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Lack of trophic release with large mammal predators and prey in Borneo

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ABSTRACT

When humans reduce top carnivore abundance in insular systems, herbivore populations may increase, with cascading impacts on the community. But the prevalence of such "trophic release" effects in non-insular ecosystems remains little known, particularly in tropical ecosystems. We assessed whether areas with low top carnivore abundance were associated with greater abundance of herbivores across seven rainforest study areas in Malaysian Borneo. We deployed 134 camera-trap stations and analyzed the resulting photographic detections from 16,608 trap-days using multi-species occupancy models that estimate abundance while accounting for imperfect detectability. Estimated local abundance of Sunda clouded leopards (*Neofelis diardi*), the apex mammalian predator, varied from 0.0 to 3.5 individuals per camera location. Clouded leopard abundance was not negatively correlated with the abundance of any of the four prey species that we analyzed. Rather, sites with few or no clouded leopards also had the lowest estimated abundance of pig-tailed macaques (*Macaca nemestrina*). Estimated abundance of muntjac (*Muntiacus* spp.) and mousedeer (*Tragulus* spp.) was statistically unrelated to estimated clouded leopard abundance. Bearded pig (*Sus barbatus*) abundance was likewise unaffected by predator abundance, but pigs appear to live in larger groups when clouded leopards are common, possibly to better defend their young. We found no evidence of trophic release, an important conservation threat in other areas, in this ecosystem, particularly relative to the massive impacts of agricultural conversion, habitat degradation, and unsustainable wildlife exploitation.

1. Introduction

Trophic release, or the increase in herbivore abundance following carnivore extirpation, can have important effects on ecosystems. In some cases, human-caused trophic release can indirectly affect an entire ecosystem (Maron et al., 2006; Myers et al., 2007). Human disturbance frequently affects carnivores disproportionately to other species. This may occur because carnivores may be directly targeted – for example tigers (*Panthera tigris*) are heavily poached due to the high monetary value of their body parts. But even if not directly targeted, carnivores are often particularly vulnerable to human disturbance simply because they exist at much lower densities than their prey (Carbone and Gittleman, 2002) and are thus much more susceptible to local extirpation (Morris and Doak, 2002). The absence of apex predators sometimes triggers dramatic increases in the abundance of herbivores (Terborgh et al., 2001) or mesopredators (Brashares et al., 2010; Prugh et al., 2009), resulting in a negative correlation between predator and prey abundance across the landscape.

However, most predators also have the ability the track the availability of their prey. To the extent that this tracking is successful, it could result in a positive correlation in predator–prey abundance (Godin and Keenleyside, 1984; Ngoprasert et al., 2012). Moreover, humans consume many of the same large herbivore species that large carnivores select. Therefore even if predators are extirpated, prey numbers may remain locally low due to continued hunting by humans (Brodie et al., 2009). So actual trophic release would then only occur in those areas where both (i) predators are extirpated or have consistently low abundance, and (ii) hunting or habitat disturbance (i.e., two of the primary impacts of humans on predators) do not also negatively impact herbivores. For example, on consistently predator-free islands in a reservoir in Venezuela (i.e., islands large enough to support herbivores but too small for wider-ranging carnivores), the abundance of unhunted herbivores increased dramatically, leading to cascading impacts on plants (Terborgh et al., 2001). In a non-insular temperate system, wolves (*Canis lupus*) consistently avoided a township in Banff,

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Canada, leading to elk (*Cervus elaphus*) congregations near the town where predation rates were lower (Hebblewhite et al., 2005).

Whether the general conditions under which trophic release can occur are rare or common remains little known, particularly in tropical systems. This dearth of information is unfortunate given that tropical ecosystems, which host the majority of species on earth (Dirzo and Raven, 2003), are being threatened by numerous forces such as habitat alteration (Ernst et al., 2006), overexploitation (Brodie et al., 2009; Milner-Gulland et al., 2003), and climate change (Brodie et al., 2012; Sheldon et al., 2011). Given the importance of tropical ecosystems to the maintenance of global biodiversity, and thus their extremely high conservation value, it is important to ascertain whether trophic release presents an additional threat that is strong relative to these other anthropogenic impacts.

Trophic release of herbivores can be tested by assessing the abundance of predators relative to the abundance of their potential prey. Carnivores can alter the spatial distribution of prey either by directly altering prey population density (Myers et al., 2007) or by influencing the behavior of their prey (Calcagno et al., 2011; Creel et al., 2005). In either case, however, there should be a spatial signal of carnivores on prey local abundance, either because prey density is reduced in areas with abundant carnivores, or because prey avoid such sites (Kauffman et al., 2010). Where trophic release occurs, we would expect to see an inverse relationship between predator and prey abundance, as has been demonstrated in other systems (e.g., Prugh et al., 2009; Terborgh et al., 2001). However, other factors may lead to different predator–prey relationships. When predator mobility is not restricted for example, individual predators will likely favor areas with high prey density, leading to positive predator–prey associations (Godin and Keenleyside, 1984). In addition, human-caused disturbances such as habitat alteration and hunting can simultaneously affect many animal species in an area regardless of their trophic position. This can lead to the concurrent erosion in alpha diversity or the abundance of many species across multiple trophic levels. Either of these effects could lead to a positive correlation in the abundance of predators and prey. As many tropical forests around the world have already been so heavily hunted that they are now largely devoid of both herbivores and carnivores (Milner-Gulland et al., 2003), this is a very real concern. Alternatively, human activities could influence a single trophic level (e.g., carnivores), yet have little concurrent direct or cascading indirect impacts on other trophic levels.

Here we assess relationships in predator–prey abundance in tropical rainforests spanning a broad geographical area of Malaysian Borneo. Specifically, we tested for potential trophic release by investigating the relationship between the abundance of the ecosystem's apex predator, the Sunda clouded leopard, and four common mammalian primary consumer species. We conducted these analyses at two spatial scales. First, we examined predator–prey abundance at local scale via cameratrap stations clustered as sampling units within seven study areas. This is because prey density can often be affected at such scales by the distribution of predators (e.g., see Kauffman et al., 2010, where elk density varied greatly within the territory of a single wolf pack as a function of gradients in predation risk). However, as other responses of prey to predators may only be manifest over larger areas, for example the demographic influences of predators on large and wide-ranging herbivores, we also conducted large-scale occupancy analyses whereby each of the seven separate study areas served as sampling units. As the abundance of predators and prey anywhere in the world is likely shaped by numerous factors, our goal here was to assess whether signals of trophic release were detectable relative to the background variation in environmental conditions and human disturbance.

2. Methods

2.1. Study areas

The Malaysian states of Sabah and Sarawak contain equatorial rainforest on the island of Borneo and stretch from 0°50′ to 7°22′ north latitude. While this area was mostly covered in rainforest as recently as 1950 (Bradshaw et al., 2009), logging has since drastically altered their landscapes. Most logging in Malaysian Borneo is selective, meaning that high-value timber trees are removed while smaller or less-desirable are left standing. Variation in

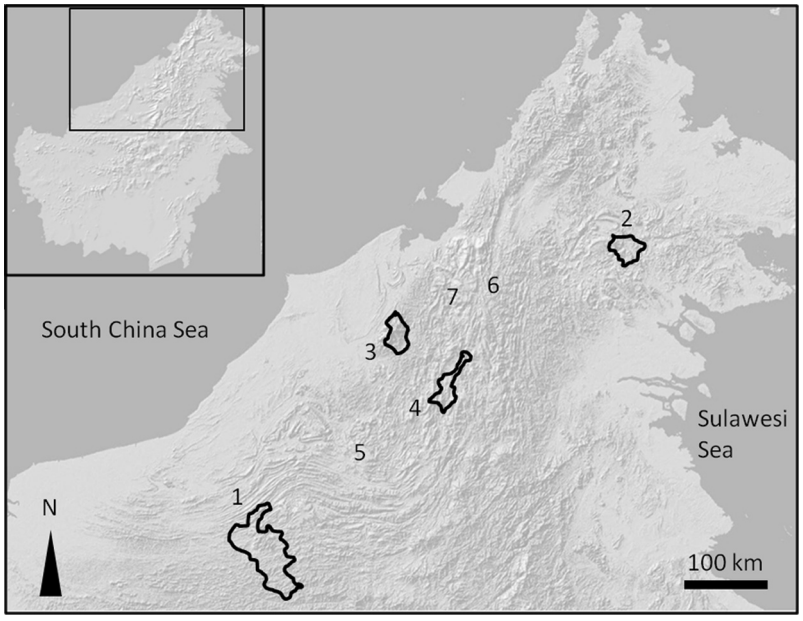

Fig. 1. Map of the study areas: (1) Hose Mountains National Park, (2) Maliau Basin Conservation Area, (3) Gunung Mulu National Park, (4) Pulong Tau National Park, (5) Ulu Baram region, (6) Ulu Padas region, (7) Ulu Trusan region. Inset shows location of region within Borneo.