing effect of resource diversity on consumer population dynamics have generally involved small-scale experimental manipulations and results have been equivocal (cf. Haddad, Crutsinger, Gross, Haarstad, & Tilman, 2011; Petchey, 2000). Our study extends this research agenda in several important ways. First, our observational study focused on an underlying demographic rate, rather than on overall abundance or population growth where effects can be masked by dispersal or vital rate correlations (Tavecchia et al., 2016). Second, our results imply that loss of biodiversity at lower trophic levels will generate stronger demographic responses to climate and greater demographic variation in higher trophic levels. Depending on the curvature of vital rate reaction norms and the structure of vital rate correlations, strengthened vital rate responses and increased demographic variance can have positive or negative effects on population viability (Doak, Morris, Pfister, Kendall, & Bruna, 2005; Koons, Pavard, Baudisch, & Metcalf, 2009; Lawson, Vindenes, Bailey, & Pol, 2015). Third, we examined these effects in a highly abundant keystone herbivore that is known to have strong effects on ecosystem function in (sub-)arctic ecosystems (Jefferies et al., 2005). If these demographic effects scale up to affect overall snow goose abundance, they could represent an important pathway through which plant diversity influences ecosystem function under climate change.

Our results are consistent with a number of other studies that have reported positive effects of seasonal warming on reproductive success and overall population growth rate in geese (e.g. Alisauskas, 2002; Gauthier, Péron, Lebreton, Grenier, & van Oudenhoove, 2016; Jensen, Madsen, Johnson, & Tamstorf, 2014; Morrisette et al., 2010). However, our study also suggests these effects will not be uniform across the breeding grounds. Warmer seasons disproportionately increase snow goose breeding success within inland freshwater habitats, which are approximately 150 times more abundant than coastal saltmarsh habitats in the Hudson Bay Lowlands (Figure 1; Brook & Kenkel, 2002). Continued climate warming could therefore substantially increase reproductive success across large expanses of the breeding area. Lesser snow geese are officially listed as “overabundant” because of their detrimental effects on high-latitude coastal ecosystems (Leafloor, Moser, & Batt, 2012). Yet, management efforts to reduce their abundance have largely been unsuccessful (Alisauskas et al., 2011; Koons et al., 2014). Breeding

season temperatures are becoming warmer and more variable at our study site (Mulder et al., 2016), and the increasing use of novel inland habitats could therefore further impede management efforts to curb population growth.

Diet contents of multiple goslings sampled during our study were highly distinct. For example, several individual goslings had uniquely fed on large numbers of *Primula* and *Salix* fruits, *Ranunculus cymbalaria* leaves, flowers of *Andromeda polifolia* and *Dryas integrifolia* and *Eleocharis palustris* culms. However, most gosling diets consisted of only a few graminoid groups. A higher frequency of distinct diets containing relatively rare plant species in coastal habitats (Figures 4 and S11) therefore contributed to the greater diet diversity we detected in these landscapes. Rare species can make important contributions to ecosystem function (Lyons, Brigham, Traut, & Schwartz, 2005), and rare species often have relatively unique traits and low functional redundancy, thereby supporting vulnerable ecosystem processes in variable environments (Isbell et al., 2011; Mouillot et al., 2013). Thus, while abundant and commonly consumed graminoids are likely necessary to support gosling growth and development, it is possible that other species may nevertheless provide important sources of nutrition in certain environmental contexts, especially in cold years where differences in reproductive success between coastal and inland areas are most pronounced (Figure 3a). A direct comparison of the phenological responses of forage species in each habitat type is needed to uncover the specific mechanisms by which resource diversity influences reproductive success (e.g. with warming experiments as in Doiron et al., 2014).

Because our study was correlational, other unexamined factors may have also contributed to the relationships we detected between resource diversity and demographic responsiveness to environmental variation. For example, variation in population responses to climate can be overestimated if coarse-scale climate metrics are correlated differently with local conditions across the landscape (van de Pol et al., 2013). This could occur, for example, if inland areas have more variable weather than coastal areas. Unfortunately, long-term data were unavailable to include fine-scale weather differences across our study area. Improved methods for interpolating historical weather over fine spatial scales will be useful for continued study of geographic differences in demographic responses to environmental variation. The predator community may also differ across the coastal–inland resource gradient, although the effects of seasonal climate on the dynamics and space use of predators are unclear at our study site. Because our analysis cannot fully rule out all possible confounding factors, experimental manipulation of forage diversity available to captive goslings would be necessary to fully isolate the effect of resource diversity on gosling responses to climate.

Characterizing population responses to environmental change is a considerable challenge, given that demographic responses are habitat-specific and environmental factors may affect population dynamics through multiple pathways simultaneously (Jenouvrier, 2013). Our study indicates that accounting for consumer–resource interactions and habitat-specific responses will provide deeper

insights into the potential effects of climate change on the population dynamics of this overabundant keystone herbivore. Further studies that integrate these effects across the entire life cycle (e.g. Gauthier et al., 2016; Jenouvrier et al., 2009) will be crucial for forecasting population trends and spatial distributions and for prioritizing management in rapidly changing climates.

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AUTHORS' CONTRIBUTIONS

All authors contributed to project development and research design; D.T.I. conducted the analyses and wrote the manuscript; D.N.K. and R.F.R. assisted with interpretation of results and contributed to drafting and critical revision of the manuscript; all authors give final approval for the submitted version of the manuscript.

DATA ACCESSIBILITY

Data and code available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8c4196f> (Iles, Rockwell, & Koons, 2018).

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SUPPORTING INFORMATION

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