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Review

Density-impact functions for terrestrial vertebrate pests and indigenous biota: Guidelines for conservation managers

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ABSTRACT

The relationship between the density of a pest and its impact on a valued resource is critical for cost-effective management. Despite their simplistic representation of dynamic and often complex systems, density-impact functions (DIFs) are appealing because they provide managers with tangible goals for pest control. Historically, these relationships have focused on agricultural resources: relatively few have been quantified for conservation assets. We provide empirical evidence for six theoretical forms of DIF. Linear functions are the default condition based on the notion that some conservation benefit will result from any level of pest control, but they comprised less than one fifth of DIFs reviewed. More than half were strongly non-linear, with substantial benefits for indigenous species when pests were suppressed to low levels. Recovery of species, however, is usually a function of multiple processes, not just removal of pests, and recovery tends to be place- and time-specific. Thus, guidelines to help conservation managers derive and use DIFs in ways that maximise their value without overextending their utility are: 1) minimise influences of factors other than pests; 2) where necessary, undertake site-specific experiments, rather than generalising from other studies; 3) use time scales that recognise delays for biota to adjust to pest control; 4) measure instantaneous responses (e.g. demographic rates) as early indicators; and 5) use DIFs to guide short-term pest management, and trophic-interactive modelling for longer-term management. DIFs derived and used in this way are a significant improvement over unguided biodiversity management, and provide managers with an evidence base for decision-making.

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1. Introduction

Calls for conservation managers to strengthen the evidence base they use for management of natural ecosystems have emerged in recent years (e.g. Ferraro and Pattanayak, 2006; Pullin and Knight, 2005). In invaded ecosystems, conservation often involves pest control, which is a major and expensive activity (Mack et al., 2000). Where eradication of pests is not possible, they are reduced to some desirable level for as long as possible (Grice, 2009; Parkes and Murphy, 2003). Desirable levels are often defined loosely in terms of abundance of the pest ('as low as possible') rather than the ecological outcome. One of the fundamental tenets of cost-effective pest management is knowing the minimum control effort, or maximum allowable pest density, that achieves a required outcome, yet this knowledge is lacking for many invaded systems (Caughley and Gunn, 1996; Grice, 2009), although see Cooke et al. (2010). Consequently, managers risk not applying enough effort, or conversely, overcommitting scarce resources.

Efforts to quantify the relationship between pest density and their impacts have focussed primarily on production resources (see Hone's, 2007 review). Production benefits are easily demonstrated in agricultural environments, and economic yields are amenable to cost-benefit modelling, which allows optimisation of management effort (see Kaboodvandpour and Leung, 2012; Yokomizo et al., 2009). In contrast, relatively few studies have quantified the responses of indigenous biota (both species and ecological processes) in natural ecosystems. This may be because insufficient resources are allocated for monitoring (Clayton and Cowan, 2010; Reddiex and Forsyth, 2006) or because techniques are inadequate (de Bello et al., 2010). Baxter et al. (2008) developed a theoretical model that examined the cost-effectiveness of controlling pest predators, and concluded that suppression of predator abundance to a 'pre-determined limit' (or threshold) can be a more cost-effective strategy than eradication. The critical knowledge gap is therefore the form of the density-impact function that allows such a threshold to be set as a tangible management target (Edge et al., 2011).

Some conservation managers already set targets for pest abundance, with the expectation of delivering specific conservation gains (e.g. Department of Conservation, 1993; Forsyth and Stuart, 2014; Otago Regional Council, 2009; Saunders, 2000). Quantifying density-impact functions provides a more direct route than trial-and-error for setting targets for pest control. However, a potential problem with density-impact functions is that they tend to be place- and time-specific, and do not include the effects of factors other than pests (see Ricciardi et al., 2013). An alternative and more robust approach than density-impact functions is to use dynamic consumer-resource models to predict pest impacts (Choquenot, 2006; Choquenot and Parkes, 2001), but these models can be difficult to parameterise because they require additional, often long-term, data that are logistically difficult or expensive to obtain, and we know of no conservation managers who use them.

Given that conservation managers are more likely to make use of targets for pest abundance than fully-fledged consumer-resource models, we aim in this paper to clarify the circumstances under which density-impact functions should be used. We begin with an outline of the theoretical types of density-impact functions applicable to many invaded systems worldwide, and provide empirical evidence for each. Throughout this paper, we use 'density-impact functions' (or DIFs) as a collective term for relationships between pest density and impact. These have been termed 'damage functions' elsewhere (e.g. Hone, 2007), where the response variable can be either economic or ecological impacts (Hone, 2007; Yokomizo et al., 2009). We discuss the advantages and pitfalls of DIFs for conservation, and suggest practical guidelines for their derivation and use.

2. Types of density-impact functions

Six types of theoretical DIFs are illustrated in Fig. 1 (although other functions are possible, e.g. Kornis et al., 2014). Technically, impacts can be either positive or negative. For clarity and ease of comparison among these functions, we discuss them in terms of positive responses of the impacted species, for example survival rates rather than mortality rates.

'Proportionate' functions represent the default condition where there are consistent, incremental changes in the response of impacted biota to incremental changes in pest density (Fig. 1a; Type III in Yokomizo et al., 2009). Non-linear functions (Fig. 1b–d) indicate disproportionate responses to changes in pest density and help determine triggers for management intervention (Suding and Hobbs, 2009). This might involve a threshold if the response variable changes rapidly with small changes in pest density. Three basic types of non-linear relationships are shown. 'Highly vulnerable' biota are characterised by major negative impacts across a wide range of pest densities. They may have few pest-avoidance or defence behaviours or lack chemical defences. Positive responses occur only when pests are suppressed to very low densities or, in extreme cases, when all pests are removed (Fig. 1b; Type I in Yokomizo et al., 2009). 'Resistant' biota suffer major negative impacts only at high pest densities (Fig. 1c; Type IV in Yokomizo et al., 2009). 'Moderately resistant' biota are intermediate between the highly vulnerable and resistant conditions — in that scenario, major negative impacts occur at intermediate-to-high pest densities (Fig. 1d; Type II in Yokomizo et al., 2009). This function demonstrates the existence of processes that can block the negative impacts of pests under some conditions. 'Insensitive' biota reflect the null hypothesis of no impact for all pest densities (Fig. 1e). A sixth DIF exists for biota that respond *favourably* with increasing pest density ('Indirectly advantaged' species; Fig. 1f). For example, some indigenous species are unaffected directly, but benefit from the removal of indigenous competitors or predators by pests.

A wide range of variables can be monitored in response to changes in pest density. The appropriate choice will depend on a clearly defined management goal. For instance, goals might be species-focused or aimed at broader community or ecosystem outcomes. They might be short-term or long-term, and relate to single or multiple pest species. Species-focused examples of response variables include occupancy, abundance, population density, vital demographic rates such as survival or fecundity, rates of increase, and distribution. At the community level, response variables could be richness and diversity of indigenous species, and the physical structure of plant communities (Forsyth et al., 2010; Wardle et al., 2001), and at the ecosystem-level, variables can include processes such as pollination (Kelly et al., 2006a,2006b; Pattemore and Wilcove, 2012), seed dispersal (e.g., Williams et al., 2010) and nutrient cycling (e.g. Fukami et al., 2006; Maron et al., 2006).

3. Protocol for literature search

We were guided by Woodcock et al.'s (2014) method for reviewing literature. Our two criteria for including terrestrial studies in this review were: (1) they were published and peer-reviewed, and (2) plotted the relationship between pest abundance and the impacted resource. Relationships were derived mostly from empirical data or by modelling, but some were schematic hypothesised relationships based on the authors'