Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios

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Abstract

Climate change poses an immediate threat to the persistence and distribution of many species, yet our ability to forecast changes in species composition is hindered by poor understanding of the extent to which higher trophic-level interactions may buffer or exacerbate the adverse effects of warming. We incorporated species-specific consumption data from 240 wolf-killed elk carcasses from Yellowstone National Park into stochastic simulation models to link trends in the El Niño Southern Oscillation (ENSO) to food procurement by a guild of scavengers as a function of gray wolf reintroduction. We find that a shift in ENSO towards the El Niño (warming) phase of the cycle coincident with increasing global temperatures reduces carrion for scavengers, particularly those with strong seasonal patterns in resource use such as grizzly bears. Wolves alleviate these warming-induced food shortages by rendering control over this crucial resource to biotic rather than abiotic factors. Ecosystems with intact top predators are likely to exhibit stronger biotic regulation and should be more resistant to climate change than ecosystems lacking them.

Key words: Canis lupus, climate change, El Niño, ENSO, global warming, kleptoparasitism, stability, trophic, Yellowstone

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Introduction

A common approach to assessing species' responses to projected climate change is to (a) link information on ecosystem types within the current distribution of selected species to contemporary climatic regimes, (b) predict how ecosystems will shift geographically under a doubling of CO_2 and associated warming, and (c) predict how species' geographic distributions will change as a consequence of geographical shifts in ecosystems (Schmitz et al., 2003). This approach may overlook changes in species interactions that will influence community dynamics onsite because it implicitly assumes that communities are 'Clementsian' super organisms (Clements, 1916), whereby whole assemblages of species move together through space and time in

response to climate change (Schmitz et al., 2003). In contrast, mammalian communities responded to late Quaternary climate fluctuations in a Gleasonian (Gleason, 1926) manner by dispersing in divergent directions and at variable rates through time (Graham et al., 1996). Hence, elements of former Pleistocene megafuanal communities of Beringia, such as caribou (*Rangifer tarandus*) and saiga antelope (*Saiga tatarica*) persist, but are no longer sympatric (Guthrie, 2003). New analyses that take biological interactions into account are therefore needed in order to more accurately predict community-level changes in response to a rapidly warming climate (Schmitz et al., 2003).

The reintroduction of gray wolves to Yellowstone National Park (YNP) 10 years ago provides a unique opportunity to study the role of a top predator in community response to climatic warming. Apex predators, such as wolves, have the potential to influence the manner in which species at lower trophic levels respond to climate change (Post et al., 1999). In YNP, reintroduced gray wolves currently subsidize 13 species

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of scavengers (Wilmers *et al.*, 2003b) (six of which are ubiquitous) during the late fall, winter and early spring through the provisioning of carrion which in the absence of wolves had been abundant only during periods of deep snow (Gese *et al.*, 1996; Wilmers *et al.*, 2003a). Winter carrion is crucial to the survival and productivity of many of these scavenger species (Newton *et al.*, 1982; Swenson *et al.*, 1986; Blanchard, 1987; Dhindsa & Boag, 1990; Crabtree & Sheldon, 1999; Wilmers *et al.*, 2003a). Recently we reported that wolves buffer climate-related changes in the amount of carrion available to the scavenger guild in YNP as increasing temperatures are yielding shorter winters with less snow (Wilmers & Getz, 2005).

Here, using a combination of field observations, empirical data, and simulation modeling, we show how carrion availability to individual scavenger species is likely to respond with and without wolves to future changes in El Niño Southern Oscillation (ENSO), the most important coupled ocean-atmosphere phenomenon contributing to global climatic variability (Wolter & Timlin, 1998), over the next 100 years.

Materials and methods

To determine how changes in ENSO will affect wolf–scavenger interactions in Yellowstone, we simulated century-long ENSO time series assuming minimum, mid-level and maximum warming scenarios as predicted in the Third Assessment Report of the Intergovermental Panel on Climate Change (IPCC) (Houghton *et al.*, 2001), and one cooling scenario (Fig. 1). These projected ENSO indices were then used as input into an empirically driven stochastic model that estimates carrion abundance by month, and species-specific consumption of carrion by year, in scenarios with and without wolves.

Simulating ENSO

The state of the ENSO is quantified monthly by the multivariate ENSO index (MEI), which is based on measures of sea-level pressure, sea surface wind and temperature, and total cloudiness fraction (Wolter & Timlin, 1998). Positive values of the index correspond to the El Niño phase of the cycle while negative values correspond to the La Niña phase. The MEI can be obtained from the climate diagnostics website (http://www.cdc.noaa.gov/people/klaus.wolter/MEI/). In order to generate predicted ENSO values for our simulations, we fit an autoregressive (AR) model with Northern Hemisphere temperature anomalies as a covariate to the monthly MEI time series. An AR (4) model was selected as the one with the smallest Akaike
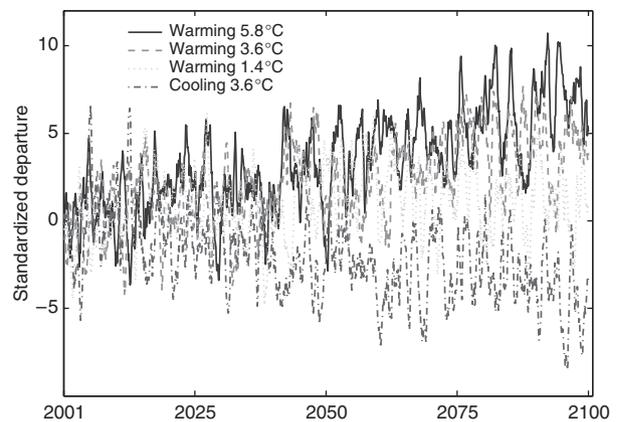

Fig. 1 Predicted El Niño Southern Oscillation (ENSO) indices based on an autoregressive model with Northern Hemisphere temperature anomalies as a covariate. These four realizations of future ENSO assume low, medium and high levels of warming based on Intergovermental Panel on Climate Change predictions as well as global cooling. Negative values of the index represent the cold La Niña phase while positive values represent the warm El Niño phase.

Information Criteria (AIC) Score (Burnham & Anderson, 2002). Projected ENSO indices were then simulated 100 years into the future using forecasted changes in Northern Hemisphere temperature anomalies as predicted in the IPCC third assessment report (Houghton *et al.*, 2001). Projected ENSO indices are stochastic with Gaussian noise generated by the error term of the fit model.

ENSO – snow depth teleconnection

In order to examine the influence of the ENSO on mean monthly snow depth, *S*, on the Northern Range of Yellowstone NP, we calculated *S* for each winter month (November–April) from both the Tower Falls and Mammoth Hot Springs weather stations for the years 1950–2000. These two meteorological stations are the only active weather stations in Yellowstone NP within the winter range of the northern Yellowstone elk herd. We then regressed snow depth at time *t* against ENSO at time *t*−1 where *t* has a monthly time step.

Stochastic simulations

We performed stochastic simulations in order to determine the effects of changes in ENSO on carrion abundance to scavengers in scenarios with and without wolves. To do so, we used the correlation between Northern Range snow depth and ENSO to generate simulated snow depths of each winter month from 2001 to 2100. Carrion abundance for each month and

year was then estimated for scenarios (a) 'without wolves' using empirical relationships established before wolf reintroduction between snow depth and carrion (Gese *et al.*, 1996, Wilmers & Getz, 2005) and (b) 'with wolves' using relationships established as wolf reintroduction between snow depth, wolves and carrion (Wilmers *et al.*, 2003a, Wilmers & Getz, 2005). Carrion abundance for the scenario without wolves, C_{wo}, is given by

$$C(t) = -14.48 + 21.04\hat{S}(t), \qquad (1)$$

and for the scenario with wolves, C_w by

$$C(t) = K(t)P(t)(1 - Q(t)), \qquad (2)$$

where K is the wolf kill rate per wolf per month, P is the wolf-pack size and Q is the percent of the edible biomass of a carcass consumed by a wolf pack where the arcsine transformation (Sokal & Rohlf, 1995) of Q is V, with

$$V(t) = 49.77 + 1.11P(t) - 0.32\hat{S}(t). \qquad (3)$$

Equation (3) is similar to that in Wilmers *et al.* (2003b) except for here we use snow depth instead of snow water equivalent. Wolf-pack sizes were assumed to be normally distributed with mean (SD) pack size of 10.6 (5) representing the current distribution of Yellowstone wolves (Smith *et al.*, 2003). Since 1997, 2 years after the reintroduction, wolf-pack size has been flat and independent of wolf density. The proportion of carrion going to each scavenger species was estimated using previously described methods (Wilmers & Stahler, 2002, Wilmers *et al.*, 2003a) with the one modification that species-specific proportions were pooled into two time periods rather than one. We split the winter into two periods: early winter when the effects of ENSO are weak (November–February) and late winter when the effects of ENSO are strong (March–April).

We simulated four different climate change scenarios. These represented low (1.4), middle (3.6) and high (5.8) levels of global warming as projected over the next 100 years by the IPCC (Houghton *et al.*, 2001). We performed multiple runs of each stochastic ENSO scenario with and without wolves to relate the effects of increased warming or cooling on carrion abundance and allocation to scavenger species with and without wolves. We ran each scenario 100 times in Matlab 6.1, which was sufficient to achieve a high signal-to-noise ratio while also keeping processing time manageable.

Previously, we used population dynamics models to understand the effects of predator–prey dynamics on the total flow of carrion to scavengers (Wilmers & Getz, 2004) and on the buffering effects of wolves on late winter carrion supply to scavengers (Wilmers & Getz, 2005). These studies revealed two key results that are relevant to this study, namely that: (a) while the pre-

sence of wolves in Yellowstone reduces the overall availability of carrion to scavengers, this reduction is small because wolf consumption of carrion is partially offset by greater turnover in the elk population (Wilmers & Getz, 2004), and (b) the buffering effect of wolves on late winter carrion appears to be independent of population dynamics of wolves or of prey. In this study, therefore, we ignore population dynamics, presenting changes in carrion availability due to climate change, and wolf presence or absence as average changes over the 100-year period. While we realize that ignoring dynamics can be risky, we feel that including the dynamics of six scavenger species as well as wolves and elk, would add so much complexity that it would obscure any important insights that might be gleaned. We emphasize as well that results reported here are based on simulation modeling. Although this effort builds upon previous empirical and modeling research, and is data-driven, we recognize that additional data collection would provide a valuable test of the patterns we present here.

Results and discussion

As global temperatures have increased, the ENSO cycle has increasingly shifted away from the cold La Niña phase towards the warm El Niño phase of the cycle (Trenberth & Hoar, 1997). Winter precipitation in the north-western United States correlates negatively with the El Niño phase of ENSO (McCabe & Dettinger, 1999). In Yellowstone, we find that El Niño years are associated with mild winters with lower than average snow depths. La Niña years, in contrast, are associated with relatively severe winters with deep snows. Long-term weather data indicate that relations between ENSO and

Table 1 Best fit linear model of mean monthly snow depth on ENSO. $\hat{\beta}$ gives the estimate of the slope

Site	Month	$\hat{\beta}$	SE	*t*-value	*P*-value
Tower	November	0.09	0.36	0.25	0.80
	December	−0.01	0.60	−0.02	0.98
	January	−0.76	0.80	10.95	0.35
	February	−1.08	0.78	−1.39	0.17
	March	−2.69	0.87	−3.11	0.003
	April	−1.79	0.76	−2.35	0.02
Mammoth	November	−0.10	0.20	−0.51	0.61
	December	−0.35	0.37	−0.95	0.35
	January	−0.89	0.61	−1.46	0.15
	February	−0.63	0.66	−0.95	0.34
	March	−1.79	0.73	−2.44	0.01
	April	−0.65	0.30	−2.18	0.03

ENSO, El Niño Southern Oscillation.

average monthly snow depth in Yellowstone increase in strength from early winter to late winter, and that ENSO exerts a significant negative influence on March and April snow pack (see slope values, $\hat{B}$, Table 1). Our model reveals that continued warming will increase the frequency of the El Niño or warm phase of the ENSO, further reducing late winter snow pack in YNP and

causing substantial reductions in late winter carrion availability to scavengers in scenarios without wolves under all warming scenarios (Fig. 2a–c). The results indicate that the greater the projected warming – and hence, the stronger the shift in the ENSO towards El Niño conditions – the more dramatic the effect of warming on carrion reduction. An increase in the La
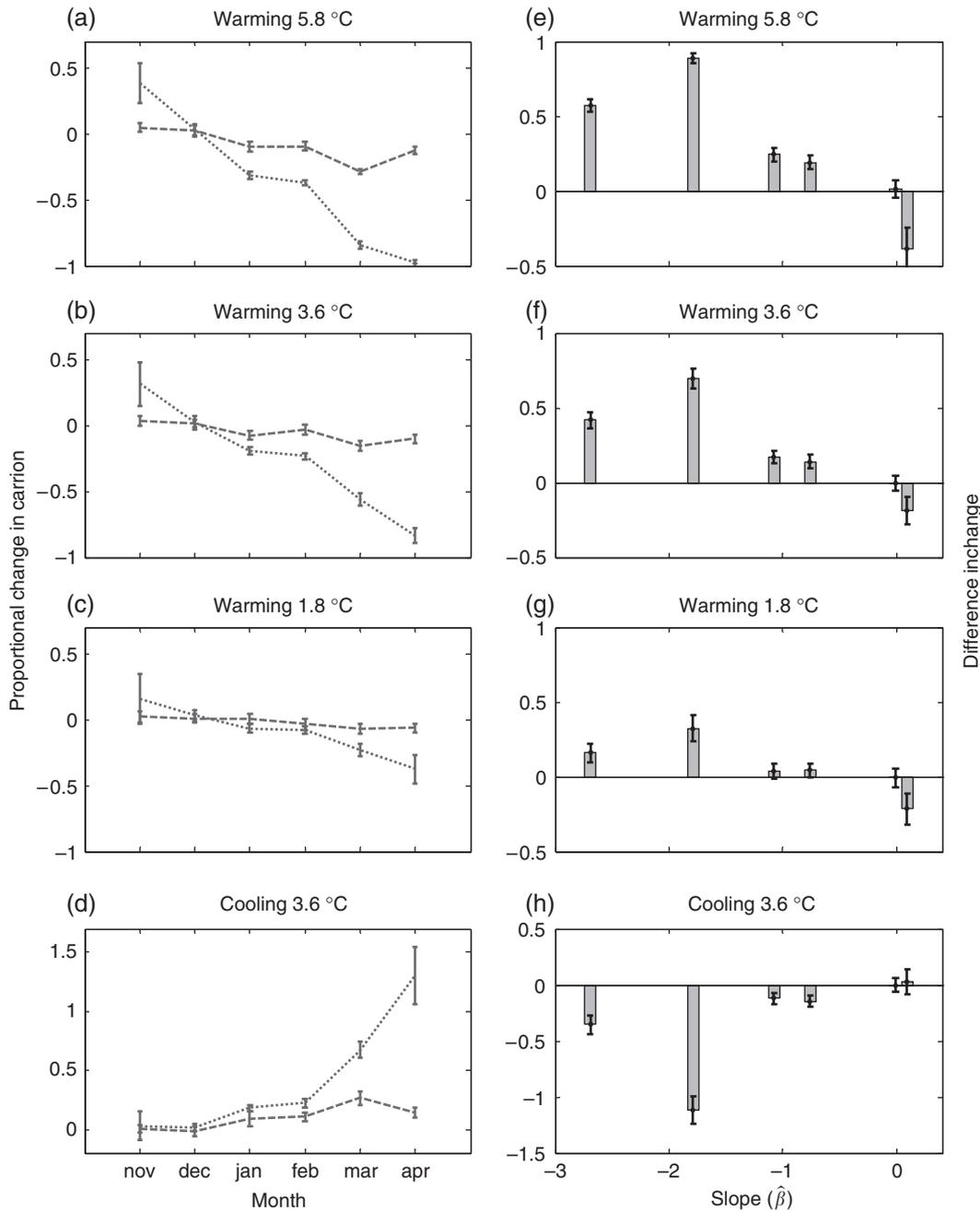

Fig. 2 (a–d) Proportional change in mean carrion abundance to scavengers (± SE) from 2000 to 2100 in scenarios with (red dashed line) and without (blue dotted line) wolves under various climate change/El Niño Southern Oscillation (ENSO) scenarios. (e)–(f) magnitude of wolf buffering of carrion to scavengers represented by plotting differences in proportional change in carrion from (a–d) against the slope of the ENSO fit on tower snow depth (see Table 1).
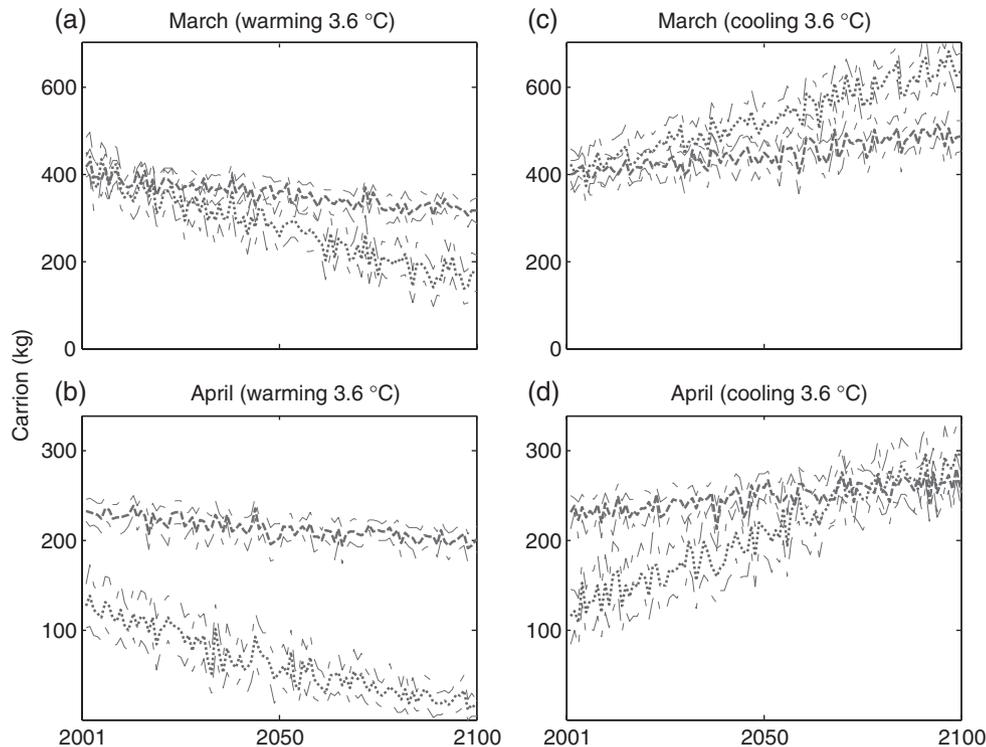
Fig. 3 Simulated average March and April carrion abundances from 2000 to 2100 in scenarios with (red-dashed line) and without (blue-dotted line) wolves assuming moderate levels of global warming (a, b) and cooling (c, d). Dotted lines represent standard errors.

Niña or cold phase of the ENSO, conversely, leads to increased snow levels and a substantial increase in late winter carrion without wolves (Fig. 2d).

The presence of wolves in both warming and cooling scenarios reduces the respective increase or decrease, in scavenge relative to scenarios without wolves (Fig. 2a–d). Climate influences on carrion availability with wolves are buffered relative to without wolves because wolf-pack size becomes the primary factor driving winter carrion availability to scavengers (Wilmers et al., 2003a). As discussed in the methods, previous simulation work revealed that, regardless of elk density, the inclusion of wolf and elk population dynamics does not alter the effects of wolf buffering on carrion availability to scavengers (Wilmers & Getz, 2005). The effects of climate change on summer precipitation, and its bottom-up effect on vegetation and elk density, is currently unknown however. Elk condition through the winter is partially mediated by summer and fall food supply; hence any effects of climate change on plant nutrition and/or fire regimes may impact the flow of winter carrion to scavengers. While we focus here on the effects of climate change on winter conditions, future work investigating the effects of global warming on summertime bottom-up and landscape level factors is needed.

Recent evidence suggests that the effect of ENSO on ecological dynamics is strengthening with increased global warming (Rodo et al., 2002). Our results indicate that the stronger the effect of ENSO on local climate variables (snow depth), the more pronounced are the effects of wolves on buffering carrion (Fig. 2e–h). Furthermore, the greater the increases in global temperatures in the future, the more important wolves become in buffering the effects of ENSO on carrion availability. In Yellowstone, the effects of warming-induced changes in ENSO on the scavenger community are strongest when carrion is regulated by abiotic factors such as winter snow fall rather than biotic factors such as wolf predation.

Wolves strongly dampen inter-annual variability in carrion availability to scavengers under climate change scenarios (Fig. 3). Under moderate scenarios of climate change, the coefficients of variation (CV) quantifying variability in carrion for the 'with-wolf' scenario in Fig. 3a–d are 0.08, 0.05, 0.08, 0.06, respectively, whereas the CV's for the 'without-wolves' scenario are 0.27, 0.54, 0.14 and 0.23. Regardless of whether the earth is warming or cooling and respective carrion levels are increasing or decreasing, wolves reduce the year-to-year variation in carrion availability. This is likely to be important to the survival and fecundity of the many
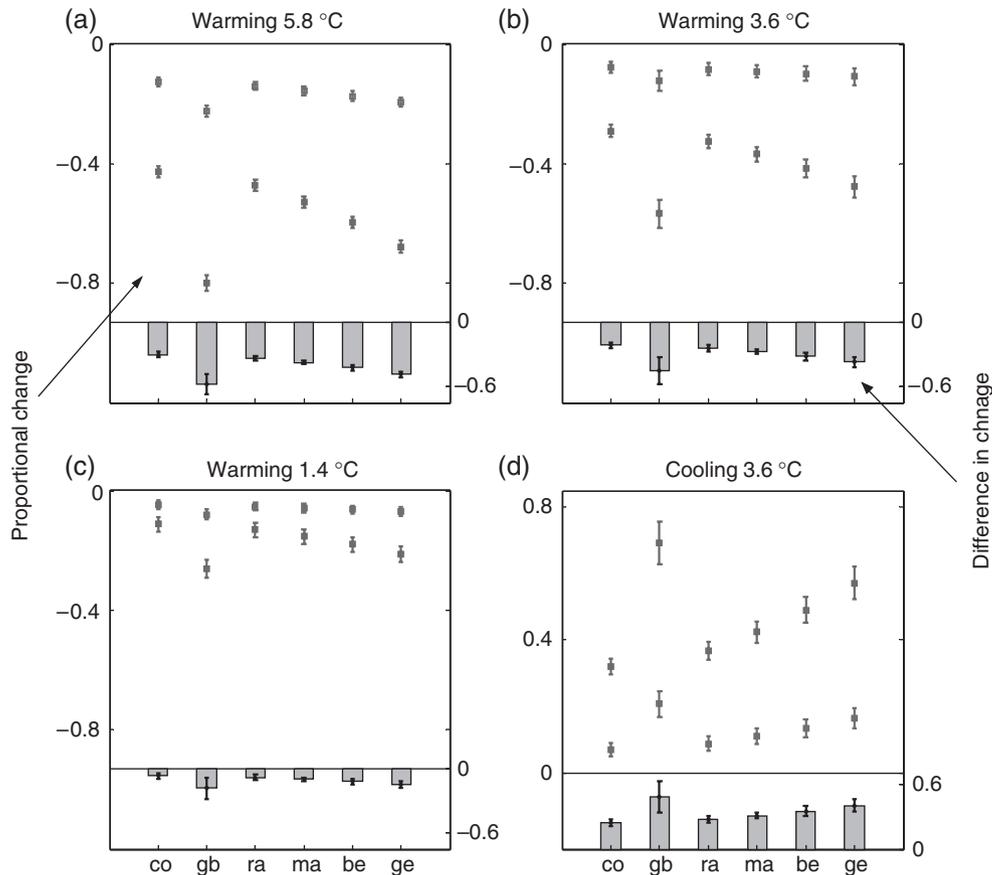
Fig. 4 Changes in carrion consumption by the six most common scavenger species under (a) maximum, (b) mid-level and (c) minimum warming and (d) moderate cooling. Top panels display proportional change in mean carrion abundance (± SE) to coyotes (co), grizzly bears (gb), ravens (ra), magpies (ma), bald eagles (be), and golden eagles (ge) from 2000 to 2100 under various climate change scenarios with (red symbol) and without (blue symbol) wolves. Bottom panels display differences in carrion availability to each scavenger species from 2000 to 2100 under scenarios with and without wolves. These illustrate the magnitude of wolf buffering against changes in El Niño Southern Oscillation.

scavenger species that depend on yearly carrion availability for over-winter survival and reproduction (Newton *et al.*, 1982, Swenson *et al.*, 1986, Blanchard, 1987, Dhindsa & Boag, 1990, Crabtree & Sheldon, 1999, Wilmers *et al.*, 2003a). While the effects of carrion on important life history parameters have been well documented elsewhere, future empirical work will focus on measuring the effects of winter carrion on the reproductive success and survival of the various scavengers in Yellowstone. Figure 3 also shows absolute changes in carrion availability to scavengers while Figs 2 and 4 show proportional changes. We use proportional changes in Figs 2 and 4 in order to directly compare both scenarios, but it should be noted that total carrion abundance in both scenarios are on similar scales, thus making comparisons of proportional changes appropriate.

The reduction in carrion because of climate change over the next 100 years will have a substantial effect on all scavenger species, particularly in scenarios without wolves (Fig. 4). In the absence of wolves, scavengers with a bias towards feeding on late winter carrion such as grizzly bears will experience the greatest losses in carrion resources, especially in comparison with species that are consistent users of carrion throughout the winter, such as coyotes and ravens. While an increase in the frequency of El Niño years leads to a larger relative decline in carrion to species with strong seasonality in resource use, an increase in the frequency of La Niña years yields the opposite pattern. Namely, grizzly bears experience a larger increase in carrion relative to coyotes and ravens as the climate cools. Regardless of the direction in which the ENSO pattern develops, the presence of wolves serves to buffer changes in the relative allocation of carrion to each scavenger species. The buffering is largest for species with the greatest expected change in carrion resources (Fig. 4, green bars). Many of the species that scavenge in the winter

become important predators during the summer. Without wolves, climate-induced reductions in carrion will lead to lower reproduction and over-winter survival by scavengers, which could have community wide spill-over effects as prey species are released from strong predation pressure.

This study shows that the reintroduction of an apex predator, the gray wolf, to Yellowstone National Park is likely to make the scavenger guild more resistant to changes in future climate. Carrion abundance, which before wolf reintroduction was determined primarily by abiotic factors (snow depth) (Gese *et al.*, 1996), is now determined primarily by biotic ones (wolves) (Wilmers *et al.*, 2003a). These results indicate, more generally, that ecosystem processes under abiotic control may be more vulnerable to climate change than those under biotic control. More biodiverse ecosystems may exhibit higher levels of biotic control, and so be more resilient to climate change than less biodiverse ones.

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