Evidence for large-scale effects of competition: niche displacement in Canada lynx and bobcat

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Determining the patterns, causes and consequences of character displacement is central to our understanding of competition in ecological communities. However, the majority of competition research has occurred over small spatial extents or focused on fine-scale differences in morphology or behaviour. The effects of competition on broad-scale distribution and niche characteristics of species remain poorly understood but critically important. Using range-wide species distribution models, we evaluated whether Canada lynx (\textit{Lynx canadensis}) or bobcat (\textit{Lynx rufus}) were displaced in regions of sympathy. Consistent with our prediction, we found that lynx niches were less similar to those of bobcat in areas of sympatry versus allopatry, with a stronger reliance on snow cover driving lynx niche divergence in the sympatric zone. By contrast, bobcat increased niche breadth in zones of sympathy, and bobcat niches were equally similar to those of lynx in zones of sympathy and allopatry. These findings suggest that competitively disadvantaged species avoid competition at large scales by restricting their niche to highly suitable conditions, while superior competitors expand the diversity of environments used. Our results indicate that competition can manifest within climatic niche space across species’ ranges, highlighting the importance of biotic interactions occurring at large spatial scales on niche dynamics.

1. Introduction

The role of competition on populations and species is a long-standing source of interest in ecology, having a fundamental influence on our understanding of a range of topics including community structure, speciation and extinction. Competition between individuals or populations is well documented for numerous taxonomic groups across diverse systems [1–3] and can result in loss of energy or reproductive output through antagonistic or exploitative relationships [3]. However, one weakness in our understanding of species response to competition is the issue of scaleability, whereby current research largely fails to inform our understanding about the effects of competition on large-scale species–environment relationships and distribution patterns [3,4]. This deficiency is problematic because it constrains our understanding of how competition is actually manifested across larger spatial scales, and whether competitive dominance is consistent irrespective of local or regional conditions. Not surprisingly, substantial debate exists regarding the extent to which climatic gradients or other environmental factors limit the expression of competition at the range-wide scale [3,5].

The standard approach for documenting the occurrence of competition is to assess levels of character displacement [6], where morphological and behavioural differences between two geographically overlapping species are found to be greater in regions of sympatry and weakened or removed in regions of allopatry [6–8]. This simple heuristic is based on the understanding that coexisting species must differ to some degree in their resource use in order to avoid competitive exclusion [9]. Therefore, a greater phenotypic difference between competitors should occur when species overlap in their distribution or space use [8]. It follows that such displacement may be a primary force in driving animal behaviour and...
interactions affect the relationship between a species and potentially more robust means for detecting whether biotic niche displacement in the presence of competitors provides an issue in distribution modelling [4,21]. Indeed, assessing information [19]. This uncertainty remains a major area of interest in ecology [20] as well as more specifically being an unresolved supposition [15–18] by demonstrating that large-scale species of abundance [5]. However, recent work has questioned this being important at smaller scales or by affecting local patterns analyses that occur at a range-wide scale should be responsive species distribution and abundance patterns. Specifically, or change their ecology when in the presence of competitors. Under understanding of how species avoid competitive interactions dynamics of species, and may act as a method for detecting the effects of competition that are otherwise masked at larger spatial scales.

Specific predictions of competition and character displacement theory can be assessed at large scales; for example, inferior competitors should shift to occupy environments where they are more strongly suited when in the presence of competitors because they are outcompeted in marginal environments [13,14]. Similarly, superior competitors should persist in their more marginal environments because they should expand their niche more or less continuously as new environment becomes available [13]. By examining these types of predictions across the entire range of species, we can refine our understanding of how species avoid competitive interactions or change their ecology when in the presence of competitors.

The expression of competitive interactions at a large spatial scale informs our understanding of the drivers of range-wide species distribution and abundance patterns. Specifically, analyses that occur at a range-wide scale should be responsive to predominantly abiotic factors, with biotic interactions mainly being important at smaller scales or by affecting local patterns of abundance [5]. However, recent work has questioned this supposition [15–18] by demonstrating that large-scale species distributions can be altered by the inclusion of biotic information [19]. This uncertainty remains a major area of interest in ecology [20] as well as more specifically being an unresolved issue in distribution modelling [4,21]. Indeed, assessing niche displacement in the presence of competitors provides a potentially more robust means for detecting whether biotic interactions affect the relationship between a species and relevant environmental variables in areas of sympatry with competitors. A more detailed understanding of the existence and magnitude of niche displacement will therefore contribute to improved appreciation of the large-scale drivers of species presence and niche characteristics, thereby refining current and future predictions of distribution patterns.

Canada lynx (Lynx canadensis) and bobcat (Lynx rufus) are logical subjects for a broad-scale analysis of competition and niche displacement, as they are closely related, morphologically similar and use similar resources throughout much of their range [22]. There is also anecdotal evidence of competition between these two species, with lynx potentially being displaced when co-occurring with bobcat [23]. Moreover, the substantive spatial overlap between marginal Canada lynx and bobcat populations (figure 1a) presents a scenario for potential competition and displacement across large spatial scales.

In this study, we use species distribution modelling, along with measures of niche similarity and breadth, to examine range-wide niche displacement between Canada lynx and bobcat. We account for background environmental differences and clinal changes in environments to address common deficiencies in studies of character displacement that are conducted across large spatial scales [7,8,11]. We test the prediction that niche displacement will be evident in regions of sympathy between both species, with lynx responding to competition by occupying a narrower environmental space that is more characteristic of their preferred environment [13,14]. By contrast, bobcat should maintain a constant niche space or even expand such space when in sympathy with lynx, depending on the nature and intensity of their competitive interactions. If bobcat presence is not limited by lynx, we expect them to expand into previously unavailable environments, thereby increasing their niche breadth when found in sympathy [13,23]. Accordingly, large-scale shifts in niche dimensions should be observed in lynx (and possibly bobcat) where their distributions are overlapping.

2. Material and methods

(a) Species data

We collected information on Canada lynx and bobcat presence across North America using museum records from freely accessible databases (MaNIS; www.manisnet.org) as well as from smaller museums that provided data through individual contact
(see the electronic supplementary material, table S1 for complete list). Presence records for the two carnivores in Canada (which were relatively sparse) were supplemented with provincial harvest records (see the electronic supplementary material, table S1 for list). To accommodate recent range shifts in Canada lynx, we also included a dataset on historic lynx occurrence in the United States based on sightings, museum records and other sources [24]. We excluded from further consideration all records (i.e. museum, harvest and historic dataset) that had more than 13 km uncertainty and were collected before 1940 to improve accuracy of the distribution models [25] and better match the time frame of our environmental data (see below). Presence data for both species were similar in their temporal distribution. Presence records were divided into two files corresponding to the sympatric and allopatric area for each species. Species geographical ranges were determined using NatureServe [26], which is an open access organization that provides information on distribution and abundance of species, and ranges were adjusted for presence records that fell outside of the range provided by this data source.

(b) Environmental data

Range-wide species distribution model (SDM) comparisons for mesocarnivores occupying most of North America require the use of niche metrics that are common to both species. Because lynx and bobcat both use a variety of prey and habitat types, and do not overlap fully across their range, we related SDMs to select climatic variables that should correspond to prey or habitat requirements for each species [27]. Climatic variables were obtained from the WorldClim database [28], which provides a variety of climatic data averaged over the years 1950–2000. An elevation layer also was obtained from the WorldClim database. In addition, we calculated long-term (1979–2000) average winter (October–March) snow depth and snow cover using data from the North America Regional Reanalysis dataset [29]. We also included information regarding the ecoregion of each grid cell. This map divided North America into 15 ecotype classes ranging from tundra to temperate forest and desert (United States Environmental Protection Agency, based on data from Omernik [30]). All environmental data were resampled to correspond to the 15 km grid cell size used to account for uncertainty in the presence records. Given the large number of potential environmental variables (particularly the bioclimatic variables), we performed an initial screening based on variable correlation ($r < 0.85$) and model importance. Such an approach eliminates correlation, and allows more interpretable models and variable responses [31]. In total, six bioclimatic variables were used in the final MAXENT modelling (maximum temperature of the warmest month; minimum temperature of the coldest month; precipitation of the warmest quarter; precipitation of the coldest quarter; mean diurnal range, i.e. mean of the monthly maximum − minimum temperature; and temperature seasonality, i.e. standard deviation of monthly mean temperature × 100), as well as snow depth, snow cover, ecoregion and elevation.

(c) Model development

The program MAXENT was used to create SDMs for each species. This program was chosen because it has been shown to outperform other algorithms for building SDMs from presence-only data [32]. MAXENT compares presence records with randomly selected points from a background extent to create maps of habitat suitability and determine the effect of environmental variables on species presence. MAXENT produces estimates of habitat suitability for each grid cell across the study region. For our models, the background was set as all Canada and the United States to cover areas potentially reachable or surveyed for either species. Therefore, the environmental attributes of our presence records were compared to environmental attributes of 10,000 random samples across this region to build our models. MAXENT assumes that sampling of presence locations is unbiased; biased sampling promotes model inaccuracy [33]. To account for the spatial bias in presence records, we first reduced the unevenness in density of presence records by randomly subsampling our presence records so that a single record was included for every 900 km$^2$ area. Bias in presence records was further addressed by creating a bias grid for use in MAXENT modelling, following procedures outlined by Elith et al. [34]. Models produced before and after we corrected for bias demonstrated a notable difference in output (see the electronic supplementary material, figure S1). Biased models were tightly linked to areas of intense sampling and did not fully represent the species’ environmental niche. We therefore continued our analysis using the subsampled records and the bias grid. We performed a 10-fold cross-validation procedure to create the MAXENT models and calculate area under the curve (AUC) statistics (performance measure). The models were run without the threshold feature (which allows abrupt step-like relationships between response and predictor) to reduce the number of estimated parameters and to allow better understanding of the variable response curves for each environmental layer. The average of the 10 models produced during the cross-validation was used to calculate model performance (see the electronic supplementary material for a more detailed description of model development).

(d) Testing the predictions

To determine whether competitors reduce their niche overlap with the disadvantaged species being disproportionately displaced where their ranges intersect, our datasets for both species were divided into two separate files, one containing presence records in the intersect area of their ranges and another in the non-intersect. We then compared the niche overlap (similarity) between the lynx model developed using only points in the intersection zone and the full bobcat model, versus niche overlap between the lynx model developed using only points in the non-intersection zone and the full bobcat model. We repeated the process for bobcat points in the intersection and non-intersection areas. Niche overlap was calculated based on logistic probabilities of occupancy in each grid cell according to the $l$ statistic implemented in ENMTOOLS [35,36]. This methodology takes as input the values of habitat suitability at each grid cell for each species across the study area and compares them using the following formula:

$$l(Px, Py) = 1 - \frac{1}{2} \sum \left(\sqrt{Px_i} - \sqrt{Py_i}\right)^2,$$

where $Px_i$ and $Py_i$ refer to the normalized suitability scores for species $X$ and $Y$ in grid cell $i$. This is essentially comparing MAXENT output (i.e. suitability scores) to any two models at all grid cells across a specified area; if there are generally large differences in suitability scores between the two models, then there is low niche overlap. The $l$ statistic ranges from 0 to 1, with 0 indicating no niche similarity between species and 1 indicating complete similarity. One potential issue with our analysis arises because niche overlap between bobcat and lynx is expected to change merely owing to differences in available environments between intersect and non-intersect zones, and not necessarily owing to any actual changes in niche space. For example, lynx models from the intersection zone will overlap more strongly with bobcat models because available environments in the intersection area (the southern portion of the lynx range) are more similar to the available environments in the bobcat range than are environments from the non-intersection (northern portion) of the lynx range. To account for this, we used a null model approach, akin to the approach advocated by Warren et al. [35]. In the intersect and non-intersect areas for both species, 100 MAXENT models were developed based on randomly generated
points (the number of randomly generated points was equal to the number of presence records for each species in the intersect and non-intersect zones). The randomly generated MaxEnt models from intersect and non-intersect sections of both species ranges were compared to random models generated from the full range of their competitor. This allowed us to determine the amount of niche overlap expected by chance and owing to overlap in the background environments of the species. The values of niche overlap from the random background environments were subtracted from our niche overlap values obtained from actual presence records to calculate niche similarity for the intersect and non-intersect portion of each species range with its competitor, controlling for the background environment. This resulted in 100 adjusted niche overlap values for both the intersect and non-intersect portions of each species’s range. We then compared adjusted niche overlap metrics to determine whether bobcat and Canada lynx become less similar to each other when occurring in sympathy.

To determine whether niche breadth is altered in areas where the competitor exists, we developed separate MaxEnt models based on presence records from the overlapping and non-overlapping areas for each species. Niche breadth of the outputs of the two models was examined through the use of Levin’s concentration metrics (implemented in EMNTOOLS [36,37]). This metric also takes the habitat suitability values for each grid cell across the range and calculates niche breadth according to the inverse concentration [38]. The values in the models will range from 0 to 1, where 0 indicates minimum niche breadth and 1 indicates the maximum. Similar to our analysis of niche overlap, the availability of environments is different in intersect and non-intersect zones for both bobcat and Canada lynx, and it is therefore necessary to account for this variability in any test examining change in niche breadth [35]. To do this, we calculated the expected niche breadth in intersect and non-intersect areas using 100 replicate datasets of randomly created presence-points located in the two zones. These replicate datasets were used to develop MaxEnt models and determine the expected niche breadth in each area, for each species (similar to above). We then subtracted the values of the 100 random pairs of intersect/non-intersect replicated models in order to obtain a distribution of expected differences in niche breadth between the sympatric and allopatric portions of each species’s range. This forms the null expectation of niche breadth change between non-intersect and intersect areas for each species, and was compared to the actual change in niche breadth obtained from models using the actual presence-points for each species in each zone [35].

To further address any possible unaccounted-for spatial factors influencing the comparison of niche similarity and breadth between lynx and bobcat, as well as to further account for potential clines or geographical variation that has affected previous displacement analysis [7,11], we followed the same procedure outlined above for comparing niche overlap and niche breadth, but with a comparably sized pseudo-intersect area for both species, which was located directly adjacent to the actual intersection zone (figure 1b). This was accomplished by buffering the intersect area to the north and south so that the size of the pseudo-intersect area for both species was equivalent to the real area of intersect. Values of niche similarity and breadth were compared between the new pseudo-intersect zone and the new pseudo-non-intersection area for both species. The pseudo-intersect analysis ensures that the patterns seen are not the result of unaccounted-for geographical clines in species distributions, or vagaries of model-fitting and extrapolation (e.g. suspected displacement in weasel guilds was actually attributed to geographical clines in morphology rather than competitive influences [11]). Moreover, this test, as well as accounting for the available background through null models, allows us to rule out the potential confounding influence of differing ecological characteristics within the sympatric and allopatric zones on our analysis.

3. Results
(a) Species distribution models
After processing lynx and bobcat locations according to the appropriate uncertainty level and excluding points within the same 900 km² grid, we had 988 and 855 observations to model lynx and bobcat distribution, respectively. The AUC value for test data of the Canada lynx model (0.853) was high, indicating that the model successfully discriminated presence from background locations. The AUC value for test data was marginally lower for bobcat (0.805), which is consistent with that expected for a generalist species [39]. Based on jackknife estimates, maximum temperature of the warmest month was the most influential variable for the Canada lynx model when considered alone, with snow depth and ecoregion also being highly influential. Lynx suitability demonstrates a bell curve with increasing maximum temperature, while increasing snow depth improved lynx suitability as would be expected. Lynx suitability was strongly linked to the northern forest and forested mountain ecoregions. The ecoregion variable reduced the performance the most when omitted, indicating that it has the most information not contained within the other predictor variables (see electronic supplementary material, figure S2). Minimum temperature of the coldest month, snow cover and temperature seasonality were most influential for the bobcat model, with ecoregion again reducing the performance the most, when omitted (see electronic supplementary material, figure S2). Bobcat displayed the opposite pattern, demonstrating decreasing suitability with increasing snow cover. Increasing minimum temperature improved bobcat suitability as would be expected. In comparison with lynx, bobcat displayed relatively high suitability throughout numerous ecoregions, which is expected from a more generalized species. The effect of ecoregion on both species’ models is predictable because it is a layer describing habitat type and would be most dissimilar to the climate layers. This causes it to reduce performance the most when omitted from the model.

(b) Niche similarity analysis
In agreement with our prediction, Canada lynx experienced a more pronounced change in niche overlap in the sympatric portion of their range compared with bobcat. In the non-intersect region of the Canada lynx range, the average difference between similarity of its niche with that of bobcat, after accounting for the background environment, was 0.222 ± 0.003 (mean difference ± CI; figure 2a). A difference of 0 would mean that a species is as similar to its competitor as would be expected from random use of the environment in both ranges. Instead, the positive value indicates that Canada lynx are more similar to bobcat in the non-intersect region than expected, based on random use of the environment. In the intersection region of the lynx range, lynx were less similar to bobcat than expected based on random use (−0.006 ± 0.002; figure 2b). By contrast, bobcat were more similar to lynx in both non-intersecting and intersecting portions of their range (non-intersect: 0.168 ± 0.003, intersect: 0.104 ± 0.002; figure 2c,d).

When considering the pseudo-intersection and non-intersection areas of the lynx range, the difference in similarity...
from random use of the environment was significantly larger than zero (pseudo-non-intersect: 0.200 ± 0.003, pseudo-intersect: 0.215 ± 0.003; figure 3a, b), indicating that in both of these regions, lynx are more similar to bobcat than the random expectation. The same result was shown for the pseudo-intersection of the bobcat range (pseudo-non-intersect: 0.255 ± 0.004, pseudo-intersect: 0.185 ± 0.005; figure 3c, d), where bobcat were more similar to lynx than random expectation. In summary, we find evidence of niche displacement (e.g. a reduction in niche similarity) of only lynx in the actual overlap zone with bobcat. By contrast, there is no evidence of niche displacement of bobcat in any of the comparisons.

(c) Niche breadth analysis
When comparing the non-intersect to intersect area of the range, the niche breadth for the Canada lynx was restricted, with the difference in Levin’s concentration metrics between the two regions equal to 0.108. However, this value fell inside the null distribution (p < 0.37; figure 4a). Therefore, niche breadth for lynx was only restricted as much as expected based on changes in the available background environment. The same results were evident in the pseudo-ranges for lynx, with the difference in Levin’s concentration metric being 0.067 falling inside the null distribution (p < 0.17; figure 4b).

Bobcat demonstrated a different trend. The difference in Levin’s concentration metric from the non-intersect to intersect populations of the species was near zero (−0.010), indicating that their niche breadth was not restricted. This value fell outside the null distribution (p < 0.01; figure 4c), indicating that the bobcat’s niche breadth increased more than expected based on random differences in available environment when moving into the intersect region of their range. For the pseudo-ranges, the niche breadth was also not restricted from moving into the pseudo-intersect (−0.119 difference between Levin’s concentration metrics), but this value fell within the null distribution (p < 0.06; figure 4d), indicating that this change in niche breadth was not any greater in magnitude than expected based on random differences in available environments. Therefore, in the area of sympatry, lynx niche breadth remained constant, while bobcat expanded their niche breadth, taking advantage of previously unavailable environments.

4. Discussion
Our results indicate that Canada lynx are subjected to niche displacement in areas of overlap with bobcat. Following predictions originally detailed by Brown & Wilson [6], the niche of Canada lynx was less similar to that of bobcat in the area
of sympatry. A similar shift was not observed for bobcat, but rather they increased their niche breadth in areas of overlap. These results demonstrate that in the presence of competition, species either expand unrestrictedly into environments that were previously unavailable, or shift their niche to use habitat less suited to their competitor. Given that we incorporated multiple environmental axes across the entire range of each species, our results suggest that niche displacement can manifest at large spatial scales, and that competition can alter fundamental relationships between species distribution and climatic or environmental variables.

This study substantially extends our understanding of how competition can influence the spatial relationships of species and suggests that niche displacement is a real phenomenon with demonstrable outcomes. Significantly, common limitations (presence of geographical clines or differences in environmental characteristics between sympatric and allopatric areas) that tend to hinder the interpretation of character displacement studies [7,8,11] were accounted for in our analysis. For example, Canada lynx were more similar to bobcat in the pseudo-intersect zone after accounting for expected similarity based on available habitats, indicating that lynx continue to increase in similarity with bobcat moving southward until they reach the real area of intersect, which unambiguously demonstrates niche shift in the area of sympathy.

By focusing on how competition influences changes in coarse-scaled niche metrics, our study not only extends previous character displacement work by addressing more fundamental outcomes of competition, but also highlights the importance of biotic interactions at large scales. Although the role of species interactions in influencing fine-scale patterns in species distribution or abundance is well documented and accepted, their role at larger spatial scales remains unresolved [3,40]. Previous work on this subject focused on more indirect measures of biotic interactions at large scales, such as incorporating competitor or predator distribution or abundance as covariates within models [16,40], identifying areas of overlap or high favourability in the niches of potentially competing species [41], examining differences in abiotic variables in zones of allopatry and sympatry [42], or assessing the degree of range filling in the presence of competitors [4]. Our study builds on such work by showing that the presence of a competitor can alter range-wide climatic niche space occupied by a species in zones of contact.

Our findings have implications for a variety of applied questions in ecology; perhaps most importantly, they highlight difficulties in predicting species range shifts (as a result of climate or land-use change) based solely on abiotic variables. Biotic interactions could alter future range shifts in a variety of ways. Habitat considered to be suitable in

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**Figure 3.** Similarity of Canada lynx and bobcat niche in comparison with the background environment in the pseudo-intersect and non-intersect zones. The histogram represents similarity (I stat.) for 100 random samples from the background environment of (a) Canada lynx pseudo-non-intersect area with the bobcat full-range, (b) Canada lynx pseudo-intersect area with the bobcat full-range, (c) bobcat pseudo-non-intersect area with the Canada lynx full-range and (d) bobcat pseudo-intersect area with the Canada lynx full-range. Arrows and corresponding numbers represent the similarity value of the actual species niches in the designated areas of their ranges.
the future could be limited based on pressure from competitors or predators [43,44]. Furthermore, population declines or increases owing to changing habitat suitability could be accelerated in the presence of competition and predation [45,46]. Our results also suggest a less obvious effect of biotic interactions, whereby competition alters range-wide species–environment relationships; this type of effect will also alter future range shifts and distribution patterns of species. The proper way to incorporate biotic interactions in SDMs remains an active area of study [19,47]. One approach that seems useful when dealing with the type of competitor effects we document in this study may be use of interaction currencies in models, whereby the strength of species interactions are mediated by certain environmental variables (e.g. snow cover in our system [47]). Regardless, projections of species habitat suitability models based on climatic changes should attempt to incorporate the effects of competition, or at least provide an argument for why such effects may not be important. However, the extent to which the area of suitable habitat is altered in the presence of competition is unknown, and more research is required to understand the full importance of biotic interactions for future projections, including how to estimate and incorporate the strength of competitive interactions into models [47].

The change in niche overlap observed for Canada lynx when in sympatry with bobcat is expected if they are spatially displaced or otherwise respond unfavourably to competitive pressure [6]. Unlike lynx, bobcat niche was not subjected to the same change in similarity with lynx in sympatric or allopatric areas. In fact, the slight change in similarity for bobcat probably reflected the opposite change in lynx, as bobcat niche similarity was still significantly greater than the background environment. This suggests that in our system, as predicted, niche displacement is stronger for lynx. As well, the increase in niche breadth for bobcat when in the area of sympathy implies that this species expanded the diversity of environments used in their northern range. Together with the observed lack of change in niche overlap in areas of sympathy, we infer that bobcat are not limited or displaced by the presence of lynx, and thus that the inability for lynx to exploit marginal resources in the overlap area potentially causes their displacement and niche breadth restriction [14].

Figure 4. Niche breadth restriction occurring for Canada lynx and bobcat from the non-intersect to intersect region compared with the background environment. The histogram represents the amount that niche breadth of the environment was restricted for the 100 random samples in the (a) real non-intersect to intersect region of the Canada lynx, (b) pseudo-non-intersect to intersect region of the Canada lynx, (c) real non-intersect to intersect region of the bobcat and (d) pseudo-non-intersect to intersect region of the bobcat. Arrows and corresponding numbers represent the amount the niche breadth was restricted for the actual species in the designated areas of their ranges.
type of asymmetry in displacement suggests that lynx are influenced more strongly by interactions with bobcat than vice versa [10], and supports anecdotal evidence of competitive displacement of lynx by bobcat [23]. A notable outcome of our study is that it provides a strong framework for future research: syntopic lynx and bobcat should be studied in the field to determine the extent of their spatial interactions and dietary overlap, and compared against non-sympatric populations of both species. We predict that lynx will exhibit clear evidence of niche displacement, manifest through spatial avoidance of bobcat or reduced exploitation of preferred habitat or prey.

The observed asymmetry between niche displacement in bobcat and lynx is also consistent with MacArthur’s hypothesis that southern range limits are influenced by biotic interactions and northern limits by physiological capabilities [48,49]. This hypothesis is further supported by the speculation that the southern range limit of bobcat is determined by competitive interactions with other felids [50]. However, we acknowledge that uncertainty remains regarding the extent to which inferior and superior competitors are correlated with northern and southern range limits or if other factors (e.g. degree of specialization) may be influencing the observed outcome. For example, body size also may influence a species’s competitive ability [51], and bobcat in particular are known to have highly variable body size across their range [52]. However, the role of such a factor would be better addressed by comparing two sympatric species with greater difference in total body size than the comparably sized bobcat and lynx [22].

The decline in niche similarity between lynx and bobcat when they co-occur regionally suggests that lynx are displaced into more extreme environments (e.g. lower temperatures, higher snow cover and snow depth), which is better suited to lynx presence [27]. It follows that exploitative and/or interference competition probably limits lynx survival or productivity in the warmer, low-elevation extremes of their tolerability. This notion is further supported by comparisons of the percentage contribution for the environmental variables of MaxEnt models for the sympatric and allopatric areas of the lynx range. Lynx presence in the sympatric region is more strongly influenced by snow than expected based on random use models; lynx presence in the allopatric region does not show the same pattern (see electronic supplementary material, table S2). Given the reliance of lynx on snow in areas of sympathy, it seems that snow cover could serve as a key factor mediating coexistence of these two competitors. Indeed, the fact that competitive interactions between lynx and bobcat result in niche displacement (as opposed to competitive exclusion) may be facilitated by high variability in resources (e.g. availability of sites within differing amount of snow cover [10]), particularly in topographically diverse regions, for example southern British Colombia, which is one of the primary contact zones (figure 1a). This could have important implications for lynx persistence and distribution considering the projected changes in snow cover and the northward expansion of bobcat in such areas [53]. We acknowledge that limitations in the availability of snow data (i.e. long-term averages were only available from the period 1979–2000) resulted in a temporal mismatch between the snow layer and species presence data, which may have biased our conclusions regarding the influence of snow. However, given the scale of our analysis, the fact that a large portion of presence records corresponded with the time frame of the snow data, and our use of null models to determine the importance of snow cover and depth, this mismatch should not greatly influence our conclusions. Furthermore, we acknowledge that we used the maximal ranges of both species for the period covered in the study, and that this may have further influenced our conclusions regarding the importance of snow, and measures of niche similarity and breadth.

We infer from our results that character displacement may be evident not only through morphological and developmental change, as previously demonstrated [1,54–56], but also in terms of niche displacement occurring across large-scale distributions. Such displacement suggests that competitive interactions do not simply operate on small scales but rather are evident across a range of spatial scales [3]. We also present a methodology for testing niche displacement that can be broadly applied across taxa (and requires limited data) to refine our understanding of the causes and consequences of competition. Such developments will improve our ability to answer key questions regarding the ubiquity of displacement in coarse-scale niche metrics as well as determine whether particular traits (e.g. body size and niche breadth) or taxonomic status predispose species to niche displacement; this remains a key outstanding question in competition research [10]. Furthermore, our results extend previous findings established at a smaller spatial scale [15,16,43], suggesting that biotic interactions can affect the distribution of species on the macroscale by showing how niche characteristics of species may change in zones of sympathy. We highlight that future studies should focus on the large-scale components of competition in an attempt to disentangle the precise influences on species range limits [4], as well as the subtle changes that competition can have on species–environment relationships. Ultimately, our study offers an important insight into how species respond to competitive interactions with congeners at large scales, as well as how they persist in the presence of competition.

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