Climate change threatens species directly through environmental changes and indirectly through its effects on species interactions. We need tools to predict which species are most vulnerable to these threats. Pairwise species associations and body size are simple but promising predictors of the relative impact of species introduced outside of their historical ranges. We examined the vulnerability of 30 fish species to the impacts of three centrarchid predators that are being introduced to lakes north of their historical range boundaries. Species that were negatively associated with each centrarchid in their historical range were more likely to be lost from lakes with centrarchid introductions. Total body length was most important in predicting impact for the most gape-limited predator. At the regional scale, our method identifies those species most vulnerable to introductions facilitated by climate change and can easily be applied to a range of taxa undergoing range expansions.

1. Introduction

For a variety of taxa around the globe, climate change has led to declines in fitness and abundance, local extinctions and biotic homogenization of communities [1–3]. Declines in abundance and local extinctions are not only the direct consequence of climate exceeding physiological tolerances but also the indirect consequences of climate change on species interactions [3]. Climate can indirectly harm species by precipitating declines in beneficial species (including forage or prey species, host species and pollinators), or by favouring harmful species (including competitors, predators and pathogens) [3,4]. The indirect impacts of climate change on biodiversity, through species interactions, have been more difficult to predict or observe than direct physiological impacts, despite evidence that they can be more important [4].

The rate that taxa have shifted their range boundaries in response to global warming has varied considerably; species in a given community often differ in their ability to track changing climate [5,6]. This variation can lead to novel species interactions in introduced ranges and creates no-analogue communities or novel ecosystems [7]. However, as species expand their range boundaries, they often encounter resident prey, predators and competitors that were also present in their historical range (i.e. range prior to recent climate changes). Because many interactions in a species’ introduced range are not novel (to the species but clearly are to the individuals), the relationships between species in regions where they historically occurred in sympatry can be used to predict the impacts of species introductions.

Ecological measures, including species traits and association patterns, can be used as tools to predict the indirect impacts of climate change through species interactions. The ecological niche concept has been used to examine patterns of species co-occurrence, competition and the interactions between native and introduced species [8,9].
effects of climate change, through competitive interactions, decreases with increasing niche differences [10]. Competitive interactions, however, may be less important for consumers than producers as vertical (predator–prey) interactions have been recognized as stronger biotic multipliers of the effects of climate change than lateral (competitive) interactions [11]. Ultimately, however, both niche differentiation and the strength of trophic interactions are difficult to measure quantitatively [12]. Alternatively, we suggest species associations and body size as simple measures which may be good indicators of the impacts of species introductions facilitated by climate change.

The interpretation of co-occurrence patterns and the identification of non-random species associations has been a topic of considerable interest in community ecology [13–18]. Measures of species association are easily derived from presence–absence species-site matrices. Negative associations can indicate strong ecological interactions including exclusion by competition, predation or herbivory. But, negative associations are not always the result of biotic interactions and can also indicate differing habitat requirements or the influence of historical biogeography [15]. Negative associations between native and introduced species observed during a single time period can reflect either the negative impact of invasive species on native species or vice versa (biotic resistance), and may also be indicative of impacts in both directions [19]. Changes in co-occurrence patterns have been used to demonstrate the consequences of exotic species introductions on ecological communities [20,21].

Functional traits often mediate the strength of species interactions and can be used to infer niche differences [8,12,22,23]. Body size is correlated with and thus indicative of a broad range of species traits including metabolism, reproductive rate, dispersal ability, trophic position, diet breadth and vulnerability to herbivory or predation [24,25]. Differences in body size can indicate niche differentiation and reduced competition [26,27]. The strength of species interactions can also increase with body size and with predator–prey body size ratios [28–30].

We hypothesize that, together, pairwise species associations and body size can predict the relative risk imposed on resident species by predators whose ranges are expanding with climate change. We test this prediction by examining species losses associated with the introductions of predatory species whose ranges are expanding through watersheds and by anthropogenic species introductions and have recently established in lakes outside of their historical distributions in locations previously too cold to sustain populations [6,31]. Although we use fish communities as an exemplar, our study demonstrates a simple method of predicting the potential effects of climate-induced species introductions and range expansions. Our method can be applied to a wide range of taxa in a variety of ecosystems where introduced and resident species have some history of range overlap and could be extended to consider ecologically similar or closely related congener species where associations are novel or poorly documented.

We focus on three primary predictions regarding the impact of range expansions by centrarchid predators. First, it has been suggested that range expansions by centrarchid predators will threaten thousands of populations of cyprinid prey species over the next century [32]. This prediction is based on the observation that these species rarely occur in smaller lakes where centrarchid predators are present [33]. Here, we test whether negative species associations are good predictors of vulnerability. Second, we test the importance of resident species' body size in predicting the risk associated with predator introductions. We expect that the impact of centrarchid introductions will decline with increasing resident size; smaller species should be threatened by predation. Alternatively, larger species may be threatened by increased competition for prey. Third, predation for many fishes is gape-limited and prey selection is related to handling time which increases with increasing prey length [34,35]. On average, for the three centrarchid predators, largemouth bass has the largest gape and rock bass the smallest [36] (electronic supplementary material, appendix S1). The range of prey sizes consumed by rock bass is also smaller than that of smallmouth bass or largemouth bass [37]. Therefore, we expect that the importance of body size for predicting associated community changes by these centrarchids will vary with gape limitation.

While predator–prey relationships and size-related differences in prey vulnerability are probable mechanisms controlling the impacts of predatory fish introductions, there are several reasons why we might not observe the relationships we have hypothesized above. For example, extinction debts may have accumulated if not enough time had passed for the impact of introductions to be observable [38]. Additionally, species interactions may be altered by novel environmental factors in the introduced range including temperature, habitat complexity, resource availability or interactions with other community members. Finally, the relationships between species associations or body size and the impact of introductions may hold for some but not all species. Outliers to these patterns should help to generate further testable hypotheses about the indirect effects of climate change through species interactions.

2. Material and methods

(a) Data collection

We assembled a dataset of 1551 lakes in Ontario, Canada, that had been sampled during a ‘historical’ survey period (between 1957 and 1986), and again during a ‘contemporary’ period (between 1981 and 2011; figure 1 and the electronic supplementary material, appendix S3). On average, a contemporary survey occurred 29 years after the historical survey. Historical surveys were performed during the Ontario Ministry of Natural Resources and Forestry (OMNR) Aquatic Habitat and Inventory (AHI) programme [39]. Contemporary surveys included the OMNR Broadscale Monitoring (BSM) programme [40], and other published and unpublished surveys from the OMNR and the Royal Ontario Museum databases. This dataset includes those lakes analysed in Alofs et al. [6] and an additional 34 lakes recently surveyed during the BSM programme. Surveys primarily used large- and small-mesh gillnets and trapnets and were designed to sample all fish habitat. They were mostly conducted over approximately 3–5 days between June and September. Across the two survey periods, 106 fish species were observed. Presence/absence data for each pair of species were organized into separate 2 × 2 contingency tables for each sampling period. These tables tabulated the number of lakes where species occurred with and without the other species (figure 2). We considered only the 30 species which...
were present in more than 5% of lakes in each time period in order to limit the number of cells with no data (listed in figure 3).

(b) Data analysis
Our analysis focused on the changes in resident fish community composition associated with the introductions of three centrarchid predators. The focal centrarchid species, smallmouth bass, largemouth bass and rock bass, are known to be expanding their northern range boundaries [6]. We developed statistical models predicting the impact of each centrarchid species on resident fish species in lakes within the expanded range using historical pairwise species associations.

To measure historical associations between each centrarchid and other fish species, we calculated the ϕ similarity coefficient (Pearson’s correlation coefficient for binary data) from a two-by-two contingency table as $(a_h d_h - b_h c_h) / \sqrt{(a_h + b_h)(a_h + c_h)(c_h + d_h)(b_h + d_h)}$, where the subscript h indicates data from the historical sampling period, a indicates the number of locations where both the centrarchid and ‘resident’ species were present, b indicates the number of locations where the centrarchid was present and the resident was absent, c indicates the number of locations where the centrarchid was absent and the resident was present and d indicates the number of locations where both species were absent (figure 2; [41]). The ϕ-coefficient represents pairwise associations between species.
northern redbelly dace
brook stickleback
fathead minnow
Iowa darter
blacknose shiner
bluntnose minnow
spottail shiner
pearl dace
logperch
trout−perch
common shiner
lake chub
creek chub
golden shiner
pumpkinseed
yellow perch
rock bass
cisco
brook trout
brown bullhead
largemouth bass
smallmouth bass
longnose sucker
black bullhead
lake whitefish
shorthead redhorse
white sucker
walleye
lake trout
northern pike

Figure 3. RR (±95% CIs) for resident species in order of total length (smallest to largest) with introductions of (a) smallmouth bass, (b) largemouth bass, and (c) rock bass.

without the confounding effect of species’ frequency [42]. The ϕ-coefficient ranges from negative one (mutually exclusive pattern in species occurrence) to one (absolute overlap in species occurrence). To calculate ϕ, for each species pair we only included lakes in tertiary watersheds (tertiary watersheds subdivide large river systems across Ontario; figure 1) where both species historically occurred. This ensured that our measure of pairwise species associations was not biased by including occurrence measures from locations where the species distributions did not historically overlap.

To estimate the impact of species introductions, we considered only lakes where the focal centrarchid was historically absent and the resident species was historically present (ci). We then tallied the number of lakes where the resident species was still present and those where it was no longer present where the focal centrarchid was and was not present in the contemporary period and those where it was no longer present where the focal centrarchid was historically absent and did not historically overlap.

The number of lakes where the resident species was still present (ci) was calculated RR as the probability of ‘loss’ (presence during the historical period and absence during the contemporary period) of the resident species given introduction and establishment of the focal centrarchid over the probability of loss given no establishment (figure 2). This calculation is analogous in epidemiology to the probability of disease occurrence given treatment over the probability of disease occurrence with no treatment. When RR equals one, there is no difference between treatment and control groups and the closer to one the smaller the difference between the two groups. For our study, RR > 1 (greater risk with treatment) indicates a negative association between centrarchid introductions and the resident species. To test the significance of the impact of centrarchid introductions, we calculated 95% CIs for RR. The standard error of ln(RR) was calculated as √[1/b − 1/(a + b) + 1/d − 1/(c + d)] [44]. Ninety-five per cent confidence intervals not including 1 indicated significant impacts.

A fish species could be lost between two sampling periods for a number of reasons, including: local extinctions due to competition, predation, overfishing and environmental impacts (including pollution or temperature changes) and sampling error or populations becoming small enough that they are no longer detected (false absences). The importance of these factors may vary among species (e.g. small-bodied species are unlikely to be vulnerable to overfishing as they are not targeted species). Using the RR allowed us to test for increased losses related to species introductions against those background losses related to other factors. This also allowed us to compare the effects of species introductions across species despite the fact that the sampling methods used, particularly in the historical AHI, probably undersampled smaller prey fishes [46] and therefore our results may be overly conservative for those species.

We fitted linear regressions with the estimated impact of each centrarchid species’ introduction (RR) on each of 29 resident species in the contemporary sampling period as the response variable and the historical species association (ϕ) for each introduced-resident pair as the predictor variable. We similarly fitted linear regressions of impact (RR) against resident species’ average total length (cm) in Ontario (from [47]). We also fitted multiple regressions combining ϕ and resident total length to predict RR. ϕ and total length were standardized (z-score) so
that effect sizes could be compared. Both RR and total length were natural log-transformed to meet normality assumptions and linearize relationships. As an indicator of multicollinearity, we calculated Pearson product–moment correlations between the \( \varphi \)-coefficient and resident total length.

Finally, we investigated the potential influence of environmental factors (including lake morphology and human impacts) on the relationship between centrarchid introductions and resident species losses by estimating odds ratios from logistic regressions using an information theoretic approach (electronic supplementary material, appendix S2). Comparing odds ratios with RR allowed us to examine the validity of our simple estimate against a more computation intensive approach having greater data requirements.

3. Results

Of 1551 lakes, there were 395 lakes where at least one of the three centrarchid species was introduced (here, we use the term ‘introductions’ to include both anthropogenic introductions and natural colonization and the population establishment) between the historical and contemporary period. Smallmouth bass populations were sampled from 195 lakes, largemouth bass populations from 75 lakes and rock bass from 198 lakes where they were not sampled previously. All three centrarchids were sampled from six lakes and two of the centrarchid species were sampled from 61 lakes that lacked them previously. Shorthead redhorse and northern pike were never lost when largemouth bass was introduced and RR could not be calculated for those species pairs.

Four species were significantly more likely to be lost from lakes where any of the centrarchid species were introduced: northern redbelly dace, brook stickleback, lake chub and brook trout (figure 3). For example, northern redbelly dace was more than twice as likely to be lost from lakes where smallmouth bass was introduced. Brook trout was the only top predator that was more likely to be lost in lakes where any of the centrarchids were introduced. Several prey fishes were also significantly more likely to be lost from lakes where particular predatory centrarchids were introduced including:

- common shiner and Iowa darter when smallmouth bass or largemouth bass were introduced, golden shiner, fathead minnow and pearl dace when smallmouth bass or rock bass were introduced, and creek chub when largemouth bass or rock bass were introduced.

For several species, risk was significantly lower in lakes where centrarchid species were introduced (figure 3). All of these resident species were 18 cm in total length or larger. Notably, there was a significantly lower risk of brown bullhead loss in lakes where any of the centrarchid species was introduced. Centrarchid introductions were also associated with significantly reduced risk for other centrarchids (including rock bass, smallmouth bass and pumpkinseed).

Simple linear regression showed historical species association (\( \varphi \)-coefficient calculated using one set of lakes) was a significant predictor of impact (natural log of RR calculated with contemporary data for a different set of lakes) for all three centrarchid predators (figure 4; smallmouth bass (\( r^2 = 0.54, d.f. = 27, p < 0.0001 \)), largemouth bass (\( r^2 = 0.58, d.f. = 25, p < 0.0001 \)) and rock bass (\( r^2 = 0.40, d.f. = 26, p = 0.0002 \))). In each case, the slope of the relationship between (\( \varphi \)) and impact (RR) declined as \( \varphi \) became more positive. When resident species’ total length was added to these models, \( \varphi \) always had a stronger effect (\( \beta \) estimate) on impact than total length (table 1). Total length appeared to be most important, that is it had the strongest effect relative to \( \varphi \), with rock bass introductions and least important with largemouth bass introductions (table 1). In these models, total length was only a significant predictor at the \( a = 0.05 \) level, in the case of rock bass introductions. In simple linear regressions, total length was only a significant predictor of RR for smallmouth bass and rock bass introductions (figure 5). Pearson product–moment correlations between the \( \varphi \)-coefficient and total length were relatively weak (smallmouth bass: \( r = 0.360 \), largemouth bass: \( r = 0.170 \), rock bass: \( r = 0.322 \)).

We found that the odds ratios associated with the introduction of centrarchids, derived from logistic regression models including environmental variables, were strongly correlated with RR (\( r > 0.8 \); electronic supplementary material,
appendix S2). Additionally, $\psi$ and resident total length predicted odds ratios and RR in a similar manner.

### 4. Discussion

In combination, historical species associations and body size appear to be good predictors of the vulnerability of resident species to introduced predators at a regional scale. Across Ontario lakes, we found that the introductions of smallmouth bass, largemouth bass and rock bass appear to threaten both prey (e.g. cyprinids) and predatory species (i.e. brook trout). In particular, species associations explained more than half of the variation in the impact of smallmouth bass and largemouth bass on losses of resident species. Many of the strong negative associations involved previously recognized predator–prey relationships between centrarchids and cyprinids or other small fish species [16]. Our models suggested these negative associations had a stronger effect than more positive associations (nonlinear, curved relationship, figure 4). The strong effect of negative species associations and the importance of total length, given gape limitation, suggest that the impacts which we demonstrate are more likely to be driven by consumption than competition. Similarly, recent meta-analysis examining a broad suite of taxa suggests that consumption is more important than competition in determining biotic resistance to aquatic invasions [48].

The method we applied aids in identifying the resident species most vulnerable to species introductions facilitated by climate change. Based on negative species associations, range expansions by centrarchid predators have been expected to threaten several cyprinid prey species [32]. We have shown that these predicted negative impacts are already occurring, over a roughly 30 year period, for northern redbelly dace, pearl dace and fathead minnow.

Traits often mediate species interactions and we have used body size, an easily measured and widely available trait, to predict the impact of species introductions. Smaller fishes appear to be at greater risk with predator introductions. Total length was most important in predicting the impact associated with rock bass, the most gape limited of the predators we examined. The apparent impact of centrarchid introductions on brook trout, despite its larger body size, suggests potential competitive interactions between these species. Interestingly, brook trout also appears to inhibit the establishment of smallmouth bass [49]. Total length is correlated with a range of traits in fishes, and is also a good predictor of range expansions by warm and coolwater fishes in Ontario [6]. In addition to total length, fish prey vulnerability is related to body depth and the presence of spines [35,50]. Incorporating these traits could improve our ability to predict the impacts of centrarchid introductions across species.

Biotic interactions may contribute to the variability in range shifts that have been seen among species [5]; specifically, predators may limit range shifts by their prey [51]. Alofs et al. [6] demonstrated that while several warm- and coolerwater-adapted predatory sportfishes have expanded their northern range boundaries northward tracking climate changes over a 30 year period in Ontario, the northern range boundaries of many warm and coolerwater prey fishes have instead contracted southward (indicating species losses). This suggested that range expansion by predatory fishes may be limiting range expansion by prey fishes. Our study supports this hypothesis.
by demonstrating that many prey species which are exhibiting range contractions (northern redbelly dace, golden shiner, creek chub, blacknose shiner) are more likely to be lost when a centrarchid species is introduced.

We have demonstrated correlations between climate-facilitated species introductions and local extinctions across a large geographical region, varied species life histories, and over approximately 30 years. As Cahill et al. [3] proposed, however, correlative studies are only the first step in documenting the indirect effects of climate change through species interactions. Our study suggests mechanisms that need to be explicitly tested. RRs greater than one indicate greater losses of a resident species where a centrarchid predator was introduced to lakes than in lakes were it was not. We attribute this pattern to species interactions, that is, the impact of these predatory species either on prey species or potential competitors. Alternatively, this pattern could be driven by changes over time in another factor that favours centrarchid introductions but concurrently harms resident species. For example, smallmouth bass introductions may be more likely in lakes where high fishing pressures threaten the persistence of brook trout. Increasing temperatures could favour the introduction of warm and coolwater centrarchid species while threatening the persistence of coldwater species (which include brook trout, burbot, cisco, lake chub, lake trout, lake whitefish, trout-perch and longnose sucker). However, most coldwater species exhibited RRs less than one which suggests this scenario has not occurred. Mechanisms favouring centrarchid introductions while threatening cyprinid prey species are difficult to envision—especially given fishing pressures tend to contribute to introductions of centrarchids and cyprinids as bait species in the same lakes; therefore, a positive bias should exist between these taxa if the strong negative predation effect were not realized. Many experiments have examined predator–prey relationships in fishes, particularly between centrarchids and cyprinids, under a variety of conditions [35,52–57]. Here, the RR helps to identify potential predator–prey relationships that should be further investigated in the context of species introductions and climate change. It is likely that the impact of centrarchid introductions on resident prey fishes will be both age- and size-dependent [58,59].

RRs less than one indicate fewer losses of a resident species in lakes where a centrarchid has been introduced. This pattern could be similarly attributed to species interactions, in this case facilitation, or to another factor favouring both the introduction of the centrarchid and the persistence of the resident species. For example, golden shiner is known as a nest associate of largemouth bass [60]. Golden shiner can gain reproductive advantage by spawning over the centrarchid’s nest where eggs will receive protection from predation. Accordingly, while smallmouth bass and rock bass introductions seem to increase the risk to golden shiner (RR > 1), largemouth bass introductions seem to facilitate its persistence (RR < 1). By contrast, the introduction of smallmouth bass does not seem to favour the persistence of its nest associate common shiner [60]. Increasing temperatures between the historical and contemporary sampling periods may favour both the introduction of centrarchid species and the persistence of other warm and coolwater fishes. This shared temperature effect seems a likely explanation for many of the RRs that indicate less species loss with centrarchid introductions (e.g. brown bullhead, yellow perch or other centrarchid species). Both biotic and abiotic mechanisms explaining the impacts we observed need to be explicitly tested.

RRs are a simple, yet useful tool for identifying the species potentially vulnerable to introductions or addressing questions in many other types of ecological studies. The data hungry and calculation intensive analysis of incorporating environmental data and estimating odds ratios supports the utility of RR by producing similar results (electronic supplementary material, appendix S2). As we have illustrated, RRs can provide insight across large regions, variable life histories, and in cases where a priori reasons suggest species introductions may increase the losses of resident species. These reasons may include established predator–prey relationships or negative historical species associations.

The method we demonstrate can be easily applied to examine the potential impacts of species introductions to any system where community data are available across sites and introduced and resident species share some part of their historical distributions. Our method can be applied to pairwise interactions both within and across trophic levels. Species associations and traits which mediate species interactions, including body size, should be good predictors of the threats to resident species imposed by introduced predators, herbivores, parasites and competitors. Similarly, species associations and traits should be useful for identifying species that may benefit from range expansions by hosts, mutualists or pollinators. Further, while body size is generalizable, other traits may be better suited to examine the strength of pairwise interactions in this and other systems and should be explored. For example, body depth and spine length may be important in fish predation, while corolla length may control pollination and toxicity or tolerance may influence herbivory. In addition to identifying the impacts of climate-induced range expansions, our method may also be used as a first step in evaluating the potential impacts of assisted migrations on resident community composition. Finally, the RR provides a general analytical approach that is used widely in the medical literature, but effectively ignored by ecologists—yet it may provide a valuable metric in evaluating results ranging from experimental to macroecological studies.

Data accessibility. The data reported in this paper are archived and maintained by the Ontario Ministry of Natural Resources and Forestry and the Royal Ontario Museum and are freely available upon the establishment of appropriate data-sharing agreements.

Authors’ contributions. K.M.A. and D.A.J. conceived the research and designed the methods; K.M.A. compiled the data and performed the analysis; K.M.A. wrote the first draft of the manuscript and both authors contributed substantially to revisions. Both authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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