Multi-trophic interactions in anthropogenic landscapes: the devil is in the detail

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1. Comments to Dorresteijn et al. (2015)

Dorresteijn et al. [1] recently addressed the question what influence humans have on predator–prey interactions in human-modified landscapes. Their study follows increasing evidence from relatively natural landscapes that large carnivores are central drivers of ecosystem structure and functioning through density-mediated and behaviourally mediated effects on their prey [2]. A key question is whether large carnivores will have similar ecological effects in human-dominated landscapes [3]. This is particularly relevant in the light of the carnivore recolonization of European landscapes [4]. We applaud Dorresteijn et al. [1] for highlighting that ecological effects of large carnivores may be quite different in human-modified landscapes. Unfortunately, we feel that there are crucial flaws with their study design, analyses and interpretation. These flaws seriously undermine the strong conclusions that they draw about the role of top-down and bottom-up processes in anthropogenic landscapes. Our main concerns include (i) lack of relevant bottom-up data, (ii) a camera trap design unsuitable for testing their hypotheses regarding community structure, and (iii) top-down and bottom-up processes that are studied at an inappropriate spatial scale.

(1) Their main aim was ‘to quantify the relative effects of top-down versus bottom-up processes in shaping predator and prey distributions’. It is surprising that the authors articulate this main objective without including actual bottom-up drivers in their analyses. Bottom-up processes were captured by variation in two land cover types, forest versus pasture cover, using the Corine Land Cover data. However, these very coarse categories do not reflect the variation in food resources (i.e. bottom-up processes) that drive the distributions of prey and predator. This variation occurs at finer spatial resolution, nested within the main land cover types that the authors used. For example, inside forest habitat (where all cameras were placed), one important fine-scale factor that drives deer distribution, and hence camera trapping rates, is variation in canopy openness, with deer strongly concentrating inside canopy gaps [5]. In addition, fox abundance (the mesopredator in this study) is driven by variation in prey availability that is linked to microhabitat variation [6]. Therefore, the Corine Land Cover data alone provide no basis for testing the importance of bottom-up effects in driving encounter rates of mesopredators and herbivores. In fact, we would argue that such land cover data may be a better proxy for top-down forces. Ungulate prey species avoid open or closed habitat depending on whether they respond to a large carnivore or human hunter [7]. Although the authors draw conclusions about bottom-up effects, we argue that these are unfounded owing to an absence of relevant bottom-up variables in their models.

(2) The main results and conclusions of this paper are based on the use of camera traps to estimate the relative occurrence of prey and predators. Design of camera trap surveys is essential because it strongly influences camera trap capture rates and thus affects inferences made at the community level [8].
The authors placed one to two cameras per 5 × 5 km grid cell, with cameras active for roughly 22 days and set along paths. There are two main problems with this design that affect the outcome of the study. First, not placing cameras randomly but along paths creates strong biases towards capturing certain species [8]. A design that leads to biases towards certain species cannot be used to infer community structure. This bias may be overcome with a large enough sample per site [8]. This leads us to the second problem of the design: the very low sampling intensity (one to two cameras per sampling unit of 25 km²). This low sampling intensity will result in a very poor estimate of species abundance at the scale of each sampling unit, particularly if cameras were not set to optimize species-specific capture rates. This led the authors to correctly conclude that wolf (with only two observations) should be excluded as response variable. However, we wonder why the same conclusion has not been drawn for most of the other species? Using the data provided through the online repository, we found that the number of camera trap detections per camera location was not correlated with alternative density estimates provided for each location for wolf, bear and humans (correlation coefficient of 0.01, 0.08 and 0.1, respectively). This indicates that the camera traps did not reflect the densities of wolf, bear and human. The same is likely true for red deer, which had an equally low sample size. This makes conclusions at the level of species’ population density or communities at the sampling unit scale of 5 × 5 km very problematic. We wonder what the relationships depicted in figure 3 of [1] really mean; do they represent ecological relations or statistical artefacts?

(3) The scale at which the authors approach their aim does not fit the scale at which predator–prey interactions operate. Dorresteijn et al. [1] use low-spatial-resolution data on predator presence, namely landscape-scale estimates of wolf and brown bear densities derived from sign surveys and direct sightings by hunters and wildlife managers. A first issue with this, as the authors acknowledge in their electronic supplementary material, is that such estimates are known to be error-prone, especially for large predators [9]. Our concerns about the used predator densities are aggravated by the unusually high wolf densities that the authors reported for the hunting grounds (figure 1 of [1]). The highest densities reported by Dorresteijn et al. [1] are sixfold to eightfold higher than the highest estimates reported in studies reviewing wolf densities across Europe, including the Carpathians [4,10]. Perhaps more importantly, however, these landscape-level data assume a homogeneous distribution of predator activity across a large scale. However, predators will use some parts of the landscape more intensively and create prey refugia in other places [10,11]. Both the distribution of predator territories and activity centres within these territories strongly affect landscape-scale ungulate distribution and habitat selection [11–13]. Predators also strongly affect ungulate distribution and behaviour at much finer scales (less than 10 m² [13]). As Dorresteijn et al. [1] assume a homogeneous distribution of predators and their (risk) effects within large hunting grounds, they can either have over- or underestimated the role of top-down effects, depending on the locations of camera traps.

Humans can strongly limit numbers of predators, such as wolf, by legal hunting or poaching [14], which undermines their ecological functionality [15]. Moreover, wolves in general spatially avoid humans [16,17], and prey may profit from these ‘human shield’ effects, leading to the redistribution of predator and prey over the landscape [13,18]. Surprisingly, however, the authors did not include humans as a driver of wolf distribution in their structural equations model because of too few camera records of wolves. We argue that this is an important limitation of the model, as human activity can strongly mediate trophic cascades caused by wolves [19]. Moreover, the location of cameras in relation to distance to human activity becomes a crucial point. For example, cameras placed at far distance from human activity, with consequently lowest deer trapping rates in case predators are present, will provide evidence for strong top-down effects of apex predators on ungulate populations. Whereas placement close to human settlements will result in high deer and low carnivore trapping rates, supporting the hypothesis that bottom-up factors prevail. Having cameras placed randomly will in fact probably mask both these patterns.

We very much appreciate the effort of Dorresteijn et al. [1] to look at the role of predators in human landscapes. Owing to a lack of studies, we currently face the risk that the role of re-colonizing carnivores in ecosystem restoration is over-romanticized [20], particularly in human-dominated landscapes in Europe and North America. The way forward is to perform rigorous scientific studies that are clearly communicated to the public. It is equally important to highlight shortcomings in published studies. Although we acknowledge that the authors recognize some of the discussed caveats, we believe that the ones we discuss in this comment are so significant that the interpretation of their results becomes questionable, especially because Dorresteijn et al. [1] draw strong conclusions about the dominant effect of humans on ecosystems relative to top-down (carnivore) and bottom-up (resource) effects. We have argued that their study design and the resulting data do not warrant the strong conclusions they draw. Answering the important, but complex, question that they pose asks for much more detailed assessments of multi-trophic interactions in anthropogenic landscapes.

References


5. Kuiper DPJ, Cromsigt JPM, Churski M, Adam B, Jędrzejewska B, Jędrzejewski W. 2009 Do ungulates preferentially feed in forest gaps in European