

Wildlife species benefitting from a greener Arctic are most sensitive to shrub cover at leading range edges

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Funding information

Aarhus University Research Foundation, Grant/Award Number: AU Ideas program; VILLUM FONDEN, Grant/Award Number: BIOCHANGE

Abstract

Widespread expansion of shrubs is occurring across the Arctic. Shrub expansion will substantially alter arctic wildlife habitats. Identifying which wildlife species are most affected by shrubification is central to predicting future arctic community composition. Through meta-analysis, we synthesized the published evidence for effects of canopy-forming shrubs on birds and mammals in the Arctic and Subarctic. We examined variation in species behaviour, distribution and population dynamics in birds and mammals in response to shrub cover (including shrub cover indicators such as shrub occurrence, extent, density and height). We also assessed the degree of heterogeneity in wildlife responses to shrub cover and synthesized the remaining literature that did not fit the criteria for our quantitative meta-analyses. Species from higher green vegetation biomass habitats (high Normalized Difference Vegetation Index, NDVI, across their distribution) were more likely to respond positively to shrub cover, demonstrating the potential for species to expand from boreal to arctic habitats under shrubification. Wildlife populations located in the lowest vegetation biomass (low NDVI) areas of their species' range had the greatest proportion of positive responses to shrub cover, highlighting how increases in performance at leading edges of invaders distributions may be particularly rapid. This demonstrates the need to study species at these leading edges to accurately predict expansion potential. Arctic specialists were poorly represented across studies (limited to 5 bird and 0 mammal species), this knowledge gap potentially explains the few reported negative effects of shrub cover (3 of 29 species). Species responses to shrub cover showed substantial heterogeneity and varied among sites and years in all studies with sufficient replication to detect such variation. Our study highlights the importance of responses at species range edges in determining outcomes of shrubification for arctic birds and mammals and the need for greater examination of potential wildlife losers under shrubification.

KEYWORDS

birds, climate change, global warming, habitat suitability, herbivory, mammals, plant–animal interactions, shrub encroachment

1 | INTRODUCTION

Climatic warming is driving increased shrub cover in many parts of the Arctic tundra region (Forbes, Fauria, & Zetterberg, 2010;

Myers-Smith et al., 2015). Despite this rapid change, we have no overview across species of the consequences for animals across this region. Increased shrub cover occurs in the form of northward expansion of shrubs and local increases in shrub density and height

(Myers-Smith et al., 2011; Sturm, Racine, & Tape, 2001). These changes are likely to drive changes in wildlife populations and communities. A few recent studies have linked range expansions of snowshoe hare (*Lepus americanus*) and moose (*Alces alces*), commonly associated with the boreal forest in Alaska, to increasing shrub cover (Tape, Christie, Carroll, & O'Donnell, 2016; Tape, Gustine, Ruess, Adams, & Clark, 2016). Furthermore, the need to consider shrub encroachment as a mechanism in arctic wildlife declines has been identified (Ballantyne & Nol, 2015; Wheeler & Hik, 2013; Wild, Kendall, Guldager, & Powell, 2015). However, it remains unclear which species will be most affected, and whether responses to shrub cover will be consistent across individual species ranges.

Climate influences shrub growth across the Arctic and is a key mechanism for increases in arctic shrub cover (Forbes et al., 2010; Myers-Smith et al., 2015). Increases in shrub cover occur in the form of northward expansion of shrubs and local increases in shrub density and height (Myers-Smith et al., 2011; Sturm et al., 2001). The degree to which shrubification is occurring and shrubs appear sensitive to climate, varies across the Arctic (Myers-Smith et al., 2011, 2015), in part as a result of differences in human, biotic and abiotic contexts (Forbes et al., 2009; Myers-Smith et al., 2015). However, prediction of vegetation shifts for the Arctic is substantial, with a projection of 52% increases in woody cover by the 2050s (Pearson et al., 2013).

Two-way interactions exist between wildlife and shrubs. In one direction, shrubs can affect wildlife habitat suitability by altering forage and vegetation structure. Shrub cover can modify forage and habitat structure directly or by affecting the composition and cover of the vegetation community (Bråthen & Lortie, 2016). A northward expansion of shrubs could increase suitability of current arctic habitats for boreal and subarctic species, with potential for greater mixing of arctic and subarctic wildlife faunas (Sokolov, Ehrich, Yoccoz, Sokolov, & Lecomte, 2012). As boreal species invade, competition between boreal and arctic wildlife species can further alter arctic wildlife community assemblages (Hamel, Killengreen, Henden, Yoccoz, & Ims, 2013). If habitats become less suitable for arctic bird and mammal species, populations of arctic specialist species may decline following further shrubification (Fauchald, Park, Tømmervik, Myneni, & Hausner, 2017). In the other direction, wildlife communities also affect vegetation composition and structure; if distributions and densities of herbivores are affected by shrub expansion, changes in herbivory and nutrient cycling could have strong feedbacks to vegetation composition and structure and wildlife habitat.

Wildlife responses to changing shrub could alter wildlife population densities and community composition, and could affect ecosystems more broadly through impacts on processes such as predator–prey interactions, grazing and browsing pressure, trampling and other disturbance and nutrient inputs. Under elevated herbivory regimes, shrub cover can substantially decline (Forbes et al., 2009; Ims et al., 2007; Kittl, Forbes, & Oksanen, 2009). Grazing-induced shrub decline has been linked to reduced bird biodiversity in the Arctic (Ims & Henden, 2012). Substantial interest surrounds the potential for herbivores to moderate arctic shrub expansion (Cahoon, Sullivan,

Post, & Welker, 2012; Christie et al., 2015; Macias-Fauria, Forbes, Zetterberg, & Kumpula, 2012; Olofsson et al., 2009). However, while experimental effects of herbivory on shrub cover at plot level have been demonstrated, the ability of wildlife to moderate shrub expansion also depends critically on the densities, distribution and behavioural responses of herbivores to changes in shrub cover and shrub density which are largely unknown. Given the impact that a number of herbivorous wildlife species could have on vegetation, it is necessary to discern how they will respond to climate-induced habitat change.

Here, we consider how shrub cover affects occurrence and abundance, as well as reproductive, behavioural and individual condition indicators of potential population change, in birds and mammals. We define shrub cover broadly as the vertical and lateral space occupied by shrub, to maximize available data, and consider variation in indicators such as shrub occurrence, extent, density and height. We employ meta-analysis and literature synthesis of existing studies and focus on spatial and temporal variation in open tundra and shrub-tundra habitats. Our focus on birds and mammals reflects the greater availability of data for these species groups. We focus on three questions: (1) How prevalent and consistent across studies are positive and negative effects of shrub cover on individual, behavioural, population, and distributional processes linked to population and distributional change in bird and mammal species? (2) What are the characteristics of species most likely to expand northwards under shrub encroachment? (3) How does the position of a population in a species' niche space affect its sensitivity to shrub cover?

Our first question addresses the fact that studies differ in their ability to identify heterogeneities in wildlife responses to shrub cover. Studies that are repeated across multiple years or sites are more likely to identify variation in responses than those from single sites and years. Similarly, studies that report responses to multiple different attributes of a phenomenon can also detect if responses are scale-dependent or only apply to certain aspects of a phenomenon (e.g. certain shrub heights or levels of cover). We incorporate this information throughout our analysis to better understand consistency in wildlife responses to shrub.

Our second question examines if species traits determine species responses to shrub cover. Predictions of how species respond to environmental variation can be greatly improved by considering species traits (Poyry, Luoto, Heikkinen, Kuussaari, & Saarinen, 2009; Sunday et al., 2015) and current habitat associations. We investigate whether a species' propensity for greener habitats affects responses to shrub cover. We predict that species from habitats with higher vegetation biomass will be more likely to respond positively to increased shrub cover, supporting the idea that species may invade the arctic tundra from more temperate biomes. We also assess if species with more direct vegetation associations through herbivory are more sensitive to shrub cover change, and if insectivory affects sensitivity to shrub cover (given changes in insect prey have been highlighted as a potential source of shrub-induced wildlife change, e.g. Boelman et al., 2015).

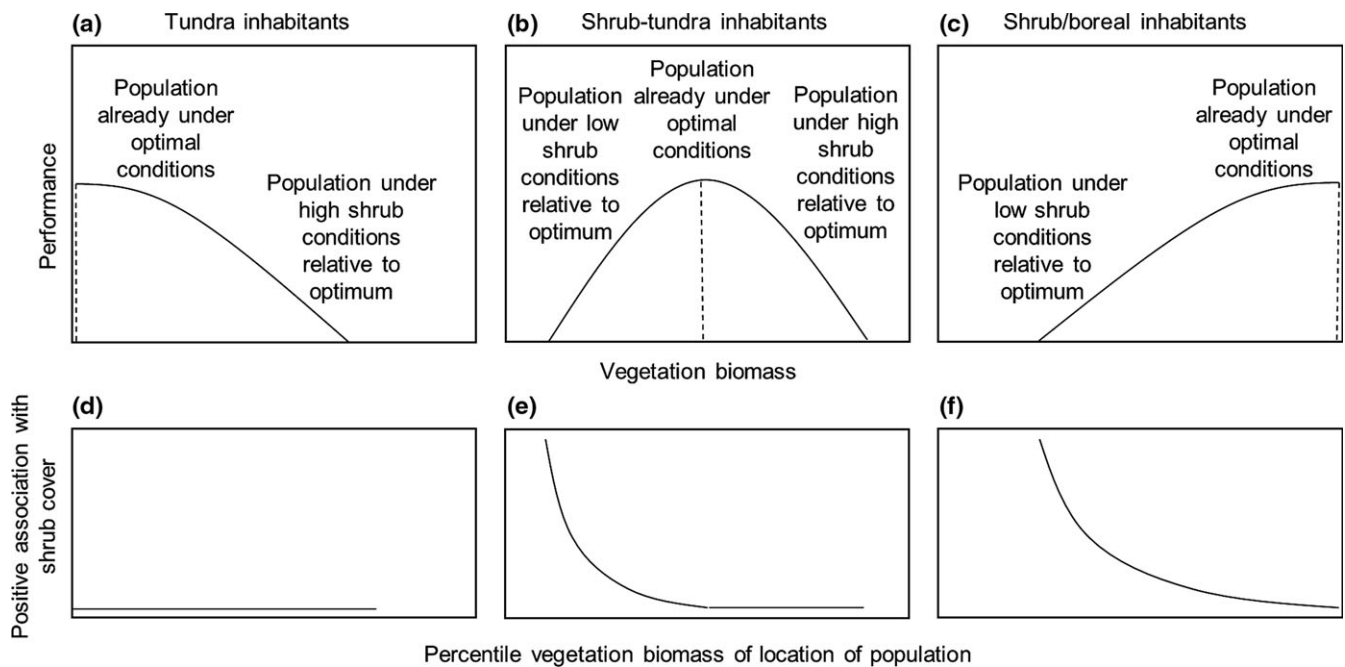


FIGURE 1 Hypothesized wildlife performance responses to shrub cover across species distributions. We show the hypothesized relationship between population location in species niche space with respect to vegetation biomass on predicted population response to shrub cover for three different species types: a, b and c: predicted relationship between vegetation biomass across the species distribution and performance for (a) extreme open habitat specialists, (b) species which perform best in intermediate closure of vegetation and (c) extreme closed-habitat specialists. For each species type, we show the likely relationship between location in niche space with respect to vegetation biomass and species probability of positive responses to shrub cover (d), (e) and (f). We expect most species in our study to conform most closely to scenario (b) and (e). Under this scenario, if optimum conditions are found at the centre of niche space, populations at lower NDVI than this optimum should be more likely to show positive responses to shrub cover. Dashed line shows theoretical optimum greenness

In our third question, we investigate if population responses vary across niche space. Species may respond differently to environmental variation across their range and populations at species range margins may be more sensitive to environmental change than populations at other parts of the distribution (Anderson et al., 2009; Scheele, Foster, Banks, & Lindenmayer, 2017). A species' sensitivity to environmental change at range edges can be driven by a combination of species interactions and climate (Thomas, 2010). In the Arctic, species may be particularly sensitive to climate-associated shrub expansion at leading and trailing range edges (Figure 1). We therefore consider how the position of a population in niche space with respect to green vegetation biomass (Normalized Difference Vegetation Index, NDVI), which is strongly related to shrub cover (Tape, Sturm, & Racine, 2006), affects the magnitude of shrub cover responses. We predict that populations in regions of a species distribution with the lowest NDVI (away from optimal conditions) will be more likely to respond positively to increased shrub cover than populations in higher vegetation biomass regions (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Wildlife responses to shrub cover

We searched the published literature on shrub and arctic wildlife indexed in Web of Science using the keywords "arctic" or "tundra"

and "shrub" or "scrub" or any word starting with "shrub" or "scrub" in combination with the singular or plural of one of the following words: "wildlife," "mammal," "bird," "animal," "herbivore," "predator". To ensure that species were not missed, we then performed searches for all genera listed to contain arctic species in the Arctic Biodiversity Assessment (Reid, Berteaux, & Laidre, 2013). We restricted our analysis to papers published in peer-reviewed journals that reported a direct association between a quantitative characteristic of shrub relevant to shrub encroachment (e.g. shrub cover, height or patchiness) and a characteristic of wildlife relevant to population density or distribution (e.g. behaviour, reproductive success, population size and occurrence) where both characteristics of shrub and wildlife were measured concurrently. We included both temporal and spatial associations within our criteria for selection. Records were accessed repeatedly from 21st May 2014 with the final access on 25th July 2016.

For each paper that fitted our criteria, we recorded the species being studied, the characteristics of shrub cover under study and characteristics of species responses and type of association being made (e.g. spatial association, comparison of sites, temporal association). We included both associations between two variables, and where shrub characteristics were included in more complex models that combined shrub-related and non-shrub-related variables to explain variation in characteristics of wildlife that could affect population density or species distribution. We also recorded what type of

associations was made in each analysis (e.g. linear, quadratic or other non-linear function). We included both publications where the primary objective was to assess an association between shrub cover and wildlife and those where this objective was secondary.

We recorded all effects sizes from models of relationships between wildlife and shrub. For studies with significance tests, we included effects that were statistically non-significant, to allow us to determine consistency of responses. For more complex models, where multiple models had been compared via model selection, we included the reported effects sizes, these were normally from the model with the lowest AIC or AIC_c following standard reporting conventions. Where effect sizes were represented only graphically and could not be extracted from papers, we contacted authors for the necessary information. For differences between two means we calculated Cohen's *d* (Borenstein, Hedges, Higgins, & Rothstein, 2009) and its associated 95% confidence interval as a measure of effect size or mean difference between treatments. For linear associations from both simple regression and more complex models, we extracted β coefficients for each single shrub-related variable and their associated confidence intervals. In models including interaction terms, such as to account for site, year and habitat-specific effects, we extracted the effects for each condition. Where authors reported effect sizes and group means from transformed data, our calculated effect sizes therefore also reflect those transformations. Where authors performed non-parametric tests, our results may differ from those reported from the author as calculation of Cohen's *d* assumes normality of data. We included results from significance tests to maximize the number of studies we could include in our analyses, as a substantial proportion of studies did not have enough information to compute a standardized effect size such as Cohen's *d*. We excluded results from model selection where there was no indication of effect size and error, as there was no opportunity for comparison with other studies.

To give an indication of the consistency and degree of contingency of effects of shrub and risk of false positives within a set of observations of wildlife responses to shrub cover for a given species and location, we recorded the combined sum of all effect sizes measured and significance tests performed as our total number of effects. We then recorded the combined sum of cases where confidence intervals for Cohen's *d* or β effect sizes had 95% confidence intervals that did not span zero or significant trends or differences at $\alpha = 0.05$ were reported as our positive and negative effects. To further help evaluate consistency in responses and differentiate between potential false positives and contingent effects we recorded the source(s) of variation in responses (e.g. differences between sites), where these were reported.

2.2 | Greenness measures, population position in niche space and diet traits

We assessed the relationship between vegetation biomass across a species' range and the likelihood of positive responses to shrub cover by performing logistic regression between the proportion of

positive responses to shrub cover and mean NDVI across a species' range. We extracted occurrences for both birds and mammals from Global Biodiversity Information Facility (GBIF, www.gbif.org). We filtered occurrence data to remove any records that did not represent locations of live individuals (e.g. fossil specimens) and duplicate locations. We then checked occurrences against distributions as defined by IUCN (2014) and we removed occurrences outside these distributions (this excluded semi-domesticated reindeer in the case of *Rangifer tarandus*, reflecting our focus on wildlife habitat selection). We took this conservative approach to quantifying niche space, given the potential for outliers and erroneous occurrences due to data quality issues (Costello, Michener, Gahegan, Zhang, & Bourne, 2013) to generate biases in our estimations of the edge of niche space. To minimize biases due to variation in recording effort across space (Jetz, McPherson, & Guralnick, 2012), we filtered our occurrences using OccurrenceThinner (Verbruggen 2012: OccurrenceThinner version 1.04. <http://www.phycoweb.net/software>) with isotropic Gaussian smoothing kernels constructed with bandwidths selected by likelihood cross-validation. This tool thins data using probabilities proportional to the density of local occurrence records (as specified by the aforementioned kernels), thereby reducing spatial biases in the data (Verbruggen et al., 2013). To characterize vegetative biomass across the wildlife species ranges, we extracted monthly cloud-free normalized difference vegetation index (NDVI) across all relevant occurrences for a species (DAAC, 2016). Specifically, we extracted mean monthly NDVI for July for the years 2010 to 2015 at a 0.05 degree resolution. For mammals, we extracted NDVI at each unique occurrence location. For migratory bird species where only breeding populations occur in the Arctic, we limited records to those taken between 15th June and 15th September in any given year and also to those within IUCN-defined breeding distributions. For migratory species with both breeding and resident populations in the Arctic, we limited records to the same dates as migratory species, (given resident and migratory individuals could not be differentiated from GBIF records), but records were allowed to occur within breeding or resident range as defined by IUCN.

To establish the position in niche space of each study with respect to vegetation biomass, we estimated the mean July NDVI from 2010 to 2015 at the scale of each study site. We first found a centre point for each study site, based on coordinates given in papers or study site descriptions, we then defined the extent of the study using site descriptions to define a study site radius. Mean NDVI was extracted across land within this radius. Where the radius was undefined in the paper, we used a 10 km radius. Where multiple study sites were used in a single study, we extracted mean NDVI at each site and then took the mean across sites. We then established the position of the population in niche space using the quantile of the study site within distribution of NDVI across the species range (herein, NDVI niche position). We extracted the broad biome associations of each species from the Arctic Biodiversity assessment appendices to determine the degree to which species were arctic specialists or also had associations with other biomes (Reid et al.,

2013). We compiled the percentage of plant, insect, or vertebrate in each species diet from data in Wilman et al. (2014).

2.3 | Statistical analysis

To assess the likely habitat characteristics and traits of species expanding northwards, we performed weighted multiple logistic regressions on the proportion of positive responses for each response type recorded from each study for each species. As predictors, we used mean NDVI across a given species' range, NDVI niche position (i.e. quantile position of the study locality in the species' niche space with respect to NDVI, as measured by NDVI quantile relative to distribution of NDVI across species range), as well as the percentage of insects and plants in diet. We did not include models with interactions of mean NDVI across species range and NDVI niche position in logistic model sets due to over-parameterization and quasi-exact separation of data using these models, which would lead to inflated estimates (confirmed by data plotting). NDVI niche positions were only included in combination with mean NDVI across the species range, reflecting the fact that quantiles were only relevant in reference to their distance from a given mean NDVI across the species range (full model set detailed in Table S3). To incorporate the fact that the number of effects studied varied substantially between species and studies, we weighted the proportion of positive responses in both models according to the number of effects estimated; this reflects the fact that the consistency of responses to shrub are likely to be more precise where multiple sites, years or characteristics of shrub are assessed and reported. We used an asymptotic function to reduce the impact of weights for studies where a large number of effects were estimated and hence scaled weights according to their logarithm (using the expression $\frac{\log(\text{Weight}+1)}{\log(2)}$). We compared models using AIC corrected for small sample size (AIC_c, Burnham & Anderson, 2002). There was no overdispersion at $\alpha = 0.05$. There was insufficient data to perform quantitative analysis on the proportion of negative responses to shrub ($n = 3$), but we also performed analogous weighted multiple linear regressions on the proportion of positive and negative wildlife responses to shrub cover variables (reported in Table S4). We processed spatial data using packages "sp," "raster" and "spstat" and statistical analyses were performed in base package "stats" using function "glm" in R version 3.3.1 (Baddeley & Turner, 2005; Bivand, Pebesma, & Gómez-Rubio, 2013; Hijmans, 2014; R Core Development Team, 2016).

3 | RESULTS

Our data comprised 174 different effects grouped in to 48 different species responses to aspects of shrub cover within studies covering 21 species of birds and eight species of mammals (Tables S1 and S2). All studies reported spatial associations between shrub cover and wildlife characteristics; we found no papers that reported direct associations between concurrent temporal change in shrub cover

and wildlife characteristics. However, a number of studies both within and outside our criteria for inclusion in the meta-analysis made links between recent temporal changes in shrub and wildlife (Forbes et al., 2009; Ims et al., 2007; Tape, Christie, et al., 2016; Tape, Gustine, et al., 2016). For most species, associations were made between species occurrence and shrub cover attributes (31/48 species responses). Studies ranged in complexity from testing a single spatial association between shrub cover and wildlife characteristics or making independent comparisons of single variables between two sites, to selection between complex models describing multisite and temporal variation in wildlife responses to multiple aspects of shrub cover. All except two studies assumed linear wildlife relationships with shrub cover and tested linear associations or compared two habitats or conditions. An additional three studies had the capacity to identify location- or habitat-specific effects by incorporating the possibility for variation between more than two sites or habitats into models.

Both positive and negative responses to shrub cover were recorded within the existing literature, but positive responses greatly exceeded negative responses for both mammals (Figure 2a) and birds (Figure 2b). Mammalian studies focused on species that inhabited only boreal biomes (*L. americanus* and *Lepus timidus*) or both boreal and arctic biomes (all other species). None of the 16 mammal species that are considered to have the Arctic as their dominant biome (Reid et al., 2013) have been studied with respect to shrub cover responses. For bird species, studies spanned from species breeding exclusively in the Arctic ($n = 5$), through species where the majority of populations breed in the Arctic ($n = 3$) and species where only part of the population breeds in the Arctic ($n = 6$) to species considered boreal or temperate where breeding ranges occasionally penetrate in to arctic areas ($n = 7$). None of the species breeding exclusively in the Arctic showed responses to shrub cover. For species that were not associated solely with the Arctic, at least one positive response to shrub cover was observed in 62.5% of species and a negative effect of increased shrub was found in just three species (12.5%).

Studies of wildlife responses to shrub cover spanned the circum-polar Arctic (Figure 3). Positive responses to shrub cover were generally observed further north than negative responses and occurrences of no significant response to shrub cover were more common than positive or negative responses (Figure 3). Wildlife responses to shrub cover spanned a wide range of population positions in species niche space with respect to NDVI (NDVI niche position range: 0.004–0.832, Figure 3), but most studies represented the lower-NDVI extent of species niche space (i.e. niche space towards leading range edges, mean NDVI niche position = 0.247 ± 0.036).

In all studies where analytical models allowed for variation in responses to shrub cover (18 species/study combinations) in different contexts (e.g. sites, years, habitat types), heterogeneous responses were observed (Tables S1 and S2). For those species where more than one effect was examined, across all studies for that species, a maximum of 50% of effects tested had 95% confidence intervals that did not include zero (mean percentage of 95%

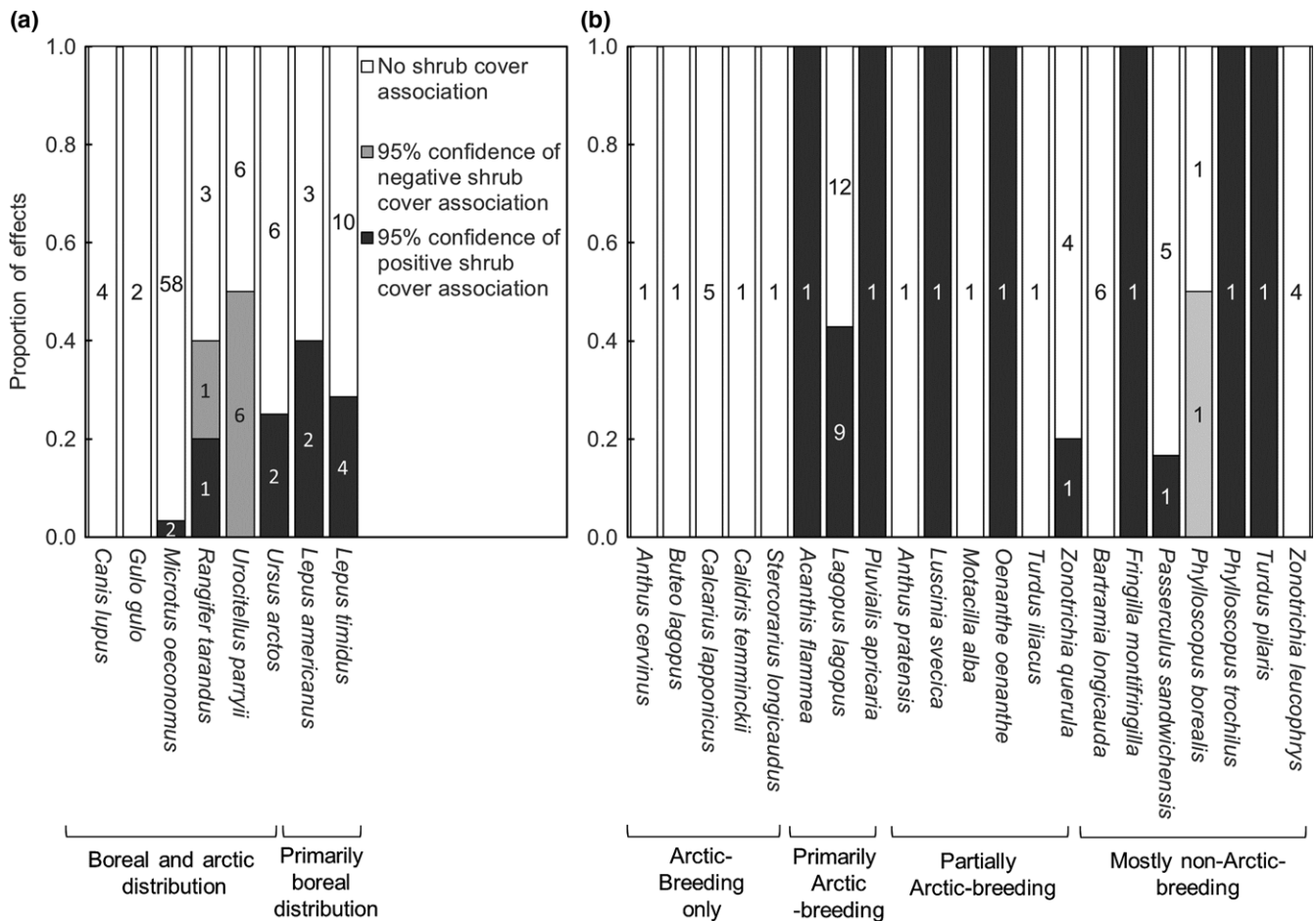


FIGURE 2 Summary of effects of shrub cover on responses of bird species relevant to population or distributional change for mammals (a) and birds (b). Percentage of positive and negative effects at $\alpha = 0.05$ are shown in addition to the percentage of occasions where no effect was observed. The frequencies of each of these outcomes for each species are shown inside bars. The degree of species association with the Arctic is shown in the bottom of the figure

confidence intervals for a species not spanning zero = $18.4\% \pm 5.1$). No more than 80% of effects were positive within any given single study for a species where more than two effects were examined. Sources of variation in wildlife responses to shrub cover included variation in responses between sites, habitat types, and years, and also reflected that many species responses were limited to specific shrub cover characteristics (Tables S1 and S2).

The proportion of positive responses to shrub cover was best described by a positive effect of mean NDVI across the species distribution (Figure 4; Tables 1 and S3, standardized effect size: 8.51 ± 3.37) and a negative relation to NDVI niche position (the quantile of NDVI at the study site relative to NDVI across the species range, standardized effect size: -5.42 ± 3.84). Species associated with a higher mean NDVI across their distribution were more likely to respond positively to shrub cover. When studies were located in areas of relatively low NDVI values within the species' range, species were also more likely to respond positively to shrub cover (Figure 4). The next most supported model under AIC_c was a model that contained only mean NDVI across the species range and had only slightly lower AIC_c than the best

supported model ($\Delta AIC_c = 0.61$). There was no evidence that degree of herbivory or insectivory affected responses to shrub cover.

Contrary to our predictions (Figure 1), positive responses to shrub cover still showed an increasing trend with mean NDVI across species range when populations studied were at the 0.5 quantile (Figure 4). This was a relatively weak trend and our predictive power is weaker for studies conducted in the more productive regions of species ranges, given studies were more likely to have been performed at the lower vegetation biomass extents of species ranges. Most importantly, we found that positive responses were more likely when species were at the lowest vegetation biomass extent of their range (Figure 4). Populations showing negative responses to shrub characteristics were predominantly from the highest vegetation biomass parts of their niche space (2/3 species). For instance, the Arctic ground squirrel (*Urocyon parryi*) was studied in the 83rd percentile of NDVI relative to NDVI across its distribution and in the reindeer study where a negative effect was observed, the study was located in the 54th percentile relative to NDVI across its distribution. These species were two of only four species studies in the

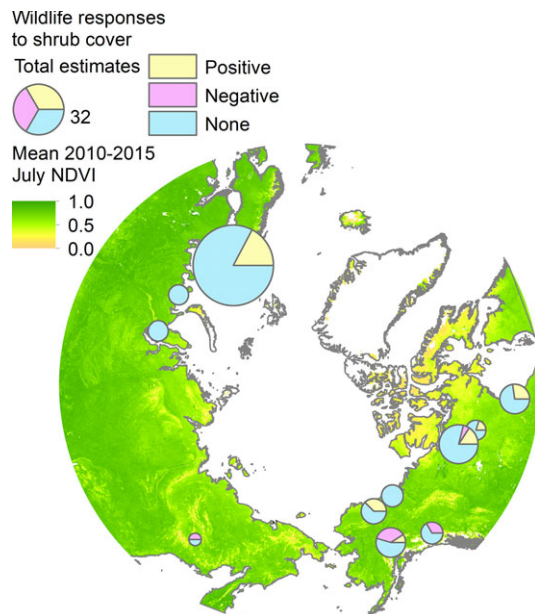


FIGURE 3 Summary of the proportion of effects size measured showing statistically significant positive or negative effects of shrub cover on birds and mammals across the Arctic and subarctic (note some nearby locations are combined to avoid excessive overlap of pie charts, in total 19 unique locations are summarized in these charts). Pie chart size reflects the number of effects sizes measured

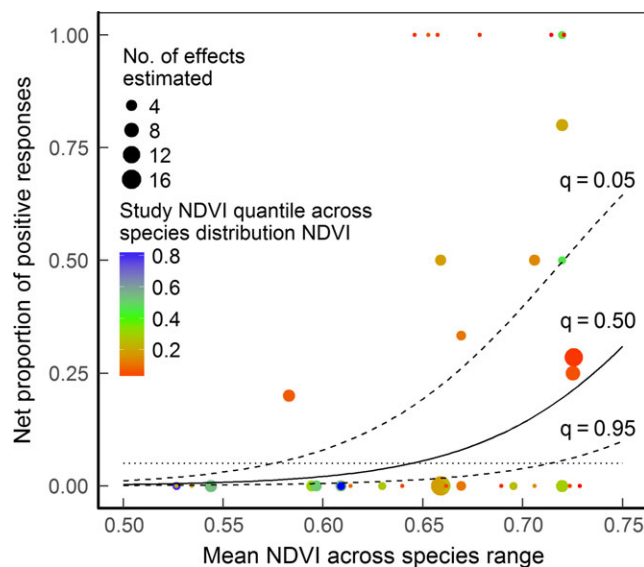


FIGURE 4 Relationship between NDVI and proportion of positive responses to characteristics of shrub associated with shrubification. A greater proportion of positive responses are for species with high mean NDVI across their range. NDVI niche position is depicted by broken and solid lines. Predictions at 0.05, 0.05 and 0.95 quantiles of study sites relative to distribution of NDVI across species ranges are shown. Grey dotted line represents expected type I error rate

more productive percentiles of their range (higher than the 50th percentile). The Arctic warbler study, where a negative response to shrub cover was observed was conversely located in the 24th

TABLE 1 Summary of top five models for the proportion of positive responses of wildlife to shrub characteristics related to shrubification in published literature for arctic and subarctic bird and mammal species. Terms are mean Normalized Difference Vegetation index across the species distribution (Mean NDVI), NDVI niche position (i.e. quantile position of the study locality in the species' niche space with respect to NDVI, as measured by NDVI quantile relative to distribution of NDVI across species range) and proportion of diet that comprises insects (Insectivory) or vegetation (Herbivory). Models are ordered from lowest AIC_c, top 5 models only are shown in addition to a null model. For full model set and effect sizes see Table S3

Model	k	AIC _c	ΔAIC _c	Deviance	AIC weight
Mean NDVI + NDVI niche position	4	72.60	0.00	50.62	0.35
Mean NDVI	3	73.20	0.61	52.93	0.26
Mean NDVI + Insectivory	4	74.94	2.34	52.12	0.11
Mean NDVI + NDVI niche position + Insectivory	5	75.02	2.42	50.42	0.10
Mean NDVI + NDVI niche positions + Herbivory	5	75.11	2.52	50.61	0.10
Null	2	84.19	11.59	67.42	0.00

percentile of NDVI relative to NDVI across its range. When both positive and negative responses to shrub cover were analysed together, our linear analysis was consistent with, and supported the same models as, our logistic models of positive responses to shrub cover (Table S4; Fig. S1). Responses to shrub cover became increasingly positive as mean NDVI across wildlife species range increased (standardized effect size: 0.82 ± 0.48) and when species were in the lowest NDVI regions of niche space (Table S4; Fig. S1, standardized effect size: -0.85 ± 0.49).

4 | DISCUSSION

Our study provides the first quantitative comparison of the degree to which species across the Arctic are responsive to shrub cover. We demonstrate how the strongest positive responses to shrub cover may be seen at low-NDVI leading edges of species ranges, that are associated with lowest vegetation biomass. We also identify the need for greater investigation of the potential effects of shrubification on open tundra specialists. It is important to differentiate the lack of information on negative effects of shrub cover on arctic wildlife from the assumption that species will not be negatively affected by shrubification. The observed spatial associations between shrub cover and indicators of wildlife population performance support the idea that substantial change in wildlife communities is likely to occur with further shrubification in the Arctic, with increased shrub cover favouring subarctic species associated with niches characterized by higher vegetation biomass. Associations with shrub cover were species- and context-specific, highlighting the uncertainty in future responses the shrubification, the large number of cases where

species were not strongly responsive to shrub cover and the likelihood of location- and species-specific outcomes.

4.1 | Responses to shrub cover

Our study shows that a number of subarctic species in the Arctic respond positively to shrub cover. Species with a higher mean NDVI across their range were more likely to respond positively to shrub cover and showed less contingency in their responses than species with a lower mean NDVI across their range. The vast majority of positive responses to shrub cover were observed for species primarily found in areas with NDVI higher than that characteristic of the arctic region, where only rare occurrences of maximum NDVI greater than 0.62 are observed (Epstein et al., 2015; Walker, Gould, Maier, & Reynolds, 2002). However, small patches of high vegetation biomass within a lower biomass landscape may provide opportunities for species to expand, if those patches are sufficiently large to maintain populations or facilitate dispersal. From our current data, we do not find positive responses to shrub cover in exclusively arctic species and this suggests that shrub encroachment could create a homogenization of arctic fauna with more boreal habitats (Sokolov et al., 2012). Invasion of boreal and temperate climate-associated wildlife into arctic-like environments has been observed during periods of warming of over geological timescales alongside expansion of woody species (Sommer, Kalbe, Ekström, Benecke, & Liljegren, 2014; Sommer & Zachos, 2009; Willerslev et al., 2014) and is likely to occur with current rapid warming and vegetation change in the Arctic. This study provides a first step to quantitatively predicting the characteristics of some of the species that may expand under shrub expansion.

Our study also highlights that shrub encroachment can have negative effects on widely distributed species. All species (Arctic ground squirrel, *U. parryi*; reindeer/caribou, *R. tarandus*, Upland sandpiper, *Bartramia longicauda*) that had any negative association with shrub cover are widely distributed, with arctic and subarctic populations. The distribution of some of these species may extend beyond their fundamental niche (for example where sink populations exist). Understanding species population dynamics may aid projection of long-term change in such species (Anderson et al., 2009; Keith et al., 2008). Source-sink dynamics may render a species with relatively wide distribution dependent on core populations in optimal habitat (as for arctic ground squirrels: Gillis, Hik, Boonstra, Karels, & Krebs, 2005; Donker & Krebs, 2012; Werner, Krebs, Donker, Boonstra, & Sheriff, 2015; Wheeler, 2012; Wheeler, Chipperfield, Roland, & Svenning, 2015), particularly in areas of high topographic variation. If habitat conversions to more woody vegetation become contiguous such that source populations are lost, rapid distributional changes could occur in these species. Conversely, if shrub expansion is spatially limited, such as to riparian corridors or certain soil types (Tape, Hallinger, Welker, & Ruess, 2012) then landscape-level change in persistence of species exhibiting source-sink dynamics species may be more limited, as source populations continue to sustain populations in shrubbier habitat.

4.2 | Responses to shrubification across niche space

We found the position of a population in niche space contributes substantially to its response to environmental variation. Positive responses to shrub cover were more likely for populations located in low vegetation biomass areas relative to biomass across their range and two of three populations with negative responses to shrub characteristics were located in a substantially higher vegetation biomass part of the species distribution. This may explain why positive responses to shrub cover (generally from species at the lowest vegetation biomass extent of their niche) were mostly observed further north than negative responses (from species generally at higher vegetation biomass extents of their niche). This has two core implications: Firstly, projections of wildlife change based on responses to variation at the core of their range may underestimate magnitudes of change in response to shrub cover at leading edges of species ranges. Secondly, an individual's ability to disperse to extremities of suitable habitat (e.g. lowest NDVI) should exert strong influence over the speed and magnitude of population and distribution change under shrubification (Urban, Zarnetske, & Skelly, 2013).

4.3 | Mechanisms of shrub-effects on wildlife

Transitions from tundra habitats to shrubbier habitat have the potential to create a wide variety of changes in habitat suitability for wildlife (Table 2). These include indirect effects on prey and predators, snow cover and phenology and soil quality such as drainage affecting substrates for burrowing mammals. Changes occurring outside the summer are particularly overlooked with respect to effects of shrub cover on wildlife species due to challenges of data collection during that period.

Responses to shrub cover were characterized by low consistency across sites and over time. Heterogeneous responses to changing climate in the Arctic have similarly been found in long-term study sites (Gauthier et al., 2013), suggesting climate-related transitions in the Arctic will be difficult to predict. The high degree of contingency that we observed in response to shrub cover may limit the extent to which species can benefit from shrub encroachment (e.g. root voles, *Microtus oeconomus*, Henden, Ims, Yoccoz, Sørensen, & Killengreen, 2011). In order for expansion of species in to the Arctic to occur, other ecological conditions must also be favourable. Environmental stressors which co-occur with shrub encroachment, as expected under warming, may moderate or subsume those driven by shrub. For arctic warblers, fledging success was greater in open compared to closed-shrub habitats; however, in a year with extreme weather, this effect was entirely lost, possibly due to changes in phenology affecting nest building opportunities (Hagelin, Perry, Ewen-Campen, Sikes, & Sharbaugh, 2010). Given greater occurrences of extreme weather are projected in the Arctic and likely effects on wildlife (Hansen et al., 2013), care needs to be taken to compare the magnitude of effects of shrub encroachment with those of other drivers

TABLE 2 Summary of some of the key potential and reported mechanisms of shrub encroachment effects on wildlife

Process affected by shrub	Consequence	Example	Reference(s)
Foraging	Benefits for species which consume shrub as preferred forage	No specific links to forage yet made	
	Costs for species which consume species that are negatively associated with shrub cover increase.	Decreased protein availability and higher toxin load in diet forage for reindeer	Thompson and Barboza (2014)
		Loss of winter lichen forage for reindeer if shrub promotes more frequent fire	Gustine et al. (2014)
Habitat for preferred prey	Benefits for species consuming shrub-associated prey	Enhanced arthropod prey for migratory songbirds	Boelman et al. (2015)
Increased vertical vegetation structure	Benefits for species which use shrub to avoid detection by predators	Shrub cover provides concealment of nests for the Upland Sandpiper, increasing breeding success.	Miller et al. (2015)
	Costs for species which rely on detecting predators at distance	Arctic ground squirrels burrow less, and have lower density and survival and alter foraging behaviour shrubbier habitats	Wheeler (2012); Wheeler and Hik (2014); Wheeler et al. (2015)
Changing plant root structure	Benefits for species that require more stable or better drained soils	Roots from shrub provide improved grizzly bear denning sites due to soil stability	McLoughlin et al. (2002)
Changing snow depth and cover	Unclear consequences due to complex relationships between shrub and snow. The physical structure of shrub can trap snow, causing accumulation, but protrusions of dark shrubby branches and foliage also lower albedo, enhancing melting.	For hibernating species (e.g. arctic ground squirrel), increases in snow depth could alter hibernation energetics. Females select burrows with higher snow cover (associated with greater shrub cover), followed by males and juveniles, (NB: no relationship was found in energetic costs of hibernation in relation to snow depth within the range of hibernacula snow conditions currently observed)	Buck and Barnes (1999); Wheeler and Hik (2013)
		Snow cover timing variation can affect the phenology of arctic wildlife life-history	Sheriff et al. (2011)
		Insulative properties of sub-nivean space are essential to winter survival of some small and medium sized mammals	Pruitt (1957)

before linking spatial associations with shrub to projected temporal change.

Contingency arose where species only responded to specific attributes of shrub cover, effects were landscape-dependent, or were determined by multiscale shrub characteristics. Some species are sensitive to shrub cover over a certain height, or are affected by overhead but not lateral visibility (Miller, Nol, Nguyen, & Turner, 2015; Wheeler et al., 2015). For some species, local shrub cover may influence prey survival and foraging efficiency by providing cover from predators where vegetation structure is open and prey exposed, but once shrub cover becomes denser, benefits of local increases in shrub cover may be lost or reversed (e.g. arctic ground squirrels, Wheeler & Hik, 2014). The presence of high landscape-level shrub cover may also alter the magnitude and mode of predation risk (as suggested for willow ptarmigan, Ehrich et al., 2012). These effects could create non-linear responses to shrub cover as height thresholds are reached or infilling leads to canopy closure; however, few studies addressed the potential for non-linear responses.

4.4 | Herbivory and shrubification

Knowing how the performance of wildlife species responds to changes in shrub cover is core to predicting the large-scale potential for wild herbivores to limit shrub expansion through herbivory. There has been considerable discussion about the role of herbivory in limiting shrub in the Arctic and the potential of certain herbivores (notably ungulates) to limit shrub expansion (Cahoon et al., 2012; Olofsson et al., 2009). Herbivore suppression of shrubby vegetation is a key potential mechanism for limiting shrub encroachment in the Arctic, given strong human intervention is largely unfeasible. Plot-level and relatively local grazing effects of wildlife have been demonstrated for a number of species (Christie et al., 2015). Greater focus has been given to ability of herbivores to suppress shrub than how densities of, and foraging intensity from herbivores will respond to changing vegetation structure. While large-scale grazing studies have demonstrated the current role of herbivores in limiting shrub through herbivore exclusion (Ravolainen, Bråthen, Yoccoz, Nguyen, & Ims, 2014; Ravolainen

et al., 2011), for non-domesticated species, understanding the likely changes in distribution and density of herbivores at large scales will also be key to projecting future grazing effects in potentially novel environments. Our data suggest that grazing pressure may be altered by the addition of new herbivore species from more temperate latitudes and also highlights the lack of information on how existing arctic herbivores will respond to changing shrub cover, which is essential to predict future grazing regimes and their potential to suppress shrub.

4.5 | Data gaps

In addition to showing how responses to shrub cover vary across niche space, our study highlights the lack of information on shrub cover associations of arctic specialists and the need for studies that can identify complex wildlife responses to shrub cover change. It may be particularly informative to investigate high-arctic species responses to shrub cover at the higher NDVI extents of their range, where our study predicts negative responses will be strongest. Increased emphasis on multiannual, multisite examinations of shrub responses or studies stratified by different ecological contexts will help to identify key sources of contingency and improve projections of future change (Ehrich et al., 2012).

ACKNOWLEDGEMENTS

This article is a contribution by the Center for Informatics Research on Complexity in Ecology (CIRCE), funded by the Aarhus University Research Foundation under the AU Ideas program. JCS also considers this work a contribution to his VILLUM Investigator project “Biodiversity Dynamics in a Changing World” (BIOCHANGE) funded by VILLUM FONDEN.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Wheeler HC, Høye TT, Svenning J-C. Wildlife species benefitting from a greener Arctic are most sensitive to shrub cover at leading range edges. *Glob Change Biol*. 2018;24:212–223. <https://doi.org/10.1111/gcb.13837>