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Abiotic and biotic interactions determine whether increased colonization is beneficial or detrimental to metapopulation management

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ABSTRACT

Increasing the colonization rate of metapopulations can improve persistence, but can also increase exposure to threats. To make good decisions, managers must understand whether increased colonization is beneficial or detrimental to metapopulation persistence. While a number of studies have examined interactions between metapopulations, colonization, and threats, they have assumed that threat dynamics respond linearly to changes in colonization. Here, we determined when to increase colonization while explicitly accounting for non-linear dependencies between a metapopulation and its threats. We developed patch occupancy metapopulation models for species susceptible to abiotic, generalist, and specialist threats and modeled the total derivative of the equilibrium proportion of patches occupied by each metapopulation with respect to the colonization rate. By using the total derivative, we developed a rule for determining when to increase metapopulation colonization. This rule was applied to a simulated metapopulation where the dynamics of each threat responded to increased colonization following a power function. Before modifying colonization, we show that managers must understand: (1) whether a metapopulation is susceptible to a threat; (2) the type of threat acting on a metapopulation; (3) which component of threat dynamics might depend on colonization, and; (4) the likely response of a threat-dependent variable to changes in colonization. The sensitivity of management decisions to these interactions increases uncertainty in conservation planning decisions.

1. Introduction

Modifying landscape connectivity has long been considered an effective conservation strategy for species occupying metapopulations. Metapopulations, which consist of distinct populations subject to extinction and connected by colonization (Levins, 1969), occur naturally, but are also becoming increasingly prevalent due to habitat loss and fragmentation (Hanski and Gilpin, 1997). To improve metapopulation persistence, restoration strategies often focus on enhancing colonization by developing habitat corridors or 'stepping stone' patches between populations (Beier and Noss, 1998; Dennis et al., 2013; Simberloff et al., 1992; Townsend and Levey, 2005). Implementing such measures can be beneficial to metapopulation persistence by increasing movement of individuals to new habitats and lowering the re-colonization time of vacant patches. These changes can in turn, increase equilibrium density, reduce local extinction rates, increase genetic variation

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and increase rescue effects (Brown and Kodric-Brown, 1977; Carroll et al., 2014; Hanski and Simberloff, 1997; Wade and McCauley, 1988).

Increased colonization can also have a negative impact on metapopulation persistence, although this link has received less attention in the conservation literature (Resasco et al., 2014). Metapopulations may be subject to abiotic or biotic threats that may adversely impact on species' extinction and colonization rates. Abiotic threats include landscape-level processes such as fire, flood and drought (Elkin and Possingham, 2008; Harrison, 1991; Vuilleumier et al., 2007; Wilcox et al., 2006), while biotic threats include disease, pathogens and predators (Davis et al., 2007; Hess, 1996; Kareiva, 1987; McCallum and Dobson, 2002; Ruokolainen et al., 2011). Biotic threats can be either specialists or generalists depending on the degree to which they rely on a specific prey type or host. Generalist threats can be relatively benign in some hosts but cause serious declines in others (McCallum, 2005), whereas specialist threats rely on a single prey type or host to survive. Both abiotic and biotic threats have caused the decline of many threatened species around the globe.

There is theoretical and empirical evidence to suggest that changes in colonization can influence the spread, abundance and exposure of threats to metapopulations (Atobe et al., 2014; Elkin and Possingham, 2008; Lopez et al., 2005; Resasco et al., 2014; Vuilleumier et al., 2007). For example, in marine systems such as coral reefs, both the movement of organisms and abiotic disturbances depend on ocean currents (Fausch et al., 2002; Le Corre et al., 2015; McClanahan et al., 2005; Pringle, 2001). In terrestrial systems, the incidence of landscape processes such as fire is often landscape-dependent (Holling, 1992). In the epidemiology literature, it is well-known that increased colonization can facilitate exposure of a metapopulation to a pathogen or disease, thereby reducing long-term persistence (Andreasen and Christiansen, 1989; Heard et al., 2015; Huang et al., 2015; Lopez et al., 2005; Sattenspiel and Castillochavez, 1990). In a similar manner, exposure to predators can increase when metapopulation colonization is increased. This could be due to either increased movement of prey to patches occupied by the predator or an increased ability of the predator to invade previously uninvaded patches (Holyoak and Lawler, 1996; Ruokolainen et al., 2011).

A plethora of studies have examined the effect of habitat loss and fragmentation on predator–prey and host–pathogen metapopulations (Bascompte and Sole, 1998; Nakagiri et al., 2001; Nee et al., 1997; Prakash and de Roos, 2002; Rushton et al., 2000; Schneider, 2001; Swinton et al., 1998); however, relatively little attention has been given to the potential negative effects of increased colonization in the context of conservation management. Some studies have used susceptible–infected (SI) and susceptible–infected–recovered (SIR) models to determine when it is beneficial or detrimental to increase colonization as a landscape restoration strategy. This work has focused on optimizing colonization for metapopulations subject to a specialist pathogen (Hess, 1996) with a constant input of infectious propagules from more abundant hosts outside the system (Gog et al., 2002), and for a generalist pathogen (McCallum and Dobson, 2002) with spillover from a secondary host (Harding et al., 2012). The results of these studies are contradictory; whether to increase (McCallum and Dobson, 2002) or decrease (Hess, 1996; Park, 2012) metapopulation colonization depends on the type of threat (specialist or generalist) and assumptions made regarding the dynamics of the network.

While these studies provide useful insight into the interaction between threats and colonization on metapopulation persistence, they are specific to host–pathogen systems and are not generally applicable to other types of threat that may act on metapopulations, such as predators, or abiotic processes (i.e. fire, flood or drought). By modeling host–pathogen systems, these studies assume threats respond at the same rate, or in constant proportion to changes in metapopulation colonization (McCallum and Dobson, 2002). While it is reasonable to expect colonization rates of a specialist disease or pathogen to equal colonization rates of a host, this is not necessarily true when considering changes in colonization rates of specialist predators, generalist threats or abiotic threats. Rather, colonization of threats that disperse independently to that of their prey/hosts are likely to respond non-linearly to changes in host/prey colonization rates. The importance of non-linear interactions among components of ecological systems is well-recognized (Didham et al., 2007); however, the effect of such interactions among threats, metapopulations and colonization is yet to be considered in landscape connectivity studies.

This study determined when it is desirable to increase metapopulation colonization while accounting explicitly for non-linear dependencies between a metapopulation and threat. We expand on previous modeling efforts to account for three types of threat: an abiotic threat, a generalist biotic threat, and a specialist biotic threat. Our approach is split into three parts. Firstly, we developed a novel method for determining the effect of increased colonization on metapopulation persistence while accounting for non-linear dependencies between a threat and metapopulation. We present this method generically for a susceptible metapopulation, then developed a method to find a 'tipping point' that determines when it is beneficial or detrimental to increase colonization. Secondly, we applied our rule to simulated metapopulations susceptible to the three types of threat. To do this, we identified which parameter describing the dynamics of each threat might depend on changes in colonization. Finally, we tested the sensitivity of metapopulation persistence to alternative plausible responses of the colonization-dependent threat variable. By doing this, we examined whether management decisions regarding colonization are sensitive to the nature of abiotic and biotic interactions.

2. Materials and methods

2.1. Patch occupancy metapopulation models

We constructed patch occupancy metapopulation models for three qualitatively different threat dynamics; an abiotic threat, a generalist threat and a specialist threat. First, we established a general model extending the original metapopulation model proposed by Levins (1969), and then we specified the model for each threat type. In each model, the proportion of patches occupied by the susceptible metapopulation h depends on the colonization rate of vacant patches c_h, and the extinction rate of occupied patches. In the absence of a threat, the extinction rate is given by e_h. When a threat is present, the extinction rate due to the threat is given by e_k (Bascompte and Sole, 1998). In the abiotic case, all patches are constantly exposed to a threat which means there are no threat dynamics to consider; the background extinction rate is uniformly inflated giving a combined extinction rate of $e_h + e_k$. In the generalist and specialist cases, we assumed a threat occupies the same patches as the susceptible species and explicitly modeled the dynamics. The proportion of patches occupied by the threat p is determined by the extinction rate e_p and the colonization rate c_p of the threat. We assumed a metapopulation is exposed to one threat at a time and not combinations of each. A summary of model parameters is provided in Table 1.

2.2. Accounting for dependencies between a threat and colonization

Our aim was to investigate how changes in the colonization rate of a metapopulation affect persistence (i.e. the proportion of