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Top-down and bottom-up control on cougar and its prey in a central Mexican natural reserve

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Abstract Top-down and bottom-up controls are hypothesized to regulate population structures in many ecosystems. However, few studies have had the opportunity to analyze both processes in the natural environment, especially on large carnivores like the cougar (*Puma concolor*). Previously, studies show that cougar diet in the Sierra Nanchititla Natural Reserve (SNNR), central Mexico, is mainly armadillo, coati, and white-tailed deer. We assess whether top-down and/or bottom-up control regulate this endangered food web: (a) we predicted that seasonal *per capita* changes in abundance (*pca*) of cougar will be positively affected by the abundance of their main prey; (b) primary productivity in SNNR will affect the *pca* of prey species, driving bottom-up control; and (c) armadillo, coati, and white-tailed deer *pca* will be affected by the abundance of cougar, generating top-down control. Using 15 camera traps for 6 years in the SNNR, we calculated a relative abundance index (RAI) and *pca* for cougar and each of the focal prey, and we used the normalized difference vegetation index (NDVI) as a proxy of primary productivity. We constructed multiple regression models and selected the best linear models based on ranking the AIC_c values. Our analysis suggests that *P. concolor pca* is best explained by bottom-up control and intraspecific feedback. White-tailed deer and armadillo *pca* were both significantly affected by cougar abundance, indicating top-down control for these prey species, but NDVI was not retained in any of the models selected for prey *pca*. Our results indicate that both bottom-up and top-down control are involved in regulating this endangered food web in the SNNR, Mexico.

Keywords Competition · Food web · Mexico · NDVI · Predator-prey · Species interactions

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Introduction

Large carnivores are critical functional components of their ecosystems, exerting both direct and indirect effects across a wide range of taxa and habitat features (Ripple et al. 2014). Top-down and bottom-up ecosystem control generate trophic cascades and regulate population structure, constituting a classic theme in ecology (Lindeman 1942; Power 1992; Hunter et al. 1997; Denno et al. 2002; Vucetich and Peterson 2004; Keeler et al. 2006). Top-down describes the control of primary resources and intermediate consumers by consumers at higher trophic levels, while bottom-up control describes how the amount and quality of resources control the dynamics of consumers on higher trophic levels (Dawes-Gromadzki 2002; Sinclair and Krebs 2002; Keeler et al. 2006). The importance of understanding what factors drive population growth through top-down and bottom-up controls is necessary for effective ecosystem management to preserve biodiversity (Sinclair and

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Krebs 2002; Elmhagen and Rushton 2007). Understanding top-down and bottom-up controls can provide useful information to control top predators, e.g., by translocating to other areas, or to conserve threatened prey species by reintroducing native species (Gasaway et al. 1992; Sinclair et al. 1998).

Some studies have reported that only top-down or bottom-up control regulates population structures (Hunter et al. 1997; Huryn 1998; Menge 2000; Walker and Jones 2001; Vucetich and Peterson 2004), but the patterns and processes of bottom-up control are less well documented (Brose 2003; Scherber et al. 2010). Large mammalian herbivores and their predators are important for studying top-down and bottom-up relationships. Some studies of insect parasitoids and other invertebrates (e.g., Dyer and Letourneau 2003; Gratton and Denno 2003; Gruner 2004) have tried to extrapolate their results to give insight into predator-prey dynamics for large mammal population regulation, which has been questioned (Bowyer et al. 2005). Some experimental studies have simultaneously manipulated productivity and predation to assess their top-down and bottom-up controls on prey assemblages in the lab (Horppila et al. 1998; Jiang and Morin 2005), but few studies have analyzed both effects in the natural environment, where it is difficult to manipulate biotic and abiotic factors (but see Mduma et al. 1999; Sinclair et al. 2003; Grange and Duncan 2006). Top-down predation by *Canis lupus*, *Puma concolor*, and *Ursus arctos* has been shown to affect ungulate density, foraging patterns, and plant species in North America (Peterson 1999; Ripple and Beschta 2008) where top-down and bottom-up forces have also been shown to act simultaneously between cougar and mule deer (*Adocoileus hemionus*) populations (Pierce et al. 2012). In the latter case, the availability of forage, which was linked to environmental effects, generated bottom-up control of the herbivore dynamics, with a slight, but time-lagged impact on the cougar population. The top-down effects of cougar limited, but did not prevent, increases in the mule deer population.

In the Sierra Nanchititla Natural Reserve (SNNR), central Mexico, 10 years of trophic niche studies have determined that the cougar (*P. concolor*) is an generalist predator, consuming 21 different mammal species, of which the armadillo (*Dasypus novemcinctus*) is the most highly predated (54% occurrence in cougar scats), followed by coati (*Nasua narica*, 16% occurrence) and white-tailed deer (*Odocoileus virginianus*, 8% occurrence), with other species contributing less than 5% (Monroy-Vilchis et al. 2009a; Gómez-Ortiz et al. 2011). Here, we assess the relative influence of top-down and bottom-up controls on these mammals in the endangered pine-oak woodland food web, based on three a priori biological hypotheses: (1) Given that the cougar is a strict carnivore, dependent on prey availability, is dominant over resources in the environment, and shows territorial behavior (Sunquist and Sunquist 2002), we predicted that the *per capita* changes in cougar abundance (*pca*) would be positively affected by

increasing relative abundance of their main prey species (interspecific interactions) and negatively by individuals of the same species (intraspecific interactions/self-regulation); (2) since focal prey species are herbivorous/insectivorous, depending on vegetation directly or indirectly (Valenzuela 1998; Aguilera-Reyes et al. 2013), we predicted that seasonal normalized difference vegetation index (NDVI), as an approximation of primary productivity in SNNR, will affect the *pca* of prey species, resulting in bottom-up control of intermediate consumers. This index has been found to provide a strong vegetation signal and is a good indicator of plant biomass (Oindo and Skidmore 2002); and (3) the *pca* of the three prey species, *D. novemcinctus*, *N. narica*, and *O. virginianus*, will be affected by the relative abundance of cougar, indicating top-down control. Our overall objective was to determine whether top-down, bottom-up, or both controls regulate this endangered pine-oak woodland food web in the SNNR, México, assessed through the strength and direction of intraspecific and interspecific feedbacks among the populations.

Materials and methods

Study site

The study was carried out in the SNNR, located in central Mexico in the Balsas River basin, at altitudes ranging from 410 to 2080 m a.s.l. (Fig. 1). The SNNR has an area of 663.93 km^2, with marked seasonality characterized by a wet season from June to October and dry season from November to May, with an average annual temperature of 14 °C. The main vegetation types are pine-oak forest, which account for 47.9% of the total area, deciduous low land forest (37.1%), grassland (8.4%), and agriculture (6.6%). This study was conducted only in the pine-oak forest, because it is an area protected by the State Government of México (Comisión Estatal de Parques Naturales y de la Fauna (CEPANAF): http://cepanaf.edomex.gob.mx/parques_turisticos) with no human disturbance. Logging and hunting of feline species and their prey have not been permitted since 1977. SNNR has 53 mammal species, which comprise 10% of Mexico's mammalian diversity (Monroy-Vilchis et al. 2011a), including 5 out of 6 feline species recorded for Mexico (*Puma concolor*, *Puma yagoaroundi*, *Panthera onca*, *Leopardus pardalis*, and *Leopardus wiedii*). Of these, cougars are of interest as one of the most abundant felines, taking advantage of existing knowledge about its trophic ecology in SNNR (Monroy-Vilchis et al. 2009a; Gómez-Ortiz et al. 2011).

Sampling design

Fifteen camera traps (Camtrakker® 35 mm and ScoutGuard Digital) using passive movement and temperature detectors
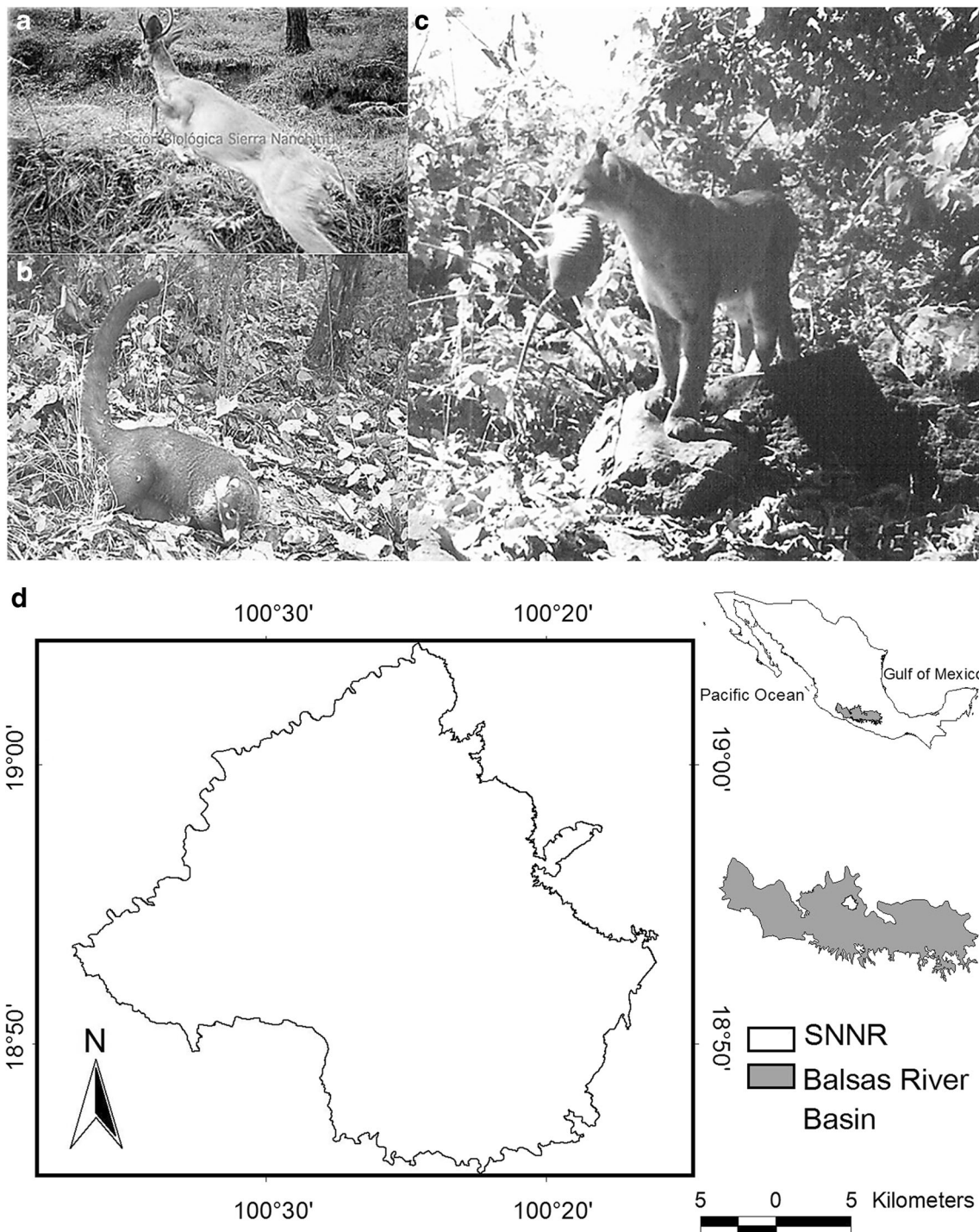
Fig. 1 Sample camera trap photographs of **a** male *O. virginianus*, **b** male *N. narica*, and **c** juvenile *P. concolor* predating a *D. novemcinctus*. Geographical location of Sierra Nanchititla Natural Reserve in the Balsas River basin (central Mexico) are shown in panel **d**

recorded data photographs from January 2004 to December 2009. Due to the rugged topography, accessibility to study sites, and the movement distances (home range) of the different species, the distance between traps was variable, with a mean of 5.5 ± 4.2 (SD) km. Each camera was attached to tree trunks at 30–40 cm off the ground. During the first year, all camera traps were placed by wide roads, but no armadillo photographs were obtained. Seven camera traps were later moved 400 m from the initial location, to trails made by wildlife and gorges near water bodies, to maximize capture probability and photograph armadillo. We were careful to have a camera trap in the home range of each species, to have a

probability greater than zero of being captured. The cameras worked continuously over 24 h, and date and time were recorded in each photograph. Cameras were checked once a month to assess their functioning and batteries.

A relative abundance index (RAI) per season (wet and dry) was calculated for cougar and each of the focal prey (*D. novemcinctus*, *N. narica*, and *O. virginianus*; Fig. 1). The RAI is defined as the number of independent photographs of each species per 100 camera trap days of sampling effort, calculated as the sum of trap days each camera was active plus the photographic records (see Monroy-Vilchis et al. 2011b; O′ Brien et al. 2003). Only the following two cases were considered in the analysis as independent photographs: (1) consecutive photographs of different individuals or species (where individuals could be distinguished by coat marks or sex, e.g., cougars and deer) and (2) consecutive photographs of the same species taken over 24 h or longer, in individuals who cannot be identified by coat marks or sex (e.g., armadillo and coati; Monroy-Vilchis et al. 2011b).

To represent the primary productivity of the SNNR, we used the seasonal average NDVI during the sampling period; these data are available from time series MODIS NDVI (MOD13Q1) 16-day composite 250-m resolution imagery of NASA's Terra satellite (ORNL DAAC 2008; http://dx.doi.org/10.3334/ORNLDAAC/1241; Willems et al. 2009). Primary production can be inferred from remotely sensed data by using NDVI, an estimate of greenness. NDVI is a measure derived by dividing the difference between near-infrared (NIR) and visible red bands (*R*) of a satellite image. It is computed by dividing the difference between the two bands by their sum:

$$NDVI = (NIR–R)/(NIR + R) \qquad (1)$$

This index takes values between − 1 and 1, where low values correspond to an absence of vegetation, and higher, positive values signify a photosynthetically more active substrate or greater primary productivity (Oindo 2002; Oindo and Skidmore 2002).

We estimated the *pca* of cougar and their main prey at each season t (wet or dry; 2004–2009), as $pca_t = \ln(RAI_{t+1} / RAI_t)$. To assess the relative influence of top-down and bottom-up controls on the populations, we constructed multiple regression models based on a priori biological hypotheses (see above). We investigated whether the changes in cougar *pca* were affected by the RAI of their main prey species (interspecific interactions) and by individuals of the same species (intraspecific interactions). Further, we tested whether seasonal NDVI affected the *pca* of prey species, driving bottom-up control, and if the *pca* of each prey was affected by cougar RAI, generating top-down control (Table S1).

The RAI of cougar and their prey was log transformed to prior to analyses. Thus, *pca* at time (season) t for each species, i, is estimated as

$$pca_{i,t} = \alpha_i + \sum_{j=1}^{n} b_{ij} \, ln\big(RAI_{j,t}\big) + NDVI_t, \qquad (2)$$

where α_i is a constant relating to changes in each species' *pca* that are independent of abundance (i.e., the intercept estimated from the linear regression of pca_i against $\ln(RAI_j)$) and b_{ij} gives the estimated *per capita* effect of species j on the *per capita* change in abundance of species i. Recent work has suggested that the type I (linear) functional response is a plausible description of between species interactions among these species (Soria-Díaz et al. in press). This general modeling framework is closely related to the Gompertz density-dependent function, which is widely used in population ecology. The specific models examined contained relevant combinations of species and environmental interactions. In the absence of further relevant information, we have assumed that emigration from and immigration into the study area are equal.

We selected the best linear models based on ranking the AIC_c (corrected for small sample size) values, calculated using the "AICcmodavg" R package (Mazerolle 2016). Plots illustrating these relationships were created using the "visreg" R package (Breheny and Burchett 2017).

Therefore, we examined *per capita* changes in abundance across seasons as a function of trophic, non-trophic, and abiotic variables, to understand how species and environmental interactions drive dynamics in the higher trophic levels of this pine-oak woodland food web, to help us determine whether top-down or bottom-up control dominate in this time and part of the ecosystem.

Results

We obtained results from 12,576 trap days during sampling, obtaining 635 independent photographs: 57.3% for *N. narica*, 19.52% *P. concolor*, 19% *O. virginianus*, and 4.2% *D. novemcinctus*. Analyses of relative abundances across multiple wet-dry seasonal cycles of these data showed that *N. narica* was the most and *D. novemcinctus* the least abundant (Table 1; Fig. S1), while the seasonal average NDVI for SNNR ranged from 0.52 to 0.76 (Table 1). A high percentage of photographs of *P. concolor*, *O. virginianus*, and *N. narica*, were associated with large roads and *D. novemcinctus* to gorges near water bodies (Table 2).

The most parsimonious statistical model of *per capita* changes in cougar abundance accounted for 80% of the variability in *P. concolor pca* (Tables 3 and S1), showing that changes in this predator's abundance across seasons (from time t to $t + 1$) were significantly affected by both intraspecific and

Table 1 Seasonal results of relative abundance index (RAI) of *P. concolor* and their prey and seasonal average normalized difference vegetation index (NDVI) for Sierra Nanchititla Natural Reserve (SNNR)

Year and season	P. concolor	D. novemcinctus	N. narica	O. virginianus	Average NDVI
2004 D	3.33		1.35	1.85	0.53
2004 W	1.22		2.45	0.48	0.76
2005 D	1.49	0.21	3.83	1.55	0.54
2005 W	1.42	0.22	3.1	0.96	0.73
2006 D	0.82	0.28	1.1	0.57	0.57
2006 W	0.95	0.28	1.67	0.91	0.76
2007 D	1.01	0.34	1.43	1.21	0.56
2007 W	2.74	0.31	3.94	3.40	0.75
2008 D	1.08	0.27	5.38	2.43	0.52
2008 W	7.32	0.49	7.32	9.76	0.75
2009 D	1.21	0.22	4.91	3.86	0.56
2009 W	2.82	0.25	5.16	4.92	0.74

W indicates wet, and D is dry season. *D. novemcinctus* data were not available for 2004 wet season due to problems with camera placement

interspecific interactions. *P. concolor* experienced significant negative intraspecific feedback (competition), while there were positive effects of white-tailed deer (*O. virginianus*), indicating bottom-up control on this component of the endangered pine-oak woodland food web (Figs. 2 and 3).

The results for the prey community were less clear; white-tailed deer and armadillo *pca* were both significantly affected by cougar abundance, indicating top-down control for these prey species (R^2 = 0.54 and 0.74, respectively; Table 3). Cougar RAI was not retained in the best model of coati *pca* (Tables 3 and S1), indicating that there is no top-down control on this prey species. The regression models showed that NDVI was not retained in any of the best models selected for prey *pca*, suggesting that there is no evidence for bottom-up control through NVDI on the lower trophic levels of this endangered pine-oak woodland food web (Fig. 3). While NDVI was retained in a model that performed similarly to the best model for coati *pca* (ΔAIC_c = 0.54; Table S1), the NDVI parameter estimate in that model did not differ significantly from 0 (− 2.28 ± 1.55 SE).

Discussion

Top-down and bottom-up controls are commonly studied through experimental manipulation of the target species (Gruner 2004; Bowyer et al. 2005; Pierce et al. 2012). Such manipulative experiments are generally carried out with small or abundant species in carefully controlled environments. Similar manipulations to test for interactions between species are not possible in large carnivores, which are secretive and wide-ranging. With 6 years of biannual sampling effort, 12,576 trap days, and eight different cougars identified (six males and two females (see Soria-Díaz et al. 2010), we find both bottom-up and top-down controls with different species

interactions in this endangered pine-oak woodland food web in the SNNR, central Mexico (Fig. 3).

Our results suggest that variation in *per capita* changes in abundance for *P. concolor* is explained by both intraspecific and bottom-up control. The RAIs of *P. concolor* and their prey (*O. virginianus*) explained over 80% of the variation in cougar *pca* in the SNNR. This result can be understood by considering that cougars show territorial behavior (Sunquist and Sunquist 2002), leading to avoidance behavior that minimizes intraspecific competition. During our study, we recorded some young transient cougar, which could move to other areas to avoid encounters with resident adults, providing a potential mechanism and example of negative intraspecific feedback. On the other hand, we did not photograph any cases where there were fights between cougars or where males killed either cubs (infanticide) or females over the study period. However, Logan and Sweanor (2001) argue that fights between cougars or infanticide are common in cougar populations, and according to our results (Table 3, Fig. 2a), we think that it may be occurring in this system. We did not detect any other factor that showed a negative effect on cougar *pca*; the sampling area is a protected zone where human activity is low, hunting of our focal species is not permitted

Table 2 Percentage of photographs obtained with camera traps by location site for the cougar and its prey of pine-oak forest, Sierra Nanchititla Natural Reserve

	Large roads (%)	Wildlife trails (%)	Gorges near water bodies (%)
P. concolor	100		
O. virginianus	100		
N. narica	75	15	10
D. novemcinctus		38	62

Table 3 Statistical models fit to seasonal time series data for the SNNR food web

Model/parameter fitted	Parameter estimates (±SE)	AIC$_c$	R^2	F-stat	p value
$pca(P) = \alpha + \ln(P) + \ln(V)$		27.96	0.80	16.13	0.002
α	0.55 ± 0.20				0.022
$\ln(P)$	-1.94 ± 0.37				< 0.001
$\ln(V)$	0.69 ± 0.27				0.035
$pca(V) = \alpha + \ln(P)$		28.45	0.54	10.69	0.010
α	0.55 ± 0.24				0.045
$\ln(P)$	-0.99 ± 0.30				0.010
$pca(C) = \alpha + \ln(C)$		23.77	0.23	2.72	0.134
α	0.55 ± 0.30				0.102
$\ln(C)$	-0.42 ± 0.26				0.134
$pca(A) = \alpha + \ln(P) + \ln(A)$		6.82	0.74	11.14	0.005
α	-0.42 ± 0.30				0.075
$\ln(P)$	-0.32 ± 0.10				0.012
$\ln(A)$	-0.45 ± 0.20				0.054

Parameter names: α = intercept, P = cougar (*P. concolor*) RAI, V = White-tailed deer (*O. virginianus*) RAI, C = coati (*N. narica*) RAI, A = armadillo (*D. novemcinctus*) RAI; *pca* is seasonal *per capita* changes in abundance. All models represent the best from the set of candidate models, selected by AIC$_c$

Fig. 2 Partial regression relationships illustrating the food web relationships between each species' *per capita* change in abundance (*pca*) and the natural logarithm of relative abundance index, ln(RAI), from the best model selected by AIC$_c$ comparison. The partial relationships are shown for **a** Cougar *pca* and RAI (intraspecific feedback, slope = -1.94 ± 0.37 SE), **b** Cougar *pca* and white-tailed deer RAI (interspecific feedback, slope = 0.69 ± 0.27), **c** white-tailed deer *pca* and cougar RAI (interspecific feedback, slope = -0.99 ± 0.30), **d** coati *pca* and RAI (intraspecific feedback, slope = -0.42 ± 0.26), **e** Armadillo *pca* and cougar RAI (interspecific feedback, slope = -0.32 ± 0.10), and **f** Armadillo *pca* and RAI (intraspecific feedback, slope = -0.45 ± 0.20). *Shaded areas* indicate 95% confidence intervals
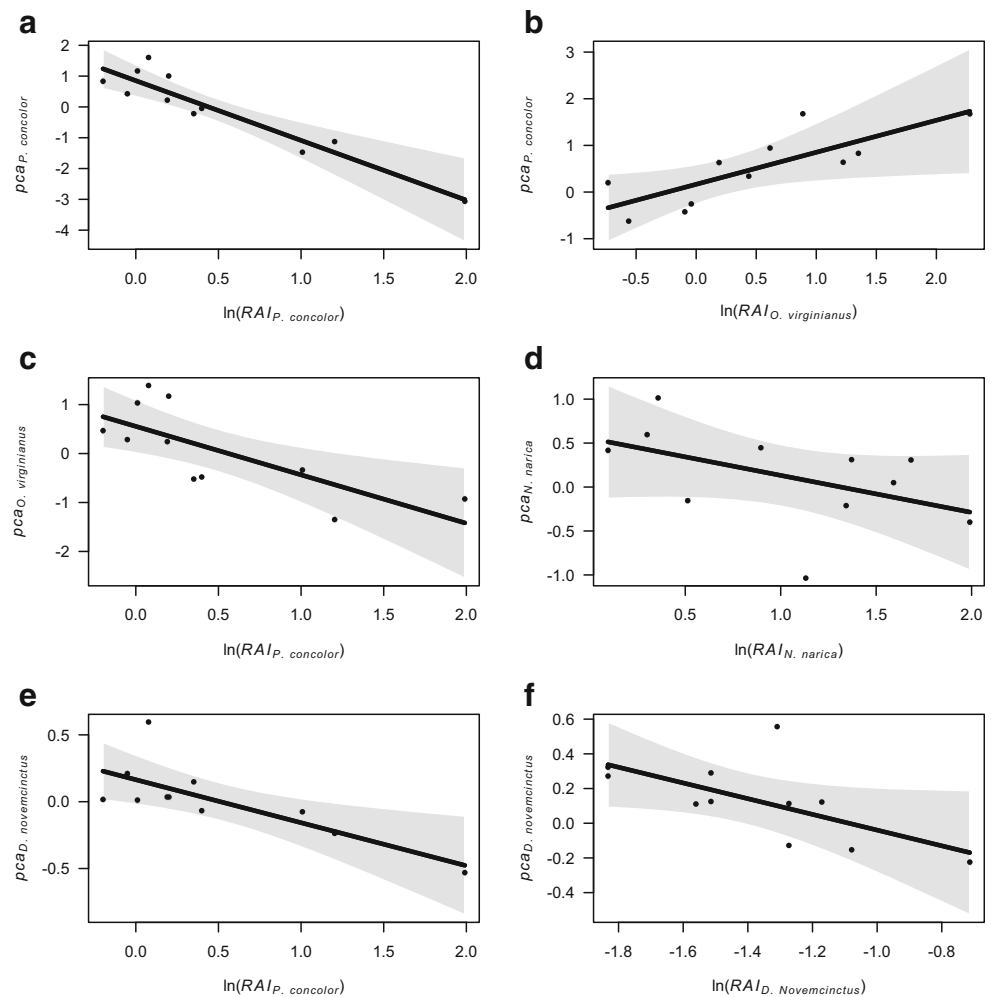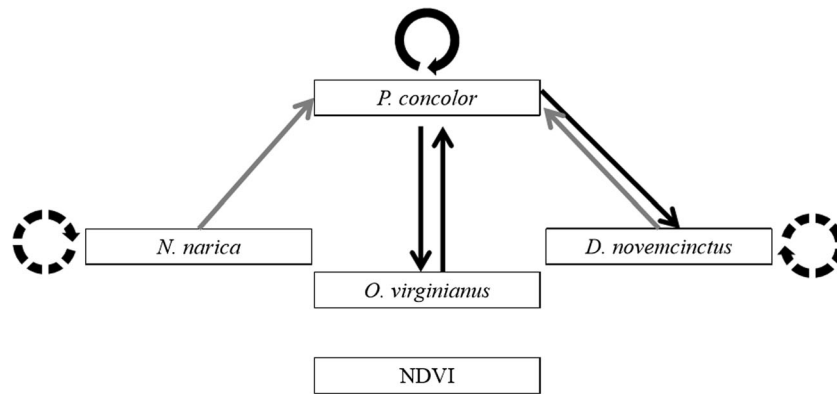
Fig. 3 A schematic illustration of the SNNR food web with *arrows* indicating the interactions among species or normalized difference vegetation index (*NDVI*). *Solid arrows* indicate statistically significant within-species or between-species interactions determined by the best fitting models (*black lines*) selected by AIC$_c$ comparison. The *double-headed arrow* indicates evidence of between-species interactions in both directions. *Solid gray arrows* indicate significant between species interactions from a similarly performing model of cougar *pca* (see Table S2). *Dashed arrows* indicate non-significant between-species interactions retained in similarly performing models of *N. narica pca* (ΔAIC$_c$ = 0.54)

(Monroy-Vilchis et al. 2011a), and no atypical changes were recorded in the climate during this study. Additionally, we also analyzed intraspecific feedback for each of the focal prey, but the best models selected by AIC$_c$ did not contain intraspecific interaction terms within prey species (Table 3; Appendix A 2–4).

White-tailed deer RAIs showed a positive effect on the cougar *pca* (Table 3; Fig. 3), supporting the assumption that cougar is an obligate carnivore (Logan and Sweanor 2001), where changes in the prey availability determine their basic demographic parameters (Gittleman et al. 2001; Bowyer et al. 2005; Gandiwa 2013). In this case, an increase in the prey abundance was associated with increases in cougar *pca* (Table 3). These results support bottom-up control of this component of the food web in SNNR (Fig. 3). Previous studies on cougar diet in our study area have shown consumption of a variety of prey, but the low value of the standardized niche breadth (*B′* = 0.203) suggests specialist habits of cougar towards a certain type of prey such as armadillo, coati, and white-tailed deer (Monroy-Vilchis et al. 2009a), which show that the cougar depends on these prey and therefore support an interpretation of bottom-up control. Another similarly performing model in this study (ΔAIC$_c$ = 1.07; see Burnham and Anderson 2002) demonstrated that coati and armadillo RAIs also significantly affected cougar *pca* (Tables S1 and S2, Fig. 2), providing further evidence supporting bottom-up control of the top predator in this system.

The NDVI was expected to be an important predictor of herbivore abundance, as higher productivity reflects extra plant resources, increasing food availability for herbivores (Oindo 2002; Oindo and Skidmore 2002). We predicted that NDVI would also be a useful predictor for the abundance of insectivorous mammals (armadillo and coati), as previous studies have indicated that the NDVI has a positive relation with the biomass, abundance, and richness of arthropods (beetles, spiders, and others; Lassau and Hochuli 2008; Sweet et al. 2015). NDVI may be an indirect indicator of

greater food availability for insectivores, and therefore, their abundances increase. However, we did not find any significant effect of primary productivity (NDVI) on the *pca* of the three prey species, although it was retained (with an estimate that did not differ from 0) in a relatively well-performing model of coati *pca* (Table S1). This result may reflect the fact that there is little variation between the NDVI of the dry and wet season (NDVI, min 0.52 and max 0.76; Table 1). The SNNR is a pine-oak forest zone, in which there is little temperature variation between the two seasons (mean 12 to 16 °C; Monroy-Vilchis et al. 2011a) and no extreme drought, so the availability of resources remains reasonably constant throughout the year and does not appear to have a strong effect on the *pca* of the prey species considered here. Other studies have argued that resource-limited conditions lead to strong bottom-up control because of reduced plant productivity in prevailing drought years (Sæther 1997; Mduma et al. 1999; Grange and Duncan 2006; Gandiwa 2013;, which may influence the next trophic level (herbivores). During wet years or those with constant primary productivity, biotic interactions become more important as the abundance of consumers increases and the forces they exert on lower trophic levels become more prominent; consumers have a greater effect on their resources, and top-down control is expected to prevail (Gandiwa 2013). It is also possible that 6 years of biannual sampling are not sufficient to detect an effect of primary productivity (NDVI) on the prey *pca* in SNNR. Other studies with over 40 years of sampling have found an effect of primary productivity on herbivore populations (Mduma et al. 1999; Vucetich and Peterson 2004; Grange and Duncan 2006). Shorter time periods (26 years) have also been sufficient to demonstrate the effects of long-term environmental change on coexistence in a bird community (Stenseth et al. 2015). Having said that, the 6-year (12 seasons) sampling period we had data available for was long enough to record strong, significant interactions between cougar and their prey (Tables 3 and S2).

The results of this study show the importance of top-down and bottom-up controls in the SNNR food web. Other studies with cougar and mule deer (*Odocoileus emionus*) in Round Valley (USA) have also found that both top-down and bottom-up controls regulate the community dynamics (Pierce et al. 2012). In Yosemite National Park in California, and in Patagonia, evidence of top-down control was found (Novaro and Walker 2005; Ripple and Beschta 2008). It is important to consider that the strength and direction of trophic control may change over time and space (Boyer et al. 2003; Meserve et al. 2003), and an important aspect is to continue to monitor the dynamics of populations during periods of extended, continuous sampling, to more accurately detect the top-down and bottom-up controls.

Another factor that could affect the prey and cougar *pca* is the jaguar (*P. onca*), also found in SNNR. However, there is little information about this felid in the study site. During sampling, only 37 independent jaguar photographs were obtained (Monroy-Vilchis et al. 2009b), and the ratio of cougar/jauguar abundance is 6:1 individuals/100 km^2 (Soria-Díaz et al. 2010). On the other hand, the jaguar is atypical in SNNR, usually inhabiting tropical and subtropical environments at lower altitudes, below 1200 m a.s.l. (Sunquist and Sunquist 2002). In the SNNR, the jaguar is found at higher altitudes (1500 to 2080 m a.s.l.) in pine-oak forest (Monroy-Vilchis et al. 2008), which is not thought to be their preferred habitat. Therefore, we believe that the jaguar has a limited effect, if any, on our analysis and interpretation.

The detectability of the species at each sampling site was different. *P. concolor*, *O. virginianus*, and *N. narica* were associated with large roads and *D. novemcinctus* with gorges near water bodies and wildlife trails (Table 1). This result was to be expected, since other studies have shown that mammals make differential use of sampling sites depending on their behavior and body size (Foster and Harmsen 2012). In addition to these results, we calculated a seasonal error rate for each species following the methodology used by Hamel et al. (2013; Fig. S2). In our case, we determined the presence/absence of each seasonal time interval across the study period (wet and dry; 2005–2009). For each species, we calculated the error rate for each of the longer season intervals as the percentage of days-sites for which a specie was classified as present based on 2005 dry (D) reference level but absent based on the longer interval. The result of this analysis showed that on average, *P. concolor* had the highest estimated error rate (28.33%), followed by *N. narica* (22.33%), *O. virginianus* (18.44%), and *D. novemncictus* (11.44%; Fig. S2). All these error rates were similar or lower than those obtained for other species by Hamel et al. (2013).

We used camera traps as a sampling tool to estimate species' RAI and determine *per capita* changes in abundance for each species. Camera traps have shown reliability in estimating abundance indices for many mammal species, if placed in suitable sampling sites (Harmsen et al. 2010; Foster and

Harmsen 2012), and their efficiency has been shown in other studies (Silveira et al. 2003; Alves and Andriolo 2005; Monroy-Vilchis et al. 2011b). We did not photograph armadillo (*D. novemcinctus*) in the first year of sampling (Table 1), as all camera traps were placed on wide roads and armadillos have since been shown not to use this type of habitat (Harmsen et al. 2010). Later, we moved camera traps to wildlife trails and gorges near water bodies and began to photograph armadillos. The mean distance between camera traps was 5.5 ± 4.2 (SD) km, varying due to the rugged topography, accessibility to study sites, and the typical movement distances of the different species. For example, we had separation distances of less than 1 km in some cases because the home range radius of the prey species is less than 1 km, e.g., white-tailed deer (Marchinton and Hirth 1984), coati (Valenzuela and Ceballos 2000), and armadillo (McBee and Baker 1982). Other camera traps had a separation distance greater than 5 km because the home range radius of the cougars is greater than 5.5 km (Núñez et al. 2002) and the cliffs and canyons in SNNR do not allow uniform distances between the sampling sites. Foster and Harmsen (2012) argue that sampling will be biased if the camera locations are only optimal for a subset of the sampled population and suggest stratified sampling design, including variables such as trail width and habitat types. With our cameras' locations in different places, we optimized the opportunity to record all species, which should help reduce any bias during sampling.

Finally, our results indicate that bottom-up control is an important influence on the seasonal variation in *P. concolor* dynamics in the SNNR and found clear evidence of top-down control of *P. concolor* on *O. virginianus* and *D. novemcinctus*. The data therefore support our first and third hypotheses: temporal changes in predator and prey abundances can be explained by considering top-down and bottom-up interactions among animals in this food web. However, a longer study or another direct or proxy variable may be necessary to detect the effect of the primary productivity on prey species and thus explain our second hypothesis. It is also important to extend the research on this topic on other areas near to the SNNR, where there is human influence, to understand the top-down and bottom-up controls in consideration with other, e.g., anthropogenic, variables.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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