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RESEARCH PAPER

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Large-scale responses of herbivore prey to canid predators and primary productivity

Mike Letnic[1] | **William J. Ripple**[2]

[1]School of Biological Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia

[2]Global Trophic Cascades Program, Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon

Correspondence
Mike Letnic, School of Biological Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, 2052, Australia.
Email: m.letnic@unsw.edu.au

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Abstract

Aim: The primacy of top-down (consumption) and bottom-up effects (primary productivity) as forces structuring ecological communities is a controversial topic. The exploitation ecosystems hypothesis (EEH) was invoked to explain biogeographical trends in plant and consumer biomass, and differs from the top-down/bottom-up dichotomy by predicting that the relative strength of these processes will vary along gradients of primary productivity. Here we test the prediction of the EEH that herbivore biomass should increase with increasing primary productivity where predators are rare, but show a negligible response to primary productivity where predators are common due to population regulation by predators.

Location: Boreal and temperate regions of North America and Eurasia, and deserts of Australia.

Time period: 1970–2016.

Major taxa studied: Cervids and kangaroos.

Methods: We obtained abundance indices of cervids at 42 locations from the literature and conducted spotlight surveys at 27 locations to derive estimates of kangaroo abundance. For analyses, herbivore abundances were converted to biomass per km^2. We tested our prediction using linear mixed effects models.

Results: Herbivore biomass showed divergent responses to increasing primary productivity and the abundance of canid predators (grey wolves, *Canis lupus*/dingoes, *Canis dingo*). The slope of the relationship between herbivore biomass and net primary productivity did not differ between Australia and the northern boreal and temperate regions. Herbivore biomass increased in response to primary productivity where canid predators were rare, but showed muted responses to increasing productivity where canid predators were common.

Main conclusions: Canid predators have strong suppressive effects on herbivore biomass that scale with primary productivity. Our study shows that the EEH has wide application to canid-predator–herbivore dynamics and may be relevant to the management of herbivores because it can provide an indication of how herbivore biomass and densities may vary in relation to ecosystem productivity and the presence and absence of canid predators.

KEYWORDS
apex predator, bottom up, large herbivore, primary productivity, top down, trophic cascade

1 | INTRODUCTION

There has long been debate over the primacy of top-down (consumption) and bottom-up effects (primary productivity) as forces structuring ecological communities (Turkington, 2009). Although often treated as mutually exclusive, top-down and bottom-up effects often operate simultaneously, and their relative importance may scale with spatial and temporal variation in primary productivity (Letnic et al., 2011). This can occur because animals and plants require nutrients and energy, and the availability of these resources may result in bottom-up limitation

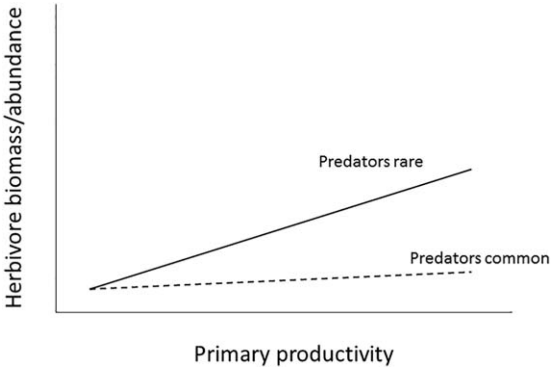

FIGURE 1 Predictions of the exploitation ecosystems hypothesis (EEH) for the relationship between herbivore biomass and primary productivity in areas where predators are common or present (solid line) and rare or absent (dashed line)

when population growth is more constrained by resource availability than by predation (Hopcraft, Olff, & Sinclair, 2010; Oksanen, Fretwell, Arruda, & Niemela, 1981; Pettorelli, Bro-Jørgensen, Durant, Blackburn, & Carbone, 2009).

The exploitation ecosystems hypothesis (EEH) was originally invoked to explain biogeographical trends in the biomass of plants and consumers in the northern boreal zone and arctic, and differs from the top-down/bottom-up dichotomy by predicting that the relative strength of these processes will vary along gradients of primary productivity (Oksanen et al., 1981 Figure 1). The EEH predicts that endothermic consumers will be absent in areas of extremely low primary productivity such as tundra, high alpine areas, steppes and deserts. As primary productivity increases, herbivore biomass is predicted to increase strongly in two-trophic-link systems where carnivores are absent or rare (Figure 1), but will show a comparatively weak response in three-trophic-link systems where carnivores are common, due to regulation of herbivores by predators (Figure 1) (Crête, 1999; Oksanen, 1992). Thus the EEH predicts that the strength of predators' effects on herbivores and herbivores' effects on plants will increase with increasing ecosystem productivity (Elmhagen, Ludwig, Rushton, Helle, & Lindén, 2010; Oksanen & Oksanen, 2000).

Previous studies have shown that the EEH is a useful predictor of biogeographical patterns in the biomasses and abundances of endothermic predators and herbivores at high and mid latitudes (Aunapuu et al., 2008; Crête, 1999; Oksanen & Oksanen, 2000; Ripple & Beschta, 2012). However, the applicability of the EEH to tropical and arid ecosystems remains largely unexplored (but see Choquenot & Forsyth, 2013). Indeed, Oksanen and Oksanen (2000) expressed concerns about the applicability of the EEH to arid environments because the dependency of herbivores on the few waterholes would make them particularly vulnerable to predators and thus limit them to even lower densities than the dearth of resources normally available in the desert would allow.

In this study we ask if the predictions made by the EEH for endothermic herbivores in relation to predation and primary productivity have application as a predictor of biogeographical patterns beyond the mid and high latitudes of the Northern Hemisphere. Our specific aim was to test predictions of the EEH for a dataset that included information on the abundance/biomass of herbivores, population status (common or present/rare or absent) of canid predators and net primary productivity (NPP) in the boreal and temperate zones of North America, Eurasia and the deserts of Australia (Figure 2).

2 | METHODS

Data on the abundance of kangaroos in Australia were collected by conducting nocturnal spotlight belt-transect surveys from a four-wheel-drive vehicle (Letnic, Koch, Gordon, Crowther, & Dickman, 2009) at 27 sites in arid regions of Australia where the mean annual rainfall was less than 300 mm (Figure 2, Table S1 in the Supporting Information). Kangaroos (*Macropus rufus*, *Macropus giganteus* and *Macropus fuliginosus*) that were sighted within a belt spanning 100 m on either side of the vehicle (total width 200 m) were counted by an observer using a 50 W spotlight while sitting on the roof of a four-wheel-drive vehicle moving at 15 km/h. The length of spotlight transects varied between sites and ranged from 10 to 60 km. Indices of kangaroo abundance at each sub-site were expressed as mean numbers of animals sighted per km^2. We converted kangaroo abundances into herbivore biomass based on the information that an average size kangaroo weighs 25 kg (Munn et al., 2009). Dingoes (*Canis dingo*) were classified as common or rare based on maps of their distribution and abundance (Letnic, Ritchie, & Dickman, 2012; West, 2008). During sampling periods when kangaroo densities were estimated we noted observations of dingoes and their tracks in order to validate our map-based classification. A histogram of dingo sightings made during spotlight surveys (Fig. S1) shows that dingoes were sighted at all of the sites where they were classified as common ($n = 13$) but were not sighted at any of the sites where they were classified as rare ($n = 14$). Dingo tracks were observed at all sites where dingoes were classified as common but only at three of the sites where they were classified as rare.

Data on the density of cervids in areas with and without wolves in North America and Eurasia (Figure 2, Table S1), were obtained from the literature. We conducted a literature search manually and using electronic databases. When selecting articles, we excluded studies of migrating cervids, non-native cervids and islands. We excluded migratory cervids because their densities are highly variable in space and time and are thus difficult to characterize for comparative purposes. We excluded islands because the size of islands can influence herbivore population density (Ariefiandy et al., 2016). We also excluded studies located in the vicinity of major human impacts such as urban areas or lands used for intensive agriculture or intensive livestock grazing. We inspected each study area with remote sensing imagery and all selected study areas that had >90% forest/grass cover. We did not exclude sites that contained forest harvesting. For comparative purposes, we normalized cervid densities to herbivore biomass densities (herbivore biomass/km^2) on the assumption that an average sized deer (*Odocoileus* spp.) weighs 45 kg, an average sized caribou (*Rangifer tarandus*) weighs 90 kg, an average sized elk (*Cervus elaphus*/*canadiensis*) weighs 135 kg and an average sized moose (*Alces alces*) weighs 270 kg

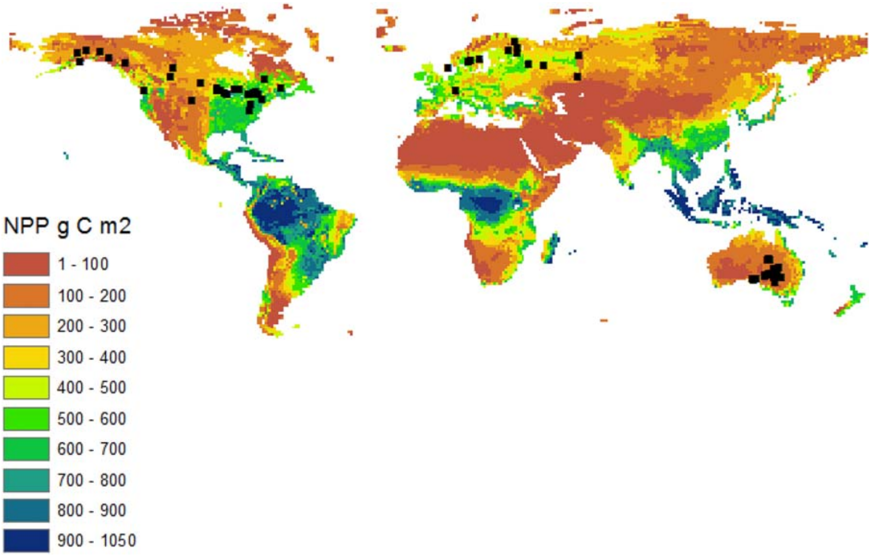

FIGURE 2 Map of global net primary productivity (NPP) predicted by a dynamic global vegetation model (MC1) and the locations of sites for which estimates of NPP and herbivore densities were obtained

(Peterson et al., 2003). For each site we classified grey wolves (*Canis lupus*) as being present or absent. Classification of wolves as being present or absent was based on study articles and maps of their current and past distribution (Mech & Boitani, 2010).

For each cervid case study and kangaroo survey location we recorded (1) an estimate of NPP, (2) whether canid predators, dingoes or grey wolves, were common or rare, and (3) the density (n/km^2) of the primary herbivore species present. NPP (Figure 2) was obtained from a dynamic global vegetation model (0.5° latitude × 0.5° longitude grid cells), MC1 (Bachelet et al., 2001; Daly et al., 2000). MC1 includes a biogeochemical module that simulates monthly carbon (C) and nutrient dynamics for a combined tree and grass ecosystem where NPP (g C/m^2/year) is a function of a maximum potential rate of plant production constrained by the effects of soil moisture, soil temperature, soil nutrients, atmospheric CO$_2$ concentration, shading and leaf area index (Bachelet et al., 2001; Daly et al., 2000). We used a dynamic vegetation model rather than satellite derived estimates of primary productivity because estimates of NPP in arid areas are often unreliable due to problems with image processing when there are large areas of bare ground and when the periods when the landscape is green are of limited duration (Pettorelli et al., 2005).

3 | STATISTICAL ANALYSES

According to the EEH, herbivore abundance should increase with increasing primary productivity where predators are rare or absent but should show a negligible response to primary productivity where predators are relatively common, due to population regulation by predators (Figure 1). We tested this hypothesis in two steps using linear mixed effects models with a Gaussian distribution and with the mean biomass of herbivores at each site as the response variable using SPSS v23.

In exploratory analyses we analysed data for kangaroos and cervids separately (Tables S2–S5, Figs S1 and S2). In our exploratory linear mixed effects models we included the fixed term canid predator (common or present versus rare or absent) in our model to test the hypothesis that herbivore abundances were suppressed by canids. We included the term NPP in our models to test the hypothesis that herbivore abundance increased with increasing NPP. We included a term representing the interaction between NPP and canid predator to test the prediction of the EEH that the slopes of kangaroo abundance plotted against NPP should show divergent responses where canid predators were common and rare (Figure 1). We included the random term genus in the exploratory model for cervids to account for differences in the body mass and behaviour of cervid genera that could have influenced the strength of the effects of wolves on cervids. For example, smaller cervids may be expected to be more vulnerable to predation than larger cervids. To select the optimal model we followed the ‘top-down’ procedure outlined in Zuur, Ieno, Walker, Saveliev, and Smith (2009) whereby non-significant terms were removed from the full model. Results for both cervids and kangaroos showed that only the interaction term between canid predator and NPP and the term NPP were significant at $P < 0.05$ (Tables S2 and S4). After removing non-significant terms, the fitted values for both cervids and kangaroos indicated that the slopes of the relationship between herbivore biomass and NPP in areas where canid predators were common and rare were divergent (Tables S3 and S4, Figs S2 and S3).

In our final analysis, we combined the datasets for kangaroos and cervids to determine if the trends in herbivore biomass evident with respect to predators and NPP were consistent between both cervids and kangaroos. In our linear mixed effects models, we included the fixed term canid abundance (common or present versus rare or absent) to test the hypothesis that herbivore abundances were suppressed by canids. We included the term NPP in our model to test the hypothesis that herbivore abundance increased with increasing NPP. We included a term representing the interaction between NPP and canid abundance to test the prediction of the EEH that the slopes of kangaroo abundance in the

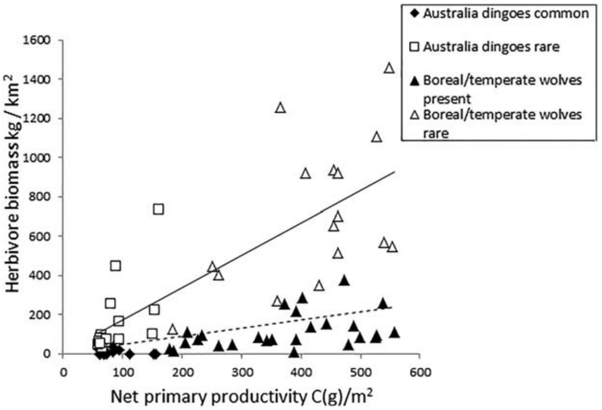

FIGURE 3 The relationship between the density of kangaroos and cervids expressed as herbivore biomass (HB, kg/km^2) and net primary productivity (NPP, g C/m^2) in areas where canid predators are common or present (closed symbols) and rare or absent (open symbols) across boreal/temperate regions of North America and Eurasia (squares) and arid regions of Australia. The lines represent fitted values of the optimized linear mixed effects model (HB $\sim$ NPP + NPP:canid predator) for areas where predators were common or present (solid line) and rare or absent (dashed line)

presence and absence of dingoes plotted against NPP should show divergent responses in the presence or absence of predators (Figure 1). We included the fixed term ‘Region’ (northern boreal/temperate, Australia) and its interactions with canid abundance and NPP to test the hypotheses that Region affected the biomass of herbivores, or had interactive effects on the relationships between herbivore biomass, canid predators and NPP. We included the random term ‘Genus’ in the model to account for differences in the ratio of body mass between the different genera and canid predators that could have influenced the strength of the effects of canids on herbivore biomass. To select the optimal model, we followed the ‘top-down’ procedure outlined in Zuur et al. (2009), whereby we first assessed the fit of the full model with ($AIC_c = 861.447$) and without ($AIC_c = 864.332$) the random factor using the Akaike information criterion corrected for small sample size (AIC_c). Then using the results of *F* tests, we removed non-significant terms from the model containing the random term to identify the optimal model structure (Zuur et al., 2009).

4 | RESULTS

Herbivore biomass plotted against NPP showed that the lowest herbivore abundances were in the low-productivity environments of the Australian desert (Figure 3). For both regions, the highest abundances of herbivores were at sites where canid predators were rare or absent (Figure 3).

Results of the full model, including the random effect Genus, showed that the only significant terms were the interaction between NPP and predator and NPP (Table S5). None of the other terms, including the term Region and its interactions with the other variables, were significant, and were thus subsequently removed from the model.

The optimal model for herbivore abundance expressed as herbivore biomass per km^2 was the model with the random factor Genus, and the fixed terms NPP (Table 1: $F = 27.22$, d.f. 1,19.32, $p < .001$) and the interaction between predator and NPP ($F = 80.31$, d.f. = 1,65.95, $p < .001$). The significant interaction term indicates a divergence in the NPP–abundance relationship (see also Figure 3). Specifically, the relationship between herbivore abundance and NPP was shallower in areas where canid predators were rare (or absent) than where they were common (or present).

5 | DISCUSSION

As predicted by the EEH, the biomasses of cervids in the boreal and temperate regions of North America and Eurasia, respectively, and kangaroos in the deserts of Australia showed divergent responses to increasing primary productivity where canid predators were common (or present) and rare (or absent). The relationship between herbivore biomass, canid predators and NPP did not differ significantly between Australia and boreal/temperate regions of North America and Eurasia. The biomass of herbivores increased in response to primary productivity where canid predators were absent or rare, but showed muted responses to increasing productivity where canid predators were abundant. The similar trends evident in the biomasses of cervids from the Northern Hemisphere and abundances of kangaroos in the comparatively unproductive desert landscapes of Australia demonstrate that regulation of herbivore populations by canids is a widespread phenomenon. Our study shows that the EEH has broad application as a descriptor of biogeographical trends in the biomasses of endothermic herbivores.

Our results provide support for the predictions of the EEH, with one exception. For the high-latitude ecosystems which it was originally intended to describe, the EEH predicts that at extremely low levels of primary productivity there will be insufficient energy to support predators and that herbivore biomass will be regulated by productivity only (Oksanen & Oksanen, 2000). Our results from the Australian deserts differ from the original thinking behind the EEH by showing that predators may still be present and regulate herbivore biomass even at low levels of primary productivity. That dingoes occupy desert ecosystems in Australia, albeit at low population densities (range 0.04–0.23 dingoes/km^2 (Corbett, 1995), may be due to the fact they have very large home ranges and thus search large areas to find food (Corbett, 1995; Newsome, Ballard, Dickman, Fleming, & van de Ven, 2013). However, despite their low densities, dingoes exert strong effects on kangaroo populations because in addition to killing kangaroos for food they also engage in surplus killing where they kill beyond their dietary needs (Shepherd, 1981).

Australia’s deserts are not alone in supporting populations of large carnivores. Large carnivores, including lions (*Leo leo*), cheetahs (*Acinonyx jubatus*), pumas (*Puma concolor*), hyaneas (*Hyaena* spp.), jackals (e.g. *Canis aureus*, *Canis anthus*), coyotes (*Canis latrans*) and wolves (*Canis lupus*), occurred historically and still occur in many of the world’s deserts (Mech & Boitani, 2010; Wilson & Reeder, 2005). Given the alignment between

TABLE 1 Parameter estimates, their 95% confidence intervals and test statistics for terms within the optimal linear mixed effects model (HB $\sim$ NPP + NPP:canid predator) investigating the relationship between herbivore biomass (HB), region, net primary productivity (NPP) and whether canid predators were common or present and rare or absent

Fixed effects	Parameter estimate	CI	d.f.	*F*
Intercept	7.06	−175.43 to 189.55	1,6.46	0.01
NPP	1.65	1.22–2.08	1,19.32	27.22***
Canid predator:NPP	−1.23	−1.51 to −0.96	1,65.95	80.31***
Random effects	Parameter estimate	CI	Wald Z	
Residual	27,241.05	19,041.84–38,970.75	5.47***	
Genus	11,476.53	1,241.17–1,106,118.53	0.88	

The genus of herbivores was included in the model as a random effect.
***$p < .001$.

the EEH and herbivore abundances in the Australian desert, we predict that the EEH may apply to some deserts on other continents and that canid predators such as wolves, jackals and coyotes, and possibly felid predators also, have similarly strong effects on prey populations as dingoes have on kangaroos in Australia. An additional caveat is that Australia's hot deserts have comparatively high but variable rainfall and hence high primary productivity when compared with deserts on other continents (Morton et al., 2011). Hence, the EEH still remains untested in the most extreme desert environments.

While our results suggest that canid predators, wolves and dingoes, can be effective at reducing herbivore population densities, the effects that felid predators have on herbivore populations are less clear. This is because fewer studies have investigated the population-level effects that felids have on herbivore prey and because their life-history traits differ considerably from canids (Bekoff, Daniels, & Gittleman, 1984; Ripple et al., 2014). Canid predators, which often hunt in packs, have a tendency to occur at higher densities than typically solitary felid predators and thus may be expected to kill more prey to meet their dietary needs than solitary felids (Bekoff et al., 1984; Gervasi, Nilsen, & Linnell, 2015; Kleiman & Eisenberg, 1973). However, studies reporting the suppressive effects that lynx (*Lynx lynx*) have on roe deer (*Capreolus capreolus*) in Europe suggest that felid predators can exert strong regulatory effects on prey populations and that these effects scale with ecosystem productivity (Melis et al., 2009). Similarly, felid predators can induce strong fear effects in their prey and in so doing trigger behaviourally mediated trophic cascades (Donadio & Buskirk, 2016). We recommend that further studies are undertaken to determine if the EEH applies in situations where felids are the dominant predator.

Our finding that herbivore abundances display consistent responses to primary productivity and the removal of canid predators in vastly different landscapes has implications for thinking about the factors that shape ecosystems and the management of herbivore populations. Applying the predictions of the EEH, we would expect that the dramatic discrepancies in herbivore abundances we report in areas where canid predators have been removed could potentially be accompanied by the depletion of palatable plant biomass and associated shifts in plant assemblages. Such trophic cascades have been reported in field studies from arid Australia and the Americas (Ripple et al., 2014). In these areas, extirpation of canid predators is associated with the reorganization of ecosystems and net loss of biodiversity due in part to excessive herbivory (Ripple et al., 2014). That the EEH has wide application to predator–herbivore dynamics is relevant to the management of wild herbivores.

In many regions of the Earth canid predators were extirpated such a long time ago that hyper-abundance of herbivores and high levels of herbivory are considered to be the norm (Chollet & Martin, 2013). Consequently, managers tasked with setting targets for herbivore population densities, natural vegetation condition and ecosystem restoration may be prone to the use of 'shifting baselines' by applying reference points that differ markedly from the state of the ecosystems prior to canid extirpation. The net result of setting high targets for herbivore population densities is that harvesting programmes designed to reduce grazing pressure by herbivores may achieve little in terms of actually reducing grazing/browsing pressure on vegetation or mitigating the threat that high population densities of herbivores pose to motorists (Klöcker, Croft, & Ramp, 2006; Letnic et al., 2012; Rowden, Steinhardt, & Sheehan, 2008).

In some places, particularly North America and Europe, large carnivores such wolves, bears and pumas are recolonizing areas where they have previously been extirpated (Chapron et al., 2014; Painter, Beschta, Larsen, & Ripple, 2015). The predictions of the EEH and the results of this study and previous studies suggest that herbivore populations may experience marked declines as carnivores re-establish (Melis et al., 2009; Painter et al., 2015). Such declines in herbivore populations are expected to be significant if carnivore populations are not persecuted. Although the expected declines in herbivore populations may in some instances bring herbivore populations down to levels that are considered 'natural', the decline of game species which are valued by hunters and changes in vegetation communities which are predicted to occur by the EEH will have considerable potential to spark conflicts between wildlife managers and other stakeholders such as those advocating for large predators and biodiversity (Melis et al., 2009; Treves, Naughton, Treves, & Shelley, 2013).

In summary our study shows that the EEH has the utility to describe predator–herbivore dynamics in boreal/temperate and arid environments spread across three continents. Our results suggest that the EEH is relevant to the management of mammalian herbivores because it can provide managers with an indication of how herbivore biomass/densities may be expected to vary in relation to ecosystem productivity and the intensity of canid predation. Such knowledge could be useful for setting population targets for herbivore populations. Although our study suggests that the EEH may have broad utility as a descriptor of herbivore abundance, little is known about its application in tropical forest and savanna environments and whether felid predators can induce similar effects on herbivore populations as has been observed for canid predators. Future studies are recommended to explore the application of the EEH as a tool to describe trophic dynamics in tropical and arid environments and the effects that felid predators have on herbivore population densities.

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BIOSKETCHES

Mike Letnic's research interests are in ecology and wildlife management.

William Ripple's research interest are in trophic cascades and biodiversity conservation.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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