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Threat webs: reframing the co-occurrence and interactions of threats to biodiversity

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Abstract

1. Interactions between threatening processes and their effects on biodiversity are a major focus of ecological research and management. Threat interactions arise when threats or their effects co-occur spatially and temporally.
2. Whether the associations between threats are coincidental or causally linked is poorly understood, but has fundamental impacts on how, when and where threats should be managed. We propose that examining threat co-occurrence, supplemented by experiments and triangulation of evidence, can help identify when and where threats interact causally, informing pressing biodiversity management goals.
3. Using case studies, we demonstrate how co-occurring and interacting threats can be visualised as networks (threat webs) and how this could guide conservation interventions at local, regional and global scales.
4. *Synthesis and applications.* Recognising that threats co-occur and interact as networks, and are potentially driven by multiple agents (e.g. other threats, shared environmental drivers), helps us understand their dynamics and impacts on ecosystems. This greater understanding can help facilitate more targeted, efficient and effective environmental management.

Introduction

Anthropogenic threats endanger biodiversity worldwide (Johnson *et al.* 2017). Threats directly affect species and the habitat they occur in (Salafsky *et al.* 2008), whereas pressures are generally considered to be broader human processes with the potential to negatively affect biodiversity (e.g. human population density). Maps of threats are often paired with biodiversity data so that threat mitigation occurs where it will reap the greatest benefit (Tulloch *et al.* 2016b). However, maps of pressures (e.g., human footprint mapping; Venter *et al.* 2016) or threats rarely consider whether the threats are linked, such that one influences, or interacts with, others (Tulloch *et al.* 2015). As species are increasingly exposed to multiple threats (Didham *et al.* 2007), management of threat interactions is recognised as critical to biodiversity conservation (Craig *et al.* 2017).

Threat associations: distinguishing between causality and coincidence

When threats interact, their effects on a response variable (e.g., individuals, populations, communities or ecosystems) can lead to non-additive effects (Côté, Darling & Brown 2016). Research on the nature of threat associations has largely focussed on pairwise threat interactions, which we term bivariate threat interactions. Threat ‘interaction types’ describe the combined effect of two threats on a response variable and can be equal (*additive*), greater than (*synergistic*), or less than (*antagonistic*) the sum of their individual effects (Côté, Darling & Brown 2016). Didham *et al.* (2007) expanded on this by describing ‘threat interaction pathways’ that distinguish between *chain interactions*, where one threat changes the prevalence of another threat (a direct interaction), and *modification interactions*, where one threat modifies the per capita impact of another (an indirect interaction), in addition to changing its prevalence.

Just as species co-occurrence arises through shared environmental constraints, or because one species facilitates or impedes the occurrence of another (Poisot, Stouffer & Gravel 2015), threat co-occurrence (i.e., the co-occurrence of threats in space and time) can be distinguished based on whether associations are coincidental or causal (Araújo *et al.* 2011). Two threats have a *coincidental* association if their co-occurrence and interaction is not the result of a causal relationship, but instead arises merely through chance or due to shared environmental and/or anthropogenic filtering (Fig. 1a). For instance, pollution and extraction of biological resources are likely to co-occur together, not because of a causal link between them, but because they have a shared anthropogenic driver — human population density (Allan *et al.* 2019). Importantly, even if threats associate coincidentally, they may nonetheless interact and affect response variables (Fig. 1b). Habitat fragmentation caused by agriculture and heat waves caused by climate change co-occur coincidentally, but interact to have synergistic impacts on woodland birds, as fragmented landscapes can have higher microclimate temperatures during heat waves (Piessens *et al.* 2009; Haslem *et al.* 2015).

Causal associations occur when one threat directly affects the occurrence, abundance or intensity of another threat. In many causally linked threat associations (e.g. logging-induced habitat fragmentation increasing the probability of vegetation structural change caused by severe fire, Lindenmayer *et al.* 2009), a *parent threat* influences the occurrence and intensity of a *secondary threat(s)* (Fig. 1c,d). By being intrinsically linked, the secondary threat might only occur in the presence of the parent threat. Causally linked threats have functional associations with one another and therefore interact to affect response variables. Teasing out causal from coincidental co-occurrence could be done by first identifying strong co-occurrence associations. Experiments and triangulation of evidence can then be used to find those strong co-occurrences that are in fact causal and the direction of their association. Threat co-occurrence can be quantified using spatially-explicit species and threat data (Bellard *et al.* 2017).

To illustrate the first step in this, we undertook a co-occurrence analysis on the threats to biodiversity in the Caribbean region (Salafsky *et al.* 2008), based on threat information for all native mammal species that occur on Caribbean islands from the IUCN Red List database (Baillie, Hilton-Taylor & Stuart 2004; IUCN 2019). We assigned threat occurrence to each island based on whether a species that is affected by that threat occurs there, to create a co-occurrence matrix. We then calculated the effect size of their co-occurrence associations using the co-occur package in R (Griffith, Veech & Marsh 2016). The results of this analysis are presented in Figure 2 and show that biological resource use (e.g. fishing, hunting) and natural system modification (e.g. installation of dams) have the strongest positive co-occurrence association. However, as we have assumed that a threat affects a species across its entire range, the results of our proof-of-concept threat co-occurrence analysis should be interpreted with caution.

Incorporating environmental drivers explicitly into models of threat co-occurrence could help determine how much of the association is driven by environment (coincidence) rather than direct causal interaction (Ovaskainen *et al.* 2016). Threats with strong co-occurrence relationships could therefore indicate causal associations (Freilich *et al.* 2018). After strong co-occurrence associations have been identified, experimental manipulation and other approaches (e.g. theory of change) would then be required to verify the presence of a mechanistic causal relationship, rather than merely a strong coincidental relationship.

‘Threat webs’: beyond bivariate interactions

Recognition that threats interact for various reasons (coincidentally or causally) and in different ways (additive, synergistic or antagonistic) fosters a more nuanced view of threats: as a network of co-occurring threats, with pairs, triplets or additional subgroups potentially having additive or non-additive effects (Fig. 3). Threat associations can vary, from no relationship (independent and some coincidental threats), to weak or strong co-occurrence (coincidental threats) or causal. From this perspective, threat associations can be viewed as a type of ecological network, which we term a ‘threat web’, analogous to food webs in which trophic interactions can vary from weak to strong (Pimm, Lawton & Cohen 1991).

A threat web is made up of threats that co-occur in an ecosystem and affect a common response variable, linked by causal and coincidental associations. For example, Fig. 3b conceptually depicts a threat web for a forest ecosystem. Like other ecological networks, threat webs allow us to envisage how threat impacts might flow through ecological systems across multiple causal and coincidental associations. That is, how a change in the occurrence or intensity of one threat might cascade through the threat web to affect other threats and the response variable of interest. An example of a *threat cascade*, following on from Fig. 3, could be triggered by alterations to the logging regime, which would then flow through to modify the fire regime and also affect invasive predators and their consumption of vulnerable prey.

To illustrate the threat web concept, we drew a conceptual web of threats affecting patch colonisation by a woodland bird, the rufous whistler (*Pachycephala rufiventris*) in the Box Gum Grassy Woodland of south-eastern Australia (Fig. 4), using parameter estimates from Tulloch *et al.* (2016a). In this example, paired threats of domestic livestock grazing and noisy miners (a hyper-aggressive bird) are coincidentally associated, as grazing has little influence on noisy miner patch colonization rates [P(col)=0.13]. Noisy miners and habitat fragmentation caused by land clearing may be causally linked [P(col)=0.60], as clearing increases the probability of noisy miners colonizing patches (Bennett *et al.* 2014), however further work is required to confirm the exact mechanism of this causality. Given this, in landscapes where noisy miners co-occur with land clearing, they are best managed as a package of mechanisms to mitigate land clearing impacts (e.g., revegetation, grazing exclusion), rather than independently (Beggs *et al.* 2019).

Without the inclusion of the spatial arrangement of threats or community data, analysis of threat co-occurrence may fail to elucidate the nature of interactions (Freilich *et al.* 2018; Rajala, Olhede & Murrell 2018). We therefore support previous calls to close gaps in knowledge of the spatial and temporal occurrence of threats (Joppa *et al.* 2016). Once threat co-occurrences are identified, network-based methods such as fuzzy cognitive maps, Bayesian networks, and structural equation modelling, will be useful for describing and quantifying the types and impacts of interactions within threat webs. These approaches provide insight into how variation in one ecosystem component (e.g. a threat) can flow through to affect another ecosystem component (e.g. another threat or response variable), and the pathway through which this interaction occurs (Bode *et al.* 2017). For example, Schweiger *et al.* (2016) used structural equation models to determine the major interaction pathways between threats (e.g. loss of predators, changes to hydrology) and wetland integrity in the Rocky Mountains, USA.

Applications for ecosystem management

Our operational framework for understanding threat co-occurrence can be embedded in structured decision-making processes used for threat mitigation by practitioners (e.g. Tulloch et al. 2015). When setting management objectives, understanding the state of the ecosystem is necessary, and knowledge of the entire web of co-occurring threats is part of this. By determining which threats are more likely to co-occur, managers can identify the relative benefit of managing particular threats, including those that are best managed as a complete web or 'package,' and those where this is not required.

The type of threat relationships present in the network can also guide management. When choosing between alternative management strategies, managers need to know the relative impact mitigating particular threats would have on the system, including how a strategy might impact the entire network. If threats are coincidentally associated, the alleviation of one threat may not impact another, whereas if they are causal, removing the parent threat would affect the secondary threat. For instance, infilling fragmented woodland can mitigate the effects of habitat fragmentation, reducing noisy miner abundance and potentially their impacts on other woodland birds (Law *et al.* 2014). Threat webs can also inform how management strategies might directly and indirectly flow through the network of threats, aiding in the prediction of unexpected outcomes. The impact of management actions on threat webs are potentially analogous to the indirect effects of disturbances on ecological networks, and could be informed by existing literature in this field (Montoya *et al.* 2009).

Understanding the full network of threats might help identify management strategies that were previously not considered, such as mitigating the distal/parent threat rather than proximal threats. For example, an invasive rodent and an invasive weed on an island could have strong co-occurrence but no casual association, except for sharing a parent threat (i.e. human tourists acting as vectors for both invasive species). Once those associations are established, a single threat management action targeted at the distal or parent threat (e.g. biosecurity) could mitigate both proximal threats. Management could therefore be guided by the hierarchy and relationship of co-occurring threats present, their relative impact on a species or ecosystem, and complementarity analyses to identify cost-effective management strategies (Chadès *et al.* 2015).

Threat webs that reasonably capture an ecosystem's dynamics and the effects of threats on a response variable can also guide decision-making. Co-occurrence network analyses can identify optimal combinations of management actions to maintain community structure (Tulloch, Chadès & Lindenmayer 2018). Management regimes that disentangle threat web networks could be identified in the same way by potentially focusing on management actions that reduce the co-occurrence, and therefore rate of interactions between threats within a web. Field experiments, especially if conducted in an adaptive management framework (McCarthy & Possingham 2007), provide a powerful approach for quantifying the nature and dynamics of threat interactions, by supressing/removing threats and monitoring the response(s) of others. Optimal eradication schedules guide invasive species management, requiring eradication efforts start at the highest trophic level and moving down the food chain (Bode, Baker & Plein 2015), and this logic could be applied to threat webs. Scenario analysis methods such as these are ideally placed to compare how different management strategies flow through a threat web and also account for threats beyond a manager's control.

Our co-occurrence approach provides policy makers and practitioners with an operational framework to understand where multiple threats might be impacting ecological communities, and helps inform when and how to best manage threats (e.g. by prioritising those places where a package of actions targeting co-occurring threats could be expected to reduce threat impacts on target conservation features and promote recovery). In situations where proximal (i.e. direct) threats are clear but uncertainty exists about distal or indirect threats, an understanding of the threat web can inform further experiments and analysis to reduce uncertainty in drivers of threats.

Conclusions

Gaining a mechanistic understanding of the reasons for why and how threats associate, and what this means for the nature and dynamics of threat interactions, can offer insight into their potential effects on species and ecosystems, and the drivers of biodiversity loss. Re-framing co-occurring threats as webs of interacting processes aids refinement of our understanding of threat interactions and can be used to guide more effective management responses to threat mitigation, particularly when embedded in structured decision-making frameworks.

Author's Contributions

All authors contributed to the development of ideas in the manuscript. WLG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

All data used in this paper are available publicly through the IUCN Red List database (IUCN 2019). The values used to create Figure 4 are reported in Beggs *et al.* (2019).

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Figures

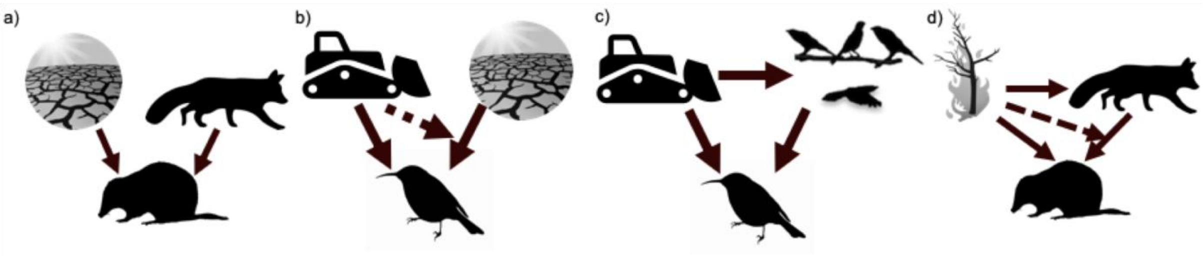

Figure 1: The different types of threat associations, illustrated conceptually. Conceptual model a) indicates coincidentally associated threats that do not interact (drought and invasive predators), b) indicates coincidentally associated threats with a modification interaction (fragmentation and drought, Piessens *et al.* 2009), c) indicates causally associated threats with a chain interaction (fragmentation and noisy miners, Mac Nally *et al.* 2012), and d) indicates causally associated threats with a modification interaction (fire and invasive predators, Hradsky *et al.* 2017). Solid lines indicate causal associations and dashed lines indicate modification interaction pathways.

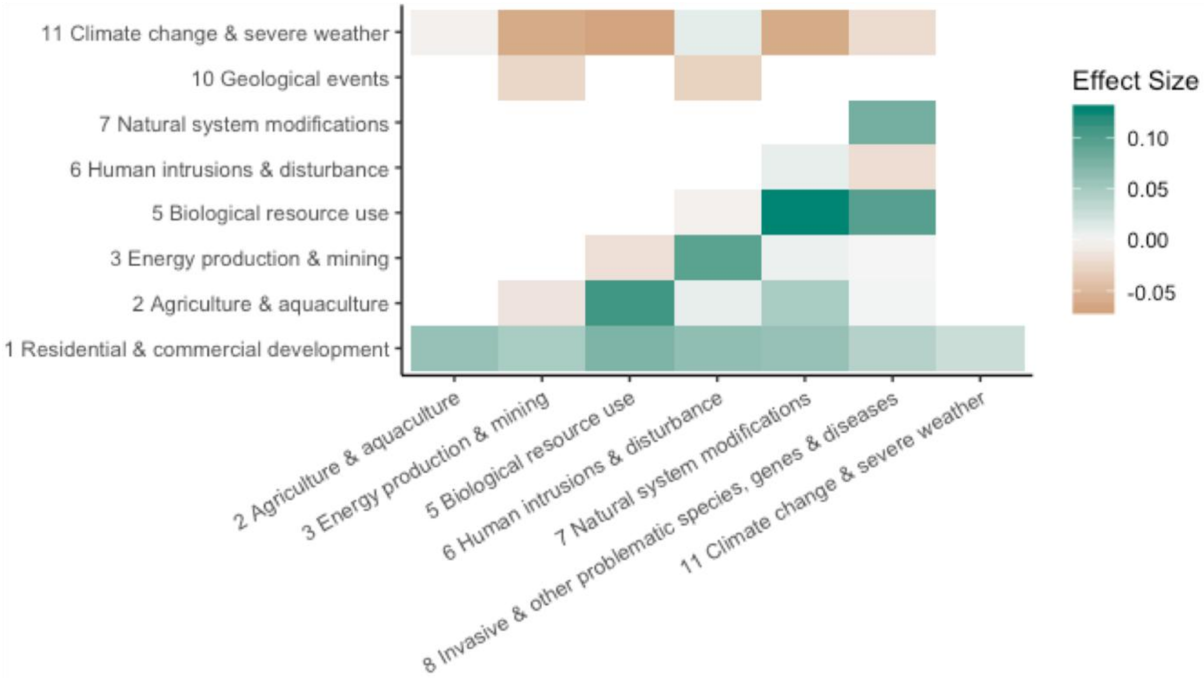

Figure 2: Effect sizes of co-occurrence relationships for threats to insular mammals in the Caribbean region, based on data extracted from the IUCN Red List of Threatened Species database. Green colours indicate a positive effect size and red colours indicate a negative effect size. Effect sizes are based on how often two threats co-occur on the same island compared with their expected rate, and were generated using co-occur (Griffith, Veech & Marsh 2016). Full methods are described in the supplementary information.

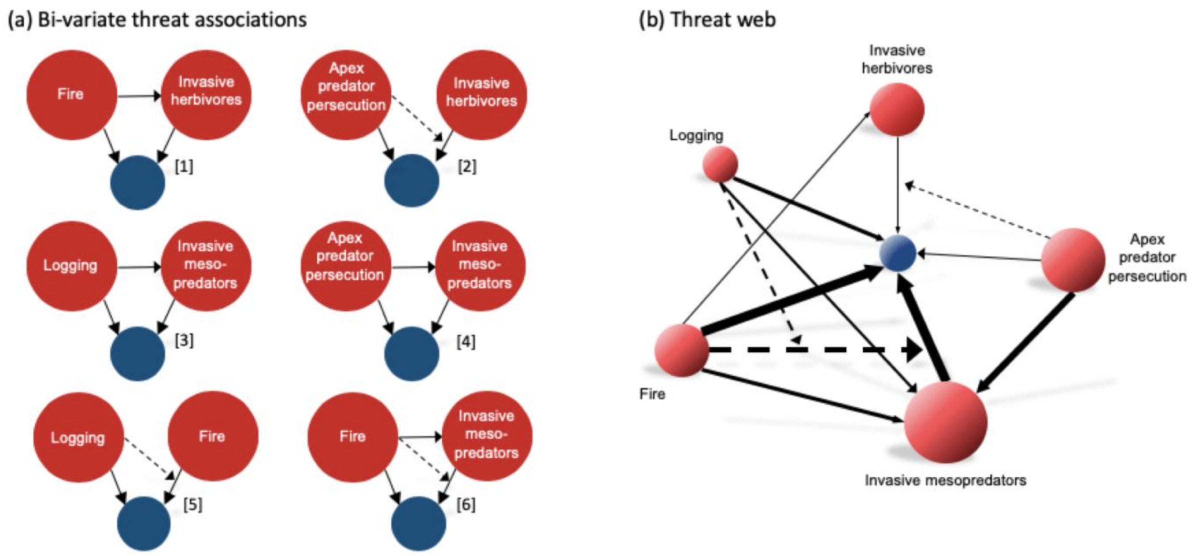

Figure 3: Conceptual illustration of different threat associations, and a threat web for a generic south-eastern Australian temperate forest ecosystem. Part a) depicts six pairs with different associations (causal/coincidental) and interaction pathways (chain/modification). Threats are represented by the red circles, and response variable (e.g. species, community or ecosystem) by the blue circle. In b) these threats are represented as a web affecting the response variable. Solid lines indicate causal associations and dashed lines indicate modification associations. Line thickness indicates the strength of the interaction between the two threats. References: [1] Forsyth *et al.* (2009), [2] Forsyth et al. 2018, [3] May and Norton (1996), [4] Colman *et al.* (2014), [5] Lindenmayer *et al.* (2009), [6] Hradsky *et al.* (2017).

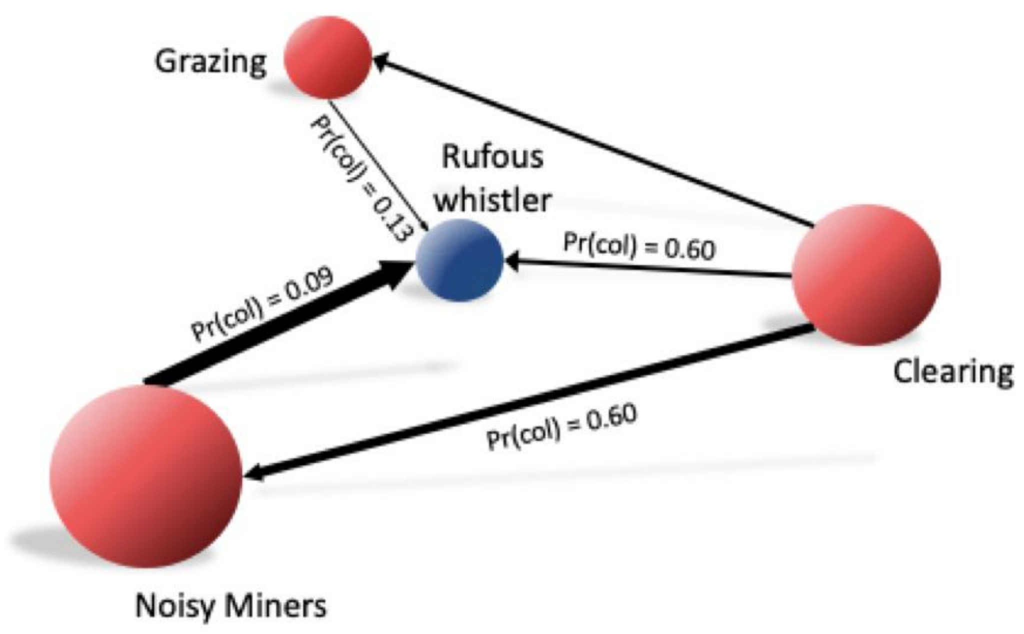

Figure 4: A parametrised threat web that interacts to affect the probability of patch colonisation [P(col)] of an Australian woodland bird, the rufous whistler (*Pachycephala rufiventris*). Shown are two threats whose co-occurrence is causally linked—noisy miners (*Manorina melanocephala*) and land clearing; and two threats whose co-occurrence is coincidental—grazing by domestic stock and noisy miners (red). Thicker lines indicate a stronger positive or negative effect. Parameter estimates shown here are from Tulloch *et al.* (2016a).