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A continental scale trophic cascade from wolves through coyotes to foxes

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Summary

1. Top-down processes, via the direct and indirect effects of interspecific competitive killing (no consumption of the kill) or intraguild predation (consumption of the kill), can potentially influence the spatial distribution of terrestrial predators, but few studies have demonstrated the phenomenon at a continental scale.

2. For example, in North America, grey wolves *Canis lupus* are known to kill coyotes *Canis latrans*, and coyotes, in turn, may kill foxes *Vulpes* spp., but the spatial effects of these competitive interactions at large scales are unknown.

3. Here, we analyse fur return data across eight jurisdictions in North America to test whether the presence or absence of wolves has caused a continent-wide shift in coyote and red fox *Vulpes vulpes* density.

4. Our results support the existence of a continental scale cascade whereby coyotes outnumber red foxes in areas where wolves have been extirpated by humans, whereas red foxes outnumber coyotes in areas where wolves are present. However, for a distance of up to 200 km on the edge of wolf distribution, there is a transition zone where the effects of top-down control are weakened, possibly due to the rapid dispersal and reinvasion capabilities of coyotes into areas where wolves are sporadically distributed or at low densities.

5. Our results have implications for understanding how the restoration of wolf populations across North America could potentially affect co-occurring predators and prey. We conclude that large carnivores may need to occupy large continuous areas to facilitate among-carnivore cascades and that studies of small areas may not be indicative of the effects of top-down mesopredator control.

Key-words: apex predator, bottom-up, interference competition, mesopredator release, species interactions, top-down, trophic cascades

Introduction

A key process that results in the direct displacement of a competitively subordinate individual is interference competition (Palomares & Caro 1999; Linnell & Strand 2000), often manifested via the direct and indirect effects of interspecific competitive killing (no consumption of the kill) or intraguild predation (consumption of the kill) (Lourenço *et al.* 2013). Such agonistic interactions are thought to be an evolved behavioural response to broad-scale exploitation competition (Peterson 1996), because species that overlap in their use of the environment and resources are at an immediate and selective disadvantage if growth or reproduction is suppressed (Conner & Bowers 1987).

Among carnivores, interference competition may be symmetrical (both species kill each other) or asymmetrical (one species kills the other), but dominance is typically based on size (Peterson 1996; Palomares & Caro 1999). This has generated interest in determining how large carnivores shape and drive community structure (Terborgh & Estes 2010; Estes *et al.* 2011; Ritchie *et al.* 2012; Ripple *et al.* 2014). It has also led to widespread predictions that the loss of large predators will release populations of smaller predators, as depicted by the mesopredator release hypothesis (Crooks & Soulé 1999; Ritchie & Johnson 2009).

The ecological effects of mesopredator release, via predation and competition, can be dramatic and affect a wide range of faunal elements (Ripple *et al.* 2013). Yet, despite great interest in such interactions, there remains considerable debate about the relative efficacy of top-down

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control in terrestrial ecosystems because the outcomes of interactions between predators may vary with resource availability, habitat structure and the complexity of predator communities (Elmhagen & Rushton 2007; Ritchie & Johnson 2009). We propose that this debate arises because few studies have been conducted at spatial scales large enough to fully detect inverse patterns between carnivore abundances. There may also be different spatial effects of competition at the local or regional scale in comparison with the scale of the entire geographic ranges of one or more species (Conner & Bowers 1987). In order to fully understand the effects of cascading species interactions, it is therefore crucial to conduct studies at multiple spatial scales.

In North America, interference competition between grey wolves *Canis lupus*, coyotes *Canis latrans* and foxes *Vulpes* spp. has been well studied at a local (landscape) scale. For example, wolves are known to kill both coyotes (Stenlund 1955; Carbyn 1982; Merkle, Stahler & Smith 2009) and less so foxes (Stenlund 1955; Mech 1966; Peterson 1977). Coyotes, in turn, may kill foxes (Sargeant & Allen 1989; Farias *et al.* 2005; Gosselink *et al.* 2007).

At a broader (regional) scale, inverse relationships between the densities of both wolves and coyotes (Berger & Gese 2007), and coyotes and foxes (Fedriani *et al.* 2000; Levi & Wilmers 2012) are supported by numerous accounts of spatial and temporal separation. For example, in northwest Montana, coyotes maintained random separation distances from wolves and there was temporal partitioning through differential arrangements of home ranges (Arjo & Pletscher 1999). Red foxes *Vulpes vulpes* have similarly been shown to select habitats which coyotes generally avoid (Sargeant, Allen & Hastings 1987; Gosselink *et al.* 2003).

At a continental scale, as wolves were eliminated by humans from much of North America, coyotes dramatically expanded their historical range (Peterson 1996; Gompper 2002). However, little attention has been given to the broader effects of competitive interactions across large geographic areas such as those now occupied by the coyote. This is critical to understand because the effects of competition could alter the distribution of multiple predator guilds at a continental scale. Therefore, we test the hypothesis that the presence or absence of wolves has caused a continent-wide shift in coyote and red fox densities due to the cascading effects of competition. We hypothesize that the spatial effects will manifest as a gradient that strengthens or weakens, depending on the level of human influence that penetrates the ranges of wolves.

To test our hypotheses, we first review long-term time series of fur return data over a 1·3 million km^2 area from the provinces of Saskatchewan and Manitoba, in central Canada. In those two provinces, there is spatial overlap in the distribution of wolves, coyotes and red foxes in the northern forested areas. To the south, red foxes and coyotes co-occur, but very few wolves exist in the crop and rangeland areas (Musiani & Paquet 2004). Thus, using the southern edge of the main distribution of wolves as our predator divide, we test the hypothesis that the presence of wolves has caused a shift in predator guilds. In particular, we predict that in the presence of wolves, there will be relatively more fur returns for red foxes than coyotes. In the absence of wolves, we predict there will be relatively more fur returns for coyotes than red foxes. We provide spatial replication and empirical support for our results by presenting fur return data from six other jurisdictions across the continent of North America.

Materials and methods

HISTORICAL BACKGROUND TO STUDY DESIGN

Over the last two centuries, widespread predator control resulted in wolves being largely restricted to the forested portions of far northern North America. Wolves only recently (post 1995) reoccupied 15% of their historic range in the conterminous United States (Bruskotter *et al.* 2013). Thus, during the 20th and 21st century, wolves have remained present in the far north of North America, but largely absent to the south (Fig. 1).

Prior to European settlement, native red foxes (including the subspecies *Vulpes vulpes alascensis*, *V. v abeitoru*, *V. v cascadensis*, *V. v necator*, *V. v macroura*, *V. v rigalis*, and *V. v rubricosa*) were distributed throughout most of the boreal and montane portions of North America (Hersteinsson & Macdonald 1992; Kamler & Ballard 2002; Statham *et al.* 2012). Since the early 1900s, red foxes may have expanded their distribution westward after non-native red foxes, of European origin, were introduced throughout the eastern United States and lowland areas in the Pacific coast states (Kamler & Ballard 2002). However, red foxes may have also expanded their range naturally from populations in Canada, perhaps due to more suitable human-altered habitat becoming available (Statham *et al.* 2012). Additionally, red foxes expanded their distribution northward into the higher latitudes and altitudes (Hersteinsson & Macdonald 1992). Thus, red fox distribution has largely overlapped that of wolves in the far north of North America throughout the 20th and 21st century, but red foxes also occur in areas where wolves are absent to the south (Fig. 1).

Coyotes were historically mostly located in central North America (Gompper 2002; Fener *et al.* 2005). However, in the early 1900s, a wolf-free corridor through Canada allowed for coyotes to disperse from the central United States to as far north as Alaska (Peterson 1996). The near-elimination of wolves from the lower 48 conterminous United States was also followed by coyote dispersal as far east as Nova Scotia, which coyotes reached by the 1980s (Parker 1995). Thus, since the early 1900s, coyotes have been dispersing into areas occupied by wolves and red foxes in the north and north-western portions of North America. There has also been a 30-year presence of coyotes in the northeast where wolves are absent, but where red foxes are present (Fig 1). The historical expansion of coyotes into areas where wolves and/or red foxes occur therefore provides the basis of a 'natural experiment' to examine.

MAIN STUDY SITES AND DATA

We first analyse the fur returns of coyotes and red foxes in two large provinces of Canada, namely Saskatchewan (651 900 km²)

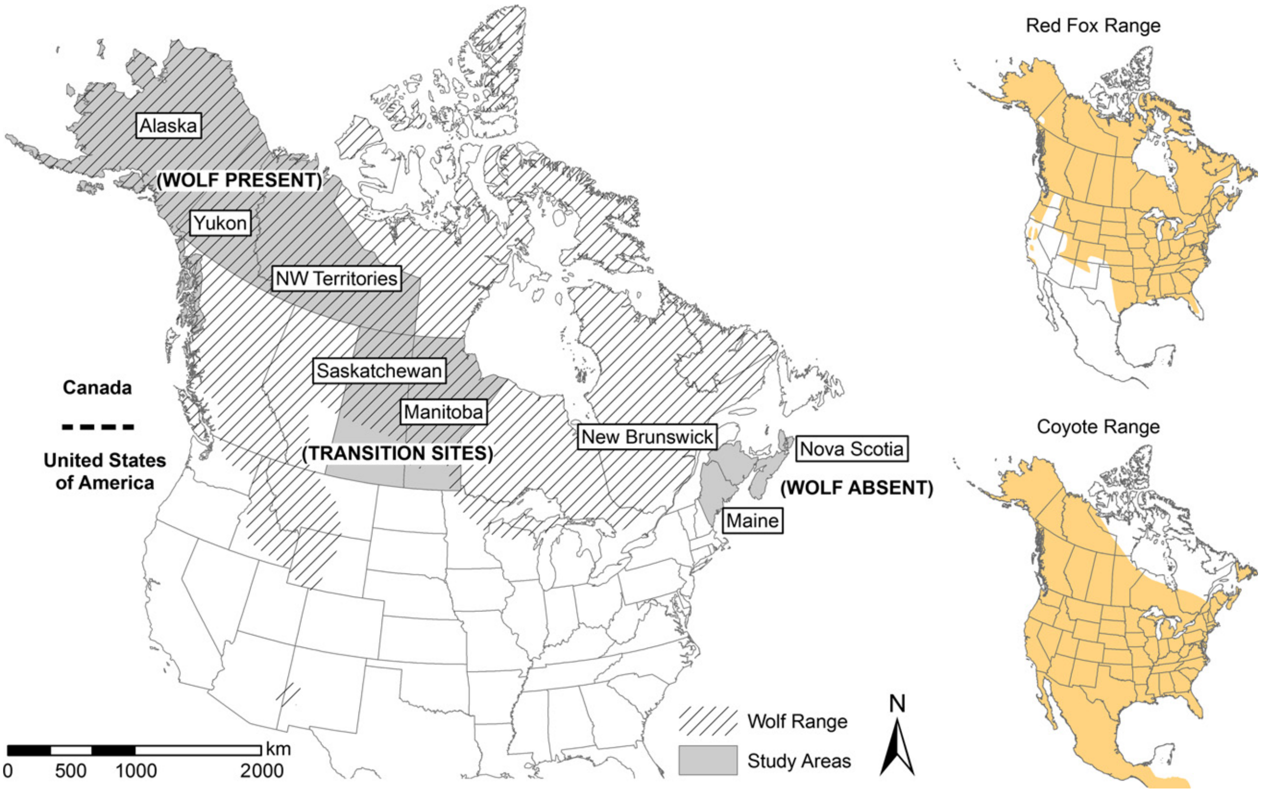

Fig. 1. Study areas in relation to the current distribution of wolves *Canis lupus*, coyotes *Canis latrans* and red foxes *Vulpes vulpes* in North America.

and Manitoba (647 797 km^2) (see Fig. 1 - 'Transition Sites'). The northern two-thirds of Saskatchewan and Manitoba are dominated by coniferous forest (>75% forest cover). The southern third is dominated by rangeland (<10% forest cover) and cropland (0% forest cover). The southern edge of the main distribution of wolves generally coincides with the boundary of the forested and open areas in both provinces (See Appendix S1 in Supporting information). Fur returns for coyotes and red foxes were collected from 136 wildlife management zones by the Government of Saskatchewan each year since 1982 (Appendix S2, Supporting information). Fur returns for coyotes and red foxes were collected from 40 wildlife management zones by the Government of Manitoba each year since 1996 (Appendix S2, Supporting information). We used these time-series data sets to test our hypotheses.

SPATIAL PATTERNS OF PREDATOR DENSITY

To broadly assess whether the presence or absence of wolves results in suppression of coyotes or red foxes, we divided the total number of coyote fur returns by the number of red fox fur returns for each wildlife management zone in Saskatchewan and Manitoba. The ratio was used because we were primarily interested in the relative abundance of coyotes and red foxes in areas with and without wolves. Thus, we assumed a ratio >1 reflects an area with relatively more coyotes than red foxes (Thurber *et al.* 1992; Peterson 1996).

For more detailed analyses, we focused on the northern predominantly forested areas where wolves were present in Saskatchewan and Manitoba (Fig. 1; Appendix S1, Supporting information). First, we calculated distance (km) from the centroid of each wildlife management zone to the closest point along the southern edge of wolf distribution. We then used a linear regression to model the relationship between coyote : fox ratios (including on the log scale) and distance from the edge of the wolf distribution using software *R* (R Development Core Team, Vienna, Austria). To test for independence (spatial correlation), we plotted the standardized residuals from the linear regression against fitted values. We also plotted the residuals versus their spatial co-ordinates (Zuur, Ieno & Walker 2009).

We then examined the spatial and temporal relationship between wolves, coyotes and red foxes across three geographic zones in Saskatchewan and Manitoba (i) the south where wolves were largely absent, (ii) a 'transition zone' (determined by the above analysis as the distance from the edge of wolf distribution where red fox fur returns started to outnumber coyote fur returns) and (iii) the north where wolves were present.

The study site in Manitoba additionally provided an opportunity to assess the relationship between wolves, coyotes and red foxes within two forested wolf-occupied wildlife management zones partially surrounded by agricultural lands on the edge of the main distribution of wolves, namely at Porcupine (1948 km^2) and Duck Mountain (3616 km^2) (see Fig. 2). To do so, we plotted yearly numbers of coyote and red fox fur returns to assess which predator consistently had more returns.

SPATIAL REPLICATION AT THE CONTINENTAL SCALE

To assess whether there is additional support for our hypotheses at a continental scale, we first plotted long-term numbers of

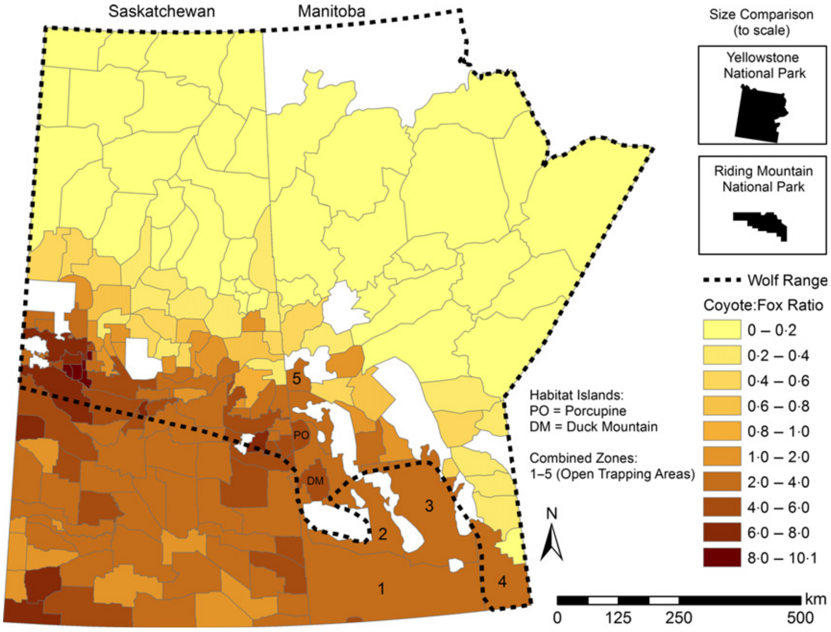

Fig. 2. The ratio of coyotes *Canis latrans* to red foxes *Vulpes vulpes* based on the total number of fur returns collected from 136 wildlife management zones by the Government of Saskatchewan from 1982 to 2011 and from 40 wildlife management zones by the Government of Manitoba from 1996 to 2010. Note that fur returns from the open trapping areas 1–5 are pooled by the Government of Manitoba.

coyote and red fox fur returns for jurisdictions in north-western North America, where coyotes and red foxes have co-occurred since the early 1900s (Hersteinsson & Macdonald 1992; Peterson 1996). We chose jurisdictions where wolves were present within the entire province or state boundary, namely the NW Territories, the Yukon and Alaska (Fig. 1). Secondly, we plotted long-term numbers of coyote and red fox fur returns for jurisdictions in north-eastern North America, where coyotes and red foxes have co-occurred since the 1980s (Fener *et al.* 2005). Here, we chose jurisdictions where wolves were absent within the entire province or state boundary, namely Nova Scotia, New Brunswick and Maine (Fig. 1) (but see also Appendix S2, Supporting information for more details on data sources).

Results

SPATIAL PATTERNS OF PREDATOR DENSITY

The spatial distribution of the coyote : fox ratio values shows that red fox fur returns outnumber coyote fur returns at sites to the north of wolf distribution in both Saskatchewan and Manitoba (Fig. 2). This is supported by the least squares regressions which showed a significant relationship between coyote : fox ratios (on the log scale) and distance to the edge of the wolf distribution in both Saskatchewan (r^2 = 0·85, $F_{1,87}$ = 506·61, P < 0·0001) and Manitoba (r^2 = 0·64, $F_{1,33}$ = 59·04, P < 0·05) (Fig. 3). There was no indication of south–north spatial correlation based on the plots of the standardized residuals against fitted values or the plots of residuals versus their spatial co-ordinates in either Saskatchewan or Manitoba (Appendix S3, Supporting information).

In Saskatchewan, the linear and nonlinear fitted lines indicates that red fox fur returns start to outnumber coyote fur returns at a distance of approximately 200 km from the edge of the wolf distribution (Fig. 3). In Manitoba, red fox fur returns start to outnumber coyote fur returns at a distance of approximately 100 km from the edge of the wolf distribution (Fig. 3). These results are supported by the plots of fur return data on a yearly basis which indicate that coyote fur returns always outnumber red fox fur returns in the absence of wolves, whereas the opposite is true north of the transitional zone distances of 200 km in Saskatchewan and 100 km in Manitoba (Fig. 4). This apparent shift occurred despite greater overall numbers of fur returns for both coyotes and red foxes in the southern agricultural region compared to the northern forested region (Fig. 5). Additionally, in the habitat islands of Duck Mountain and Porcupine, which are located within 100 km of wolf range in Manitoba, coyote fur returns consistently outnumber red fox fur returns on a yearly basis, despite the presence of wolves (Fig. 6).

SPATIAL REPLICATION AT THE CONTINENTAL SCALE

In the jurisdictions where wolves were present (NW Territories, the Yukon and Alaska; Fig. 1), red fox fur returns always outnumber coyote fur returns (Fig. 7). In contrast, in the jurisdictions where wolves were absent (Nova Scotia, New Brunswick and Maine; Fig. 1) the plots from 1970 to 2010 show that red fox fur returns generally decline as coyote fur returns increase (Fig. 7). By the year 2000, coyote fur returns outnumber red fox fur returns in all three jurisdictions in the northeast (Fig. 7).

Discussion

Our analysis supports the occurrence of a continent-wide mesopredator cascade from wolves through coyotes to red foxes. Across multiple jurisdictions and spatial scales, we show that in areas where wolves are present, red fox fur returns outnumber coyote fur returns (Fig. 7). In the absence of wolves, we show that coyote fur returns

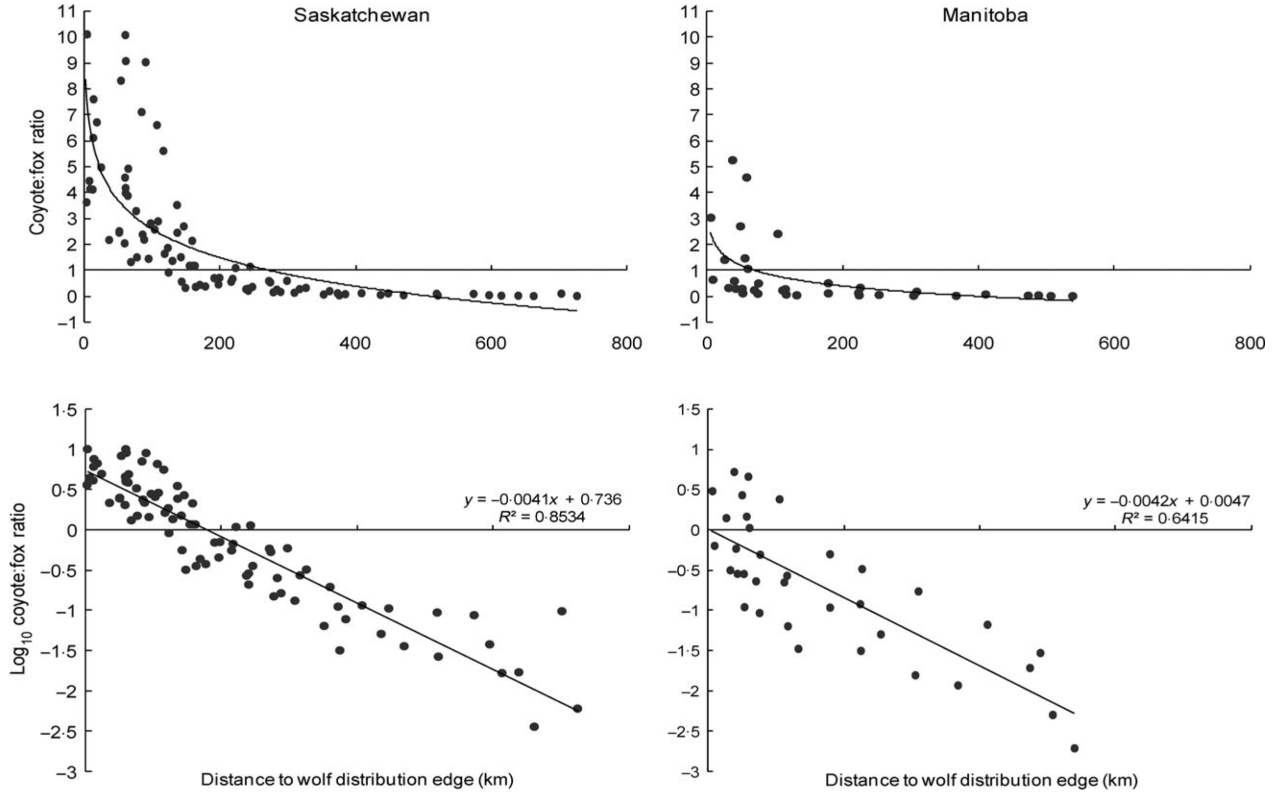

Fig. 3. The ratio of coyote *Canis latrans* to red fox *Vulpes vulpes* fur returns within wolf *Canis lupus* range in Saskatchewan and Manitoba (see Fig. 2) against the distance from the centroid of each wildlife management zone to the southern edge of wolf distribution. Data from the open trapping areas in Manitoba within wolf range (see Fig. 2) have been excluded from the analysis because fur return counts are pooled across areas with and without wolves. Three sites with no coyotes or no red foxes were also excluded from the analysis.

outnumber red fox fur returns (Fig. 7). In Saskatchewan and Manitoba, the spatial distribution of coyote and red fox fur returns was likely also influenced by the distribution of wolves (Fig. 4). However, the presence of a large transition zone on the edge of wolf distribution, where coyote fur returns outnumber red fox fur returns (Figs 2 and 3), suggest that the cascading effects of top-down control on mesopredators might only become manifest where wolves occur continuously over a large spatial area.

Although our analysis is correlative, our conclusions are based on plausible mechanisms of asymmetrical interference competition and size-based dominance among canids (Peterson 1996). For example, at a smaller spatial scale than our analyses, Levi & Wilmers (2012) showed that as wolves suppress coyote populations, foxes are released from top-down control by coyotes. A major factor potentially influencing our results is the bounty price paid for coyote and red fox fur returns. However, fur prices of coyotes and red foxes are correlated on a year-to-year basis in both Saskatchewan ($r = +0{\cdot}85$, $P < 0{\cdot}001$) and Manitoba ($r = +0{\cdot}82$, $P < 0{\cdot}05$) (Appendix S4, Supporting information). Other factors that could influence the harvest rates include (i) background fluctuations in populations, (ii) poor weather conditions for trapping and (iii) regulatory changes. However, with respect to the first two factors, these apply equally to coyotes and red foxes because of their biological similarities (McDonald *et al.* 2008; Levi & Wilmers 2012). There has also been a consistent bounty on coyotes and red foxes for the time period of our study and no regulatory changes that could have influenced their harvest rates. We are therefore confident that our ratio values reflect the relative abundance of coyotes versus red foxes in both provinces.

In any case, we provide spatial and temporal replication providing compelling support for our hypotheses. In north-western North America, where wolves are present, coyotes and red foxes have co-occurred since the early 1900s (Hersteinsson & Macdonald 1992; Peterson 1996). Whilst the northward expansion of coyotes was aided by wolf control in some areas (Peterson 1996), the fur return data suggest that coyotes never outnumbered red foxes in the northwest (Fig. 7). Indeed, in Alaska, coyotes only became common in localized areas where wolves were reduced (Peterson 1996). In north-eastern North America, where wolves are absent, coyotes and red foxes have only co-occurred since the 1980s (Fener *et al.* 2005). Despite this short time frame, the fur return data suggest that it only took coyotes 20–30 years to outnumber red foxes in the absence of wolves (Fig. 7). These trends are also independent of bounty price because coyote and red fox fur prices are generally correlated in North America dating back to the early 1900s (Appendix S4, Supporting infor-

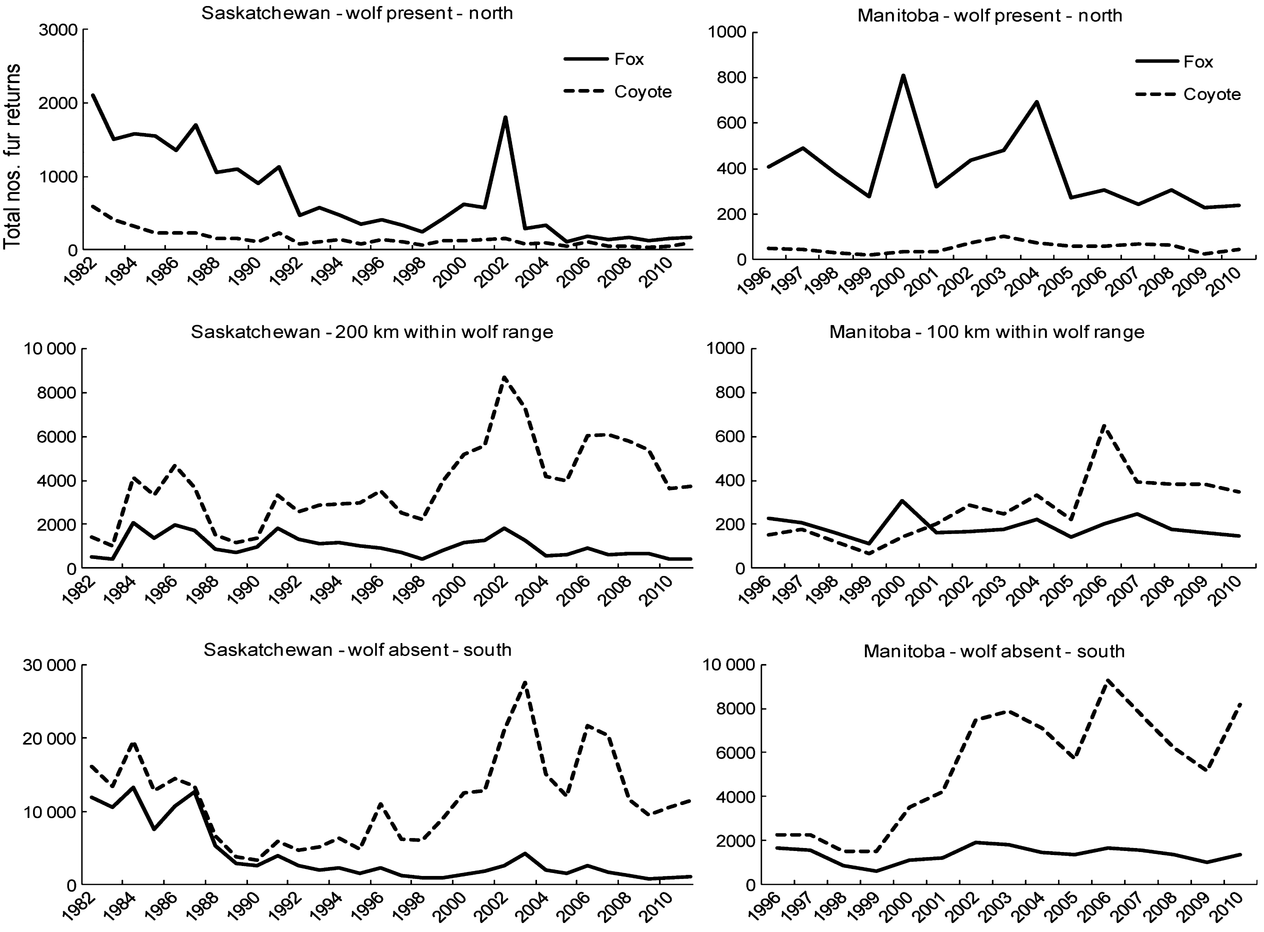

Fig. 4. Total number of coyote *Canis latrans* and red fox *Vulpes vulpes* fur returns for three comparable geographic zones in Saskatchewan and Manitoba.

mation). Additionally, our analyses does not include data from pre-20th century when all species of foxes were combined into one category, and when wolves and coyotes were also frequently misidentified (Novak *et al.* 1987) (Appendix S2, Supporting information). Nor does it include fur records from ranch (farmed) foxes, or exclude records based on whether or not they were tagged or 'sealed' (Novak *et al.* 1987) (but see Appendix S2, Supporting information for further details). Thus, we are confident that our data outside of Saskatchewan and Manitoba also reflect the relative abundance of coyotes versus red foxes.

Further support for our hypotheses is provided by comparing fur return data across three geographic regions in Saskatchewan and Manitoba (Fig. 4). In both provinces, coyote fur returns always outnumber red fox fur returns in the absence of wolves. In the presence of wolves, to the north of the transition zones, red fox fur returns always outnumber coyote fur returns (Fig. 4). The fact that red fox fur returns are lower in the north (where wolves are present) compared to the south (where wolves are absent) does not disprove our hypothesis. For example, it could be interpreted that wolves negatively affect red foxes because there are fewer red fox fur returns in the north compared to the south (Fig. 5). However, in the context of our study, it is not the direction of change in abundance that matters, it is whether or not red foxes start to outnumber coyotes as you move north into wolf range, and this is what we demonstrate. Indeed, the scale of effect is dramatic with coyote fur returns outnumbering red fox fur returns in the south by up to 7:1 and red fox fur returns outnumbering coyote fur returns at an extreme of 517:1 in the north (Appendix S5, Supporting information).

It could also be interpreted that changes in land use and habitat influence the northward expansion of coyotes. For example, it could be argued that red foxes are more suited to the northern forested areas than coyotes. However, our spatial scale analysis predominantly considers forested habitat within wolf range, and there is no change in land use or habitat at the point where red fox fur returns start to outnumber coyote fur returns in Saskatchewan and Manitoba (Appendix S1, Supporting information). Indeed, the change from predominantly coniferous forest to a transitional and tundra forest is well over 500 km from the edge of wolf distribution (Appendix S1, Supporting information). Thus, there is insufficient evidence to suggest that the northward expansion of coyotes

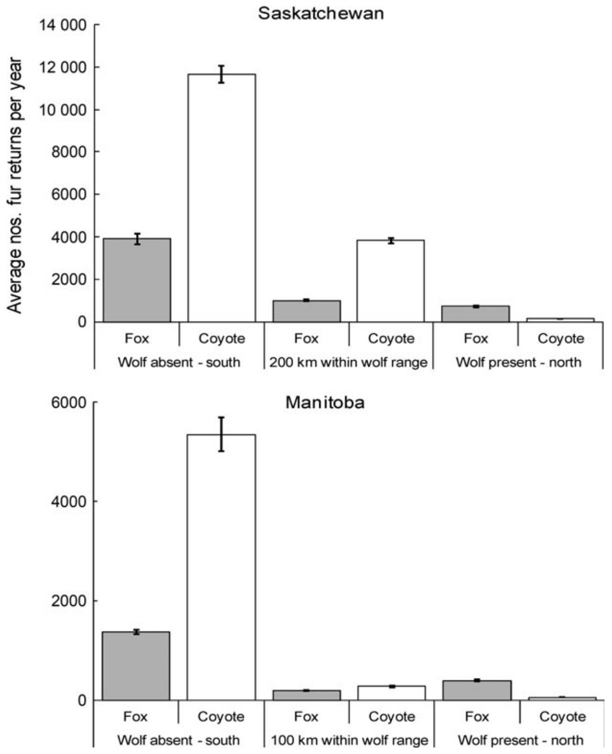

Fig. 5. Average number of coyote *Canis latrans* and red fox *Vulpes vulpes* fur returns for three comparable geographic zones in Saskatchewan (1982–2011) and Manitoba (1996–2010) (±95% confidence intervals).

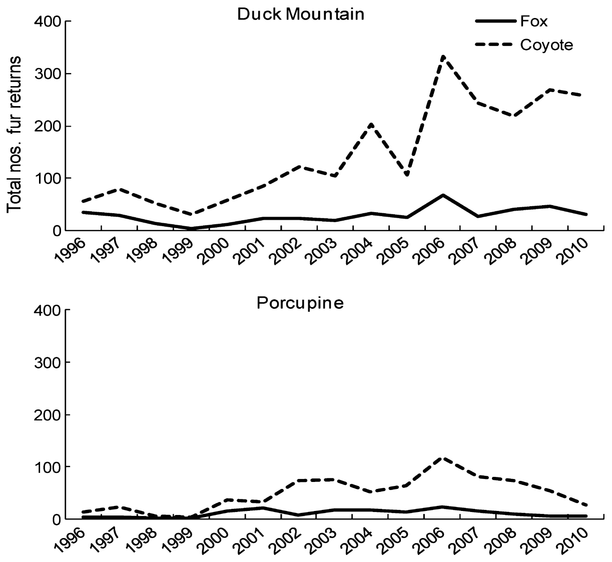

Fig. 6. Total number of coyote *Canis latrans* and red fox *Vulpes vulpes* fur returns in two forested wildlife management zones surrounded by cleared land and on the edge of wolf *Canis lupus* distribution in Manitoba (see Fig. 2 for locations).

is limited by changes in land use and habitat. This reflects the fact that coyotes and red foxes have similar habitat requirements (McDonald *et al.* 2008; Levi & Wilmers 2012). Our results therefore accord with those of Levi & Wilmers (2012) who demonstrated that bottom-up factors, land-use changes and habitat differences are insufficient to explain the pattern of spatial relationships between wolves, coyotes and foxes.

The discovery of the transition zones in Saskatchewan and Manitoba and the large scale of our analysis distinguishes our study from others. In particular, we quantified the extent to which top-down mesopredator control occurs on the edge of wolf distribution. This has implications for understanding how competitive interactions influence the spatial distribution and density of predators. For example, coexistence between wolves and coyotes may be facilitated where wolves leave carcases of large prey for coyotes to scavenge (Paquet 1992). Thus, the distribution of wolves and coyotes throughout North America could be related to the distribution, abundance and diversity of prey species, in conjunction with wolf prey selection (Paquet 1992). However, the strong negative linear relationship between the coyote : fox ratios and distance to the southern edge of wolf distribution is more suggestive of a 'ramp' effect due to very low densities of wolves on the periphery of their distribution (Caughley *et al.* 1988).

A ramp effect could occur if an attribute such as density is low at the periphery but rises progressively towards the core of distribution (Caughley *et al.* 1988). The possibility of a ramp effect in our study is strengthened by the observation that the ramp extends for 200 km in Saskatchewan but only 100 km in Manitoba, where the presence of physical barriers (lakes) produces a steeper ramp, or 'step' effect (Caughley *et al.* 1988). For example, should density step at the range boundary, the factor controlling the position of the boundary is likely to be a substrate or physical barrier (Caughley *et al.* 1988). Thus, if wolf density progressively declines towards the edge of their distribution, the strength of top-down control may also progressively decline towards the edge of wolf distribution, as indicated by the strong negative linear relationship between the coyote : fox ratios and distance to the southern edge of wolf distribution in our study (Fig. 3).

An additional factor to consider is the rapid dispersal and reinvasion capabilities of coyotes. For example, densities of coyotes may vary spatially and temporally in accordance with wolf abundance (Berger & Gese 2007), but they also may relate to coyote movements. In a insular example, lack of dispersal from adjacent areas may facilitate complete exclusion of competitively subordinate individuals, such as when coyotes were eliminated from Isle Royale a decade after wolves arrived (Peterson 1996). The opposite is true where reinvasion of coyotes is possible. In fact, despite wolves being present within the small habitat islands of Porcupine and Duck Mountain in Manitoba, red fox fur returns never outnumber coyotes (Fig. 6). Coyotes were also abundant within the wolf-occupied area of the nearby Riding Mountain National Park, but the park is also relatively small in size (2976 km^2) and surrounded by agricultural lands where coyotes were common and wolves generally absent (Carbyn 1982; Paquet 1991).

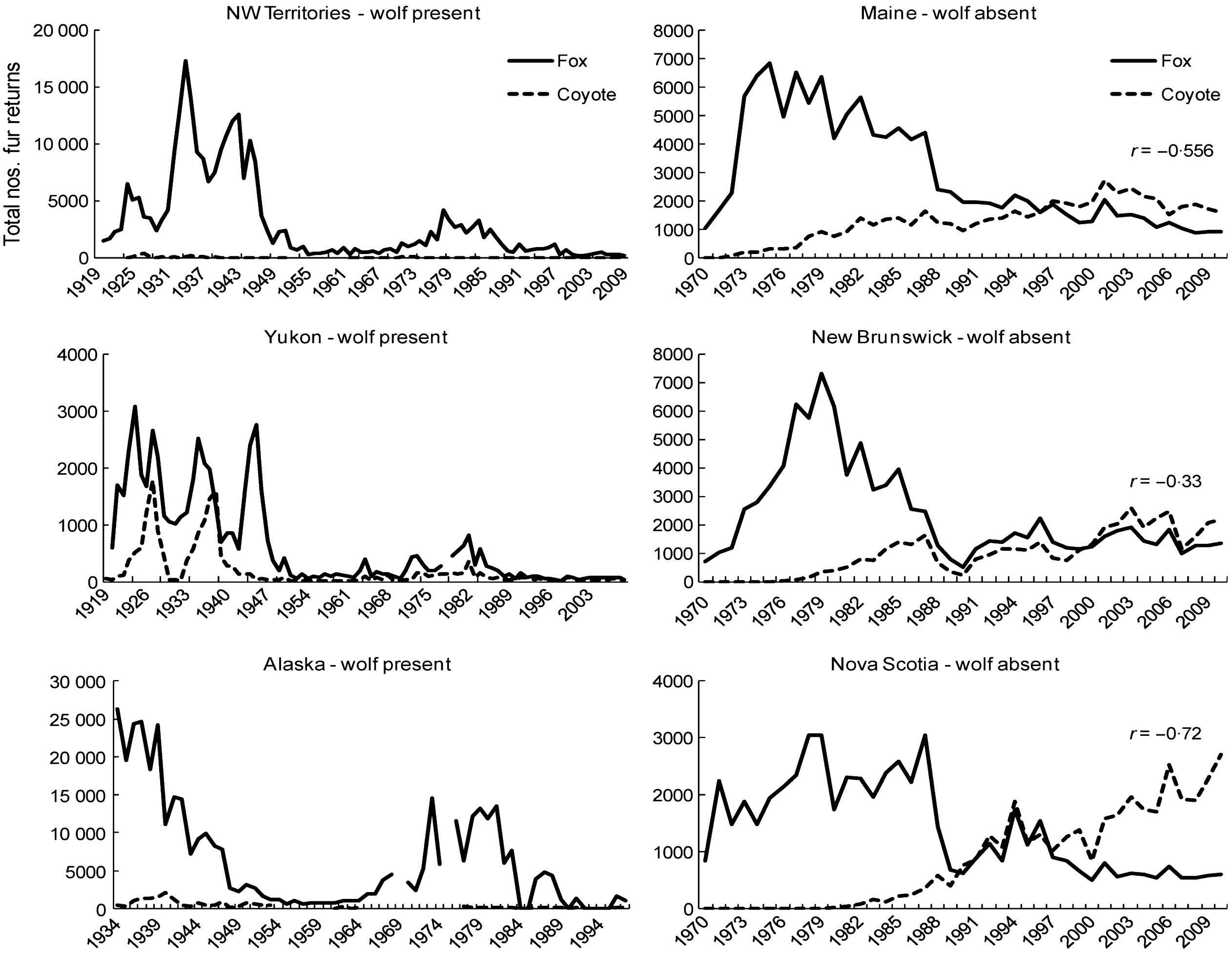

Fig. 7. Total number of coyote *Canis latrans* and red fox *Vulpes vulpes* fur returns in six jurisdictions in North America with and without wolves *Canis lupus*. Coyotes colonized the three wolf-absent areas starting in the 1970s.

Similarly, in Yellowstone National Park (8983 km^2), coyote densities declined in localized areas by up to 39% after wolf reintroduction (Berger & Gese 2007), but there was no drastic overall suppression of coyote populations in the Greater Yellowstone Ecosystem (72 519 km^2) (Berger & Gese 2007). The high dispersal capacity of coyotes potentially allows them to penetrate tens of kilometres into wolf ranges (Peterson 1996). Indeed, our data suggest that coyotes can penetrate up to 200 km within wolf range. The interactions between wolves and coyotes within Riding Mountain and Yellowstone National Park are therefore unsurprising given they are both relatively small habitat islands (Fig. 2). However, the amount of coyote dispersal into wolf range could reflect local resource conditions, especially if coyotes persist at high densities in human-altered landscapes on the edge of wolf distribution.

Our results have implications for understanding how the restoration of wolf populations in North America will affect species interaction webs. For example, coyotes were historically mostly restricted to central North America, but in less than two centuries they colonized most of the continent (Gompper 2002; Fener *et al.* 2005). As a consequence, there have been widespread predictions that in the absence of wolves coyotes will exert intense predation pressure on their typical prey (Miller *et al.* 2012; Ripple *et al.* 2013). Indeed, coyote depredation after wolf extirpation has been linked to the decline of jackrabbit *Lepus* spp., cottontail *Sylvilagus* spp. and pygmy rabbit *Brachylagus idahoensis* populations, among others (Ripple *et al.* 2013). Moreover, in the province of Nova Scotia, there has been a decline in white-tailed deer *Odocoileus virginianus*, coincident with the arrival of coyotes (unpublished data, Nova Scotia Department of Natural Resources 2013). Thus, if wolf populations expand and suppress coyotes, it is possible that a release of foxes will result in wolf- and fox-dominant prey being consumed (Levi & Wilmers 2012). The expansion of wolves may also provide positive outcomes for some lineages of montane red foxes that are potentially threatened by coyote predation (Sacks *et al.* 2010).

However, our results suggest that wolves may need to occupy large areas to facilitate an among-carnivore cascade given that the effects of top-down mesopredator control are weakened on the edge of wolf distribution for up to 200 km. No study has previously quantified the size of the 'border region' or 'transition zone' that influences the effectiveness of top-down mesopredator control. Nor has it previously been appreciated that the border region may be of this magnitude. The spatial area that wolves occupy is therefore an important factor to consider when assessing their ability to assert top-down control. For example, the apparent variation in top-down control that we found suggests that large carnivores may need to occupy large continuous areas to facilitate among-carnivore cascades and further that the spatial scale of a study can contribute significantly to variation in the results obtained. Indeed, given that wolves only occupy 15% of their former range in the United States (Bruskotter *et al.* 2013) and that much of their current range is surrounded by agricultural lands where coyotes are common, the potential for wolves to suppress coyotes may be limited.

Consideration of spatial scales also has broader implications for understanding competitive interactions between predators in other systems. For example, in Australia, the dingo *Canis dingo* is considered a top predator and potential trophic regulator that can suppress the activity or abundance of the invasive red fox and possibly also the feral cat *Felis catus* (Johnson, Isaac & Fisher 2007; Glen *et al.* 2007; Letnic & Koch 2010; Letnic *et al.* 2011). However, assessments of correlations between dingo and red fox densities typically reveal a triangular relationship whereby dingo abundance sets an upper limit on the abundance of red foxes (Johnson & VanDerWal 2009). In other words, when dingoes are abundant, red foxes are consistently rare, whereas the strength of top-down mesopredator control is weakened when dingoes are uncommon. This suggests that when control programs reduce dingo abundance, top-down suppression may be weakened (see also Wallach *et al.* 2010). Thus, where there are gradients of human influence that penetrates the size of dingo ranges over large spatial areas, similar results to those obtained in our study could be present.

Alternatively, the strength of top-down control by dingoes may be influenced by bioclimatic effects and from anthropogenic habitat change. For example, after wolves and lynx *Lynx lynx* populations declined in northern Europe, there was accelerated growth rates of red foxes in productive regions, whilst the release effect was negligible in unproductive regions (Elmhagen & Rushton 2007). But, here, we show that coyotes could feasibly disperse large distances into wolf range and that the effects of top-down control are also weakened in systems where there is a gradient of human influence that penetrates the size of wolf ranges. Thus, where there is sporadic distribution of a top predator, like the wolf in the parts of the conterminous United States (Fig. 1) and the dingo in Australia (Letnic, Ritchie & Dickman 2012), we suggest that the spatial effects of competition might be reduced. We therefore reemphasize that in order to facilitate the suppression of mesopredators, it may require establishment of top predator communities over large continuous areas where they remain at ecologically effective densities. This remains one of the greatest conservation challenges in a world where large carnivores are in significant decline because of human–wildlife conflicts (Ripple *et al.* 2014).

Data accessibility

Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.s0d20 (Newsome & Ripple 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Land cover map for Saskatchewan and Manitoba showing that there is no major change in land cover 200 km north of the wolf (*Canis lupus*) distribution edge in Saskatchewan or 100 km north of the wolf distribution edge in Manitoba. Data were sourced from the Canadian Government vegetation and land-cover-mapping project derived from the advanced very high-resolution radiometer sensor (AVHRR) (available at http://geogratis.gc.ca/geogratis/search?lang = en).

Appendix S2. Additional notes on data sources.

Appendix S3. Plots of standardized residuals obtained from the linear regression model (of coyote : fox ratios (on the log scale) and distance from the edge of wolf distribution in Saskatchewan and Manitoba) against fitted values (a) and their spatial coordinates (b). In (b), the blue circles are positive residuals, and open circles are negative residuals. In (b) for both Saskatchewan and Manitoba, there is no major indication of south–north spatial correlation because there is no spatial pattern or clustering in that direction (e.g. groups of positive and negative residuals close to each other) (see Zuur, Ieno & Walker 2009).

Appendix S4. Historical fur prices ($ CAD) for coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) for jurisdictions in North America relevant to the study. Data were not available for all years relevant to the study and no data were available for Maine and Alaska, but see trends for North America. Overall, coyote fur prices are consistently correlated with red fox fur prices. See Appendix S2 (Supporting information) for notes on data sources.

Appendix S5. The ratio of red fox (*Vulpes vulpes*) to coyote (*Canis latrans*) fur returns within wolf (*Canis lupus*) range in Saskatchewan and Manitoba against the distance from the centroid of each wildlife management zone to the southern edge of wolf distribution. Data from the open trapping areas in Manitoba within wolf range (see Fig. 2) have been excluded from the analysis because fur return counts are pooled across areas with and without wolves. Three sites with no coyotes or no red foxes were also excluded from the analysis. Here we show that red fox fur returns outnumber coyotes at an extreme of 517:1 at one site in Manitoba.