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OPINION

Integrating theory into disturbance interaction experiments to better inform ecosystem management

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Abstract

Managing multiple, interacting disturbances is a key challenge to biodiversity conservation, and one that will only increase as global change drivers continue to alter disturbance regimes. Theoretical studies have highlighted the importance of a mechanistic understanding of stressor interactions for improving the prediction and management of interactive effects. However, many conservation studies are not designed or interpreted in the context of theory and instead focus on case-specific management questions. This is a problem as it means that few studies test the relationships highlighted in theoretical models as being important for ecological management. We explore the extent of this problem among studies of interacting disturbances by reviewing recent experimental studies of the interaction between fire and grazing in terrestrial ecosystems. Interactions between fire and grazing can occur via a number of pathways; one disturbance can modify the other's likelihood, intensity or spatial distribution, or one disturbance can alter the other's impacts on individual organisms. The strength of such interactions will vary depending on disturbance attributes (e.g. size or intensity), and this variation is likely to be nonlinear. We show that few experiments testing fire–grazing interactions are able to identify the mechanistic pathway driving an observed interaction, and most are unable to detect nonlinear effects. We demonstrate how these limitations compromise the ability of experimental studies to effectively inform ecological management. We propose a series of adjustments to the design of disturbance interaction experiments that would enable tests of key theoretical pathways and provide the deeper ecological understanding necessary for effective management. Such considerations are relevant to studies of a broad range of ecological interactions and are critical to informing the management of disturbance regimes in the context of accelerating global change.

Keywords: antagonisms, compound effects, disturbance ecology, fire, grazing, higher order effects, multiple stressors, synergisms, terrestrial ecosystems

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Introduction

Disturbance is a major driver of change in ecosystems and is central to both fundamental and applied ecology. As climate change and anthropogenic pressures are driving substantial changes to disturbance regimes such as fire, severe weather and biological invasions, understanding the factors affecting disturbances and their ecological impacts will be essential to the effective future management of terrestrial ecosystems (Dale *et al.*, 2001; Turner, 2010). Recent advances in disturbance theory include improved understanding of the spatial variability of disturbance effects (Turner, 2010), and the potential for cross-scale effects (Peters *et al.*, 2007) and legacy effects (Essl *et al.*, 2015) to produce unanticipated changes in ecosystems. Another key advancement, and one with strong management applications, is the acknowledgement of the prevalence of disturbance interactions (Wisdom *et al.*, 2006; Turner, 2010), their ability to produce ecological surprises (Lindenmayer *et al.*, 2010; Doherty *et al.*, 2015), and the range of mechanistic pathways by which these interactions can occur (Didham *et al.*, 2007; Buma, 2015). An important question, however, is whether empirical studies have kept pace with theoretical advances, and the implications this has for informing effective ecological management.

As theoretical models are widely used in conservation decision-making, advances in disturbance theory

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have the potential to guide substantial improvements in the management of disturbance regimes (Driscoll & Lindenmayer, 2012). For example, several recent papers have demonstrated how a disaggregated, mechanistic understanding of the effects of disturbance and land use change on ecosystems could lead to more effective, and potentially novel, solutions for ecological management (Didham *et al.*, 2007; Fuhlendorf *et al.*, 2009; Peters *et al.*, 2011). For theory to effectively inform management, however, it needs to be paired with empirical studies that test its applicability to the local context (Driscoll & Lindenmayer, 2012). Yet, while there are many excellent examples of such studies (e.g. Mandle & Ticktin, 2012; Kimuyu *et al.*, 2014), the majority of empirical conservation studies are not well integrated with theory, and this potentially limits both theory development and management applications (Belovsky *et al.*, 2004; Fazey *et al.*, 2005; Barot *et al.*, 2015).

Here, we examine how well the experimental literature has integrated recent theoretical developments on disturbance interactions, and how this affects management implications. We focus on examples from studies of fire–grazing interactions as they are among the most commonly studied disturbance interactions in terrestrial ecosystems, and as fire and grazing are both commonly managed, much research has focussed on how prescribed fire (e.g. burn frequency) and grazing regimes (e.g. stocking density) can best be managed for biodiversity conservation. We use a mini-review of recent fire–grazing interaction experiments to highlight the gaps between theoretical and experimental studies, and the effect this has on the ability of experimental studies to inform management decisions. We then discuss how relatively simple changes to the way interaction experiments are designed and interpreted will strengthen their links with the theoretical literature, and in doing so, will improve the ability of experimental studies to provide useful information for the management of multiple disturbances.

Recent advances in disturbance interaction theory

The study of disturbance interactions has evolved largely from work on multiple stressor effects in marine systems, which is based on the 'additive' model of interactions (Folt *et al.*, 1999; Crain *et al.*, 2008). Under this model, interactive effects occur when the combined effects of two environmental stressors is greater than (synergism) or less than (antagonism) the sum of their individual effects (Folt *et al.*, 1999). Although the additive model has formed the basis of countless experimental studies of the effects of multiple stressors (reviewed by Brook *et al.*, 2008; Crain *et al.*, 2008; Darling & Côté, 2008; Jackson *et al.*, 2015; Przeslawski *et al.*, 2015), current theory recognises disturbance interactions as complex, spatially and temporally variable processes (Peters *et al.*, 2004; Wisdom *et al.*, 2006; Turner, 2010; Buma, 2015). This theory includes two recent advances which have the potential to dramatically improve our ability to predict and manage the outcomes of disturbance interactions; (1) characterisation of the different mechanistic pathways driving interactions and (2) increasing acknowledgement of the likelihood of nonlinear interactive effects.

Several recent syntheses have focussed on the mechanistic pathways by which multiple disturbances (or stressors) interact and the value of identifying interaction pathways for designing effective and novel management interventions (Didham *et al.*, 2007; Tylianakis *et al.*, 2008; Oliver & Morecroft, 2014; Boyd & Brown, 2015; Buma, 2015; Doherty *et al.*, 2015). A variety of terms have been used to describe these different interaction pathways, but despite differences in the stressors discussed, most studies separate interactions into two broadly similar 'types' (Table 1). We adopt the terminology of Didham *et al.* (2007), who separate interactions into (1) *interaction chain* effects, where one disturbance affects the occurrence or magnitude of a second disturbance, and both disturbances have a direct effect on the response variable, and (2) *interaction modification* effects, where the per-unit effect of one disturbance on the response variable depends on the environmental context of a second disturbance (Fig. 1). We use the definitions of Didham *et al.* (2007), as they are among the first presented in the literature, and while originally developed in the context of habitat modification and invasive species interactions, have been successfully adapted to characterise interactions between other stressors, both biotic and abiotic (e.g. Mandle & Ticktin, 2012; Oliver & Morecroft, 2014). Regardless of the terminology and definitions used, a focus on identifying the mechanistic pathways driving disturbance interactions has the potential to provide valuable insights for ecological management and potentially lead to novel solutions for processes that may be difficult to manage directly (Didham *et al.*, 2007; Peters *et al.*, 2011; Boyd & Brown, 2015; Doherty *et al.*, 2015). For example, feral predators have substantial impacts on many native species, but broad-scale control is often unfeasible. However, as predation success is modified by habitat complexity, it may be possible to conserve native species by improving fire management to maintain complex habitats (i.e. managing the interaction modification) (Doherty *et al.*, 2015).

The theoretical literature also acknowledges the likelihood that many interactions will have nonlinear effects on ecosystems, potentially leading to alternate

Table 1 Summary of the terms and definitions used to distinguish interaction 'types' in recent reviews of ecological interactions. Types are sorted according to how they align with the definitions of interaction chains and interaction modifications provided by Didham *et al.* (2007)

	Context		Interaction 'types' and their definitions		
Paper	Ecosystem	Disturbances/stressors	Interaction chain	Interaction modification	
Didham *et al.* (2007)	Broad range of both terrestrial and marine ecosystems	Invasive species and habitat modification	Interaction chain (numerically mediated): total impact changes because of a numerically scaled response (of the first driver) to a second driver variable	Interaction modification (functionally moderated): the per capita impact of one driver is dependent on the level of effect of a second driver	
Oliver & Morecroft (2014)	Terrestrial ecosystems	Climate change and land use change	Interaction chain: one driver changes the magnitude of another driver and both drivers have a direct effect on the response variable	Interaction modification: the per capita effect of one driver changes depending on the level of another driver	
Ban *et al.* (2014)	Coral reefs	Multiple stressors, both biotic and abiotic	Stressor interactions: where one stressor directly influences another	Synergistic effects: where two stressors interact to produce an effect on a response variable that is greater than purely additive	
Doherty *et al.* (2015)	Terrestrial ecosystems	Invasive predators and disturbance	Numerical impact: where a disturbance increases the abundance of the invasive species	Functional impact: where a disturbance changes the per capita impact of an invasive species	Compounding impacts: where the effect of disturbance on a population changes its ability to cope with invasion
Boyd & Brown (2015)	Marine ecosystems	Environmental drivers, focussing on warming and ocean acidification	Physiochemical interactions: interactions that occur directly between drivers, outside of organisms	Physiological interactions: where an organism's physiological response to one driver changes with the level of another driver	Food web interactions: where interactive effects on organisms occur indirectly, via changes in food webs or ecosystem functioning
Buma (2015)	Broad range of both terrestrial and marine ecosystems	Wide range of disturbances	Linked interactions: one disturbance increases or decreases the likelihood, spatial extent, intensity or severity of a second disturbance	Compound disturbance: recovery from a second disturbance is more or less likely, or at altered speed, due to the initial disturbance	
Jackson (2015)	Marine, terrestrial and freshwater ecosystems	Multiple invasive animals	Interactions among invaders: where the presence of one invader influences the performance of a second invader	Combined impacts: where the presence of one invader influences another's impact on the ecosystem	

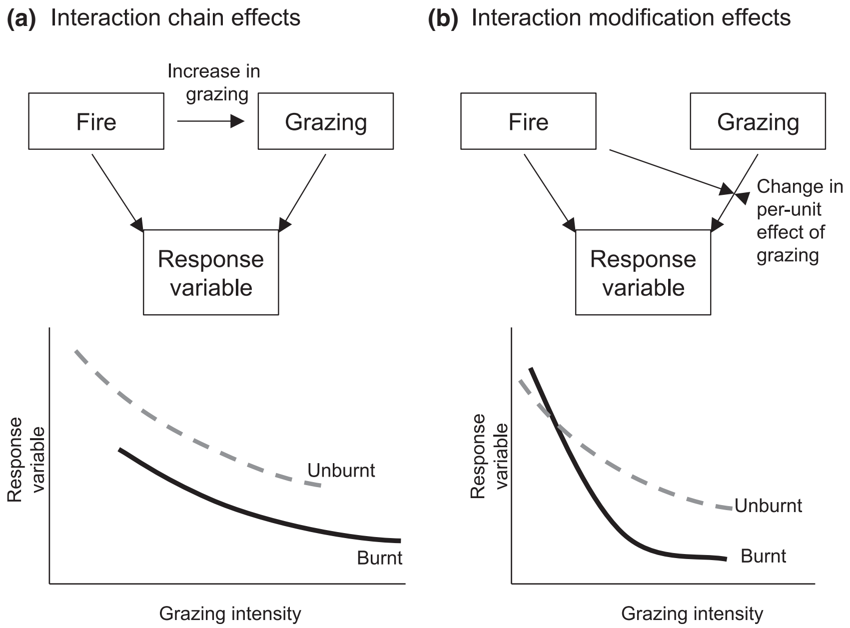

Fig. 1 The two major pathways by which fire and grazing can interact to affect biota (adapted from Didham *et al.*, 2007). (a) An interaction chain effect, where fire affects the spatial distribution or intensity of grazing, which in turn has a direct effect on the response variable (e.g. plant or animal abundance), but the per-unit effect of grazing on the response variable remains unchanged. A chain interaction also can occur in the opposite direction, with grazing affecting the spatial location, spread and intensity of fire. (b) An interaction modification, where the per-unit effect of grazing on the response variable is modified by the occurrence of fire. This interaction can also occur where grazing modifies the effect of fire on the response variable. The response curves shown are only one example of many possible relationships. The slope and direction of responses, and the direction and strength of interactions will vary depending on the ecosystem, disturbances and organisms (response variables) studied.

states (Peters *et al.*, 2004; Wisdom *et al.*, 2006; Oliver & Morecroft, 2014; Kayler *et al.*, 2015). These nonlinear effects can occur both in chain (Didham *et al.*, 2007) and modification interactions (Dunne, 2010). Further, when chain and modification interactions both occur, their net effects may become nonlinear through cross-scale interactions (Peters *et al.*, 2007). When the effects of disturbances and their interactions are nonlinear, knowledge of key points, such as when a small change in disturbance intensity has a large effect on biodiversity (or vice versa), are potentially invaluable for informing targeted and effective management (Peters *et al.*, 2004; Huggett, 2005; Groffman *et al.*, 2006; Didham *et al.*, 2007). For example, the effect of fire on the susceptibility of forests to pine-beetle attacks is nonlinear: low severity fire can increase the susceptibility of forests to pine-beetle outbreaks (Kulakowski & Jarvis, 2013), while high-severity, stand-replacing fires can reduce forest susceptibility to the same pests (Kulakowski *et al.*, 2003). Knowledge of these nonlinear effects, and estimates of the threshold at which effects switch from negative to positive would allow managers to adjust fire management practices, and/or conduct target management of local beetle outbreaks, to minimise the risk of widespread pine-beetle infestations.

Where are the gaps between theory and experimental studies?

Many experimental studies of disturbance interactions aim to inform management decisions, citing conservation challenges as motivation for the study, or providing management recommendations based on their findings. However, few studies focussing on conservation problems are well integrated with theory (Fazey *et al.*, 2005; Barot *et al.*, 2015), despite the acknowledged value of using a strong conceptual framework to guide empirical research (Driscoll & Lindenmayer, 2012; Barot *et al.*, 2015), and the popularity of conceptual models for guiding management decisions (Williams, 2011). To assess the extent of this problem among studies of disturbance interactions, we focussed on the two recent conceptual advancements highlighted previously: (1) the mechanisms driving interactions and (2) nonlinear interactive effects on ecosystems or biota, and quantified the extent to which these concepts have been addressed in recent studies of fire–grazing interactions. To do this, we reviewed 50 recent papers that focussed on fire–grazing interactions and were published between 2011 and 2015 (Appendix S1). This mini-review was conducted to obtain a representative sample of recent studies of fire–grazing interactions (most of which were experimental) which we could use to answer specific questions about the current literature and is not intended as a comprehensive literature review. The 2011 cut-off was selected as a number of key conceptual studies were published in the years 2007–2008 (e.g. Didham *et al.*, 2007; Peters *et al.*, 2007; Brook *et al.*, 2008; Crain *et al.*, 2008; Darling & Côté, 2008), and the 2011 cut-off allowed some lag time for these ideas to become integrated into experimental studies.

Mechanisms driving interactions

Do experimental studies identify interaction pathways?

Fire and grazing can interact via a number of different pathways. For example, fire can affect the intensity and spatial distribution of grazing as many herbivores preferentially graze in burnt areas (a chain interaction often referred to as fire-driven grazing or pyric herbivory) (e.g. Allred *et al.*, 2011). Similarly, grazing can affect the location and intensity of fires by modifying the distribution of fine fuels (also a chain interaction) (e.g. Kimuyu *et al.*, 2014). At a more local scale, fire and grazing, by altering the composition, traits or condition of biological communities or individual organisms, can alter each other's effects on those organisms (an interaction modification) (e.g. Eby *et al.*, 2014). However, few of the studies we reviewed identified the mechanistic pathways driving the fire–grazing interaction, despite 80% of these papers citing management applications as a motivation for the study. Of the 50 studies reviewed, only one quantified the relative contributions of both chain and modification effects in the interaction (Mandle & Ticktin, 2012), and 30 did not quantify any pathway, reporting only net effects of the interaction (Fig. 2). Of these 30 studies, five included description of more than one potential pathway driving the observed effects, 15 described only one potential pathway, and 10 did not provide any ecological definition of how the 'interaction' might be occurring (Fig. 2).

Overall, 30% of the fire–grazing studies we reviewed discussed only one interaction type, but did not provide evidence that this interaction type was driving the observed effects. For example, 13 of the 22 studies that defined only chain interactions (mostly fire-driven grazing) actually tested for net interactive effects and did not quantify the extent to which fire affected herbivory (Fig. 2). As it has been demonstrated that burning does not always affect herbivore site selection (McGranahan *et al.*, 2012), the interaction detected by such studies may be caused by a chain, or a modification, or both. By defining only one interaction type, but testing for net effects, these studies make the implicit assumption that the defined interaction is driving the fire–grazing interaction, which may or may not be true.

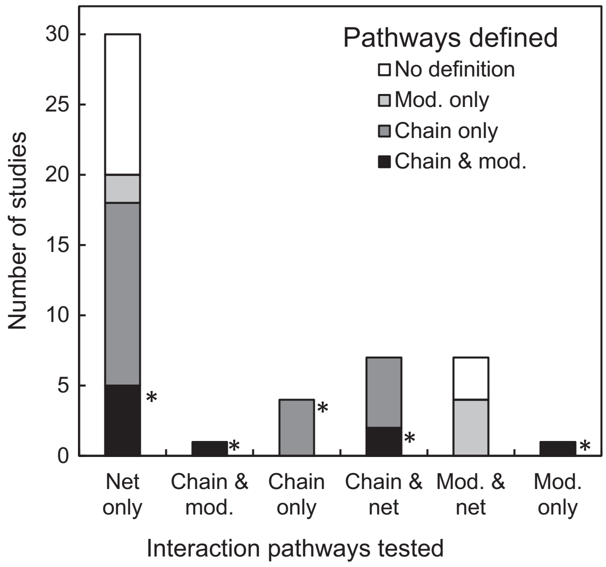

Fig. 2 A comparison of the interaction pathways described or defined by studies of fire–grazing interactions, vs. the pathways actually tested in the study (chain = interaction chain, mod. = interaction modification, net = tests for interactions that do not isolate interaction pathways, and hence may result from chain, or modification effects or a combination of the two). Numbers are based on a review of 50 fire–grazing interaction studies published between 2011 and 2015. *Indicates combinations where the definition used was appropriate for the interactions tested (n = 13).

How does not identifying the interaction pathway affect management applications?

Studies which make untested assumptions about interaction pathways could potentially be harmful, rather than useful for land management. We illustrate this with an example, based on a recent study by Foster *et al.* (2015), who found that fire and herbivory by native macropods interacted via both an interaction chain, and an interaction modification, to reduce the diversity of forest understory vegetation. If the authors had measured the net effect of the interaction and based their management recommendations on an assumption about the interaction pathway, then these recommendations would be likely to lead to little improvement, or even deterioration of biodiversity (Fig. 3). For example, if the authors had assumed that the interaction occurred through an interaction chain, they may have recommended changing fire management to prevent herbivores concentrating in burnt areas (e.g. by increasing the area burnt). However, due to the

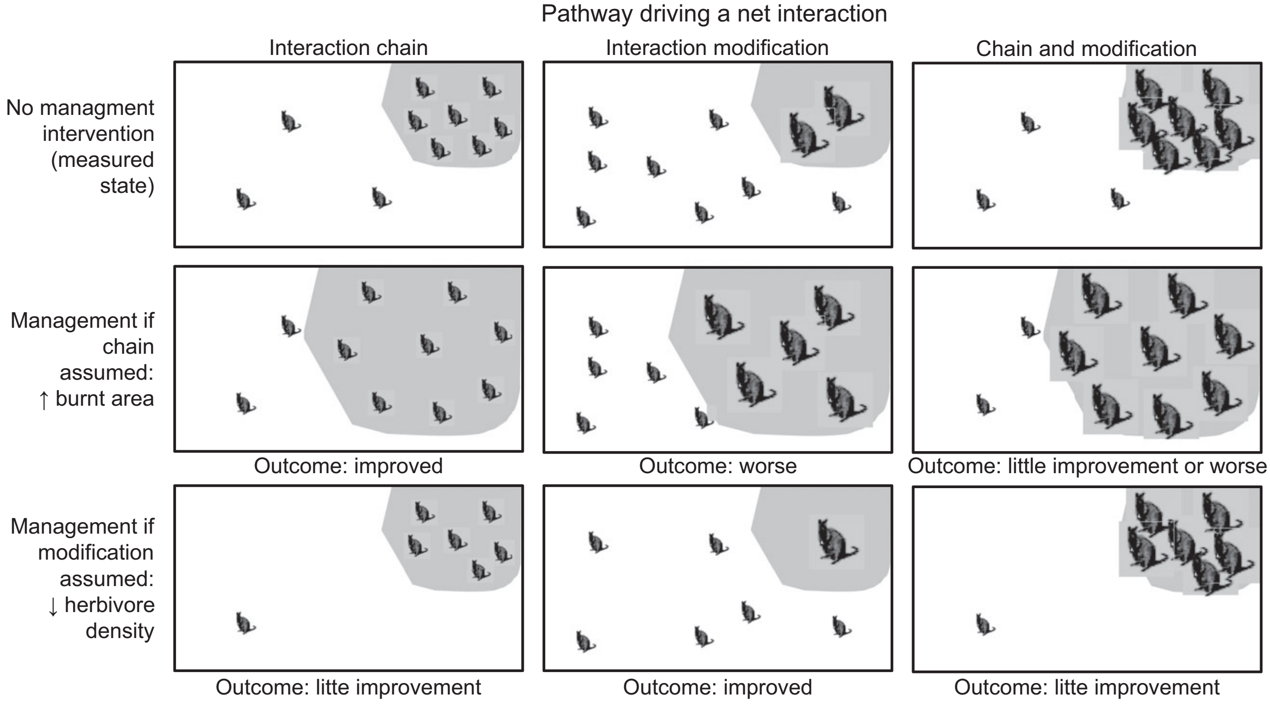

Fig. 3 Schematic diagram illustrating how incorrect assumptions about interaction pathways can lead to ineffective, or even damaging, management interventions. In the presence of an interaction chain, herbivores congregate in burnt areas (grey shading), while in the presence of an interaction modification, the per-herbivore impact is greater in burnt than unburnt areas (larger size of herbivore indicates larger per-herbivore impact). Managing for one interaction (e.g. an interaction chain), when the observed effects are predominantly driven by a different interaction pathway (e.g. an interaction modification), can result in unexpected outcomes. Note that the 'outcomes' in this example are based on the study of Foster *et al.* (2015), where fire and grazing interacted to negatively affect plant diversity, and so the aim of management interventions would be to maintain plant diversity by reducing interactive effects.

presence of an interaction modification, reducing grazing pressure in burnt sites by increasing burn size is unlikely to mitigate all interactive effects and may actually increase negative effects on plants by increasing the proportion of the population that is exposed to the interactive effects (Fig. 3).

Similarly, the converse assumption (that the interaction occurred solely through an interaction modification) also could lead to ineffective management recommendations. If an interaction modification was assumed, the authors may have recommended control measures to reduce the abundance of macropod herbivores. However, due to the presence of an interaction chain, where herbivores were attracted to burnt areas, general population control may do little to reduce grazing pressure in burnt areas, and therefore not mitigate negative interactive effects (Fig. 3). As population control of native herbivores is both resource-intensive and socially unpopular (Nugent *et al.*, 2011), a control programme that does not achieve the desired benefits for biodiversity is not only a waste of resources, but could compromise the ability of managers to implement similar programmes in the future. This example demonstrates how failure to integrate theoretical concepts on interaction pathways into the design and interpretation of experimental studies could limit their ability to effectively inform the management of multiple disturbances.

Nonlinear interactive effects on ecosystems and organisms

How well do experimental studies test for nonlinear effects?

Among the 50 papers we reviewed, there were two common study designs used to investigate fire–grazing interactions; patch-burning experiments (15 papers) and factorial experiments (27 papers). Few studies (12%) of either type were able to detect nonlinear effects. Most patch-burning studies compared 'homogenous' grazed areas with 'heterogeneous' patch burnt and grazed areas, under constant grazing intensity and burn size. Only two of the 15 studies using a patch-burning design varied any characteristics of the burns (e.g. size of the burnt area), and none tested the how interaction strength was affected by grazer density or species. While not testing for nonlinear interactions, a further three studies did test the consistency of interactive effects across sites with different management histories.

All of the studies that identified an interaction modification (nine studies), and many studies which tested net effects (18 studies), used a factorial study design, combining different levels of fire (most often burnt/unburnt) and grazing (most often grazed/un-grazed) at the plot level. To detect nonlinear interactive effects, factorial studies must use more than two treatment levels for at least one disturbance (i.e. include treatment levels in addition to grazed/un-grazed and burnt/unburnt, or measure natural variation within these levels), and ideally include that factor as a continuous variable in analyses. However, of the 27 factorial studies we reviewed, only nine used more than two levels for either fire or grazing, and only three of these used either factor as a continuous variable in analyses. Thus, only three of 27 factorial studies and two of 15 patch-burning studies were of a design that could detect nonlinear interactive effects.

How does not identifying nonlinear effects affect management applications?

The management implications of failing to detect nonlinear effects differ slightly between chain and modification interactions, but most relate to the ability to extrapolate (or interpolate) results to untested situations or locations. Studies using patch-burn designs are testing for the ecological effects of a chain interaction ('pyric herbivory'), where herbivores are attracted to the fresh growth after fire, resulting in high grazing intensity in burnt patches (Fuhlendorf *et al*., 2009). However, although it is acknowledged that the extent to which fire drives grazing patterns may vary with the intensity, duration and timing of grazing, as well as with the size, shape, intensity and timing of fire (Fuhlendorf *et al*., 2009; Sensenig *et al*., 2010; Allred *et al*., 2011) (Fig. 4), most patch-burning studies did not test whether any of these factors affected the strength of the fire–grazing interaction (but see McGranahan *et al*., 2013; Hovick *et al*., 2014), and the consistency of such relationships remains poorly understood. Most patch-burning studies are therefore able to detect the presence of an interaction at the levels of burning and grazing selected for that experiment, but cannot reliably be used for inference beyond this specific combination of conditions. A manager who is faced with different conditions from those tested in a study is therefore provided with little useful information about whether changing stocking rates, harvest quotas or prescribed burns will improve biodiversity outcomes. By comparison, studies that tested effects over a gradient of fire sizes, or a range of stocking densities, would be able to give insights into the probable outcomes of changing management practices, as well as improve our fundamental understanding of the fire–grazing interaction.

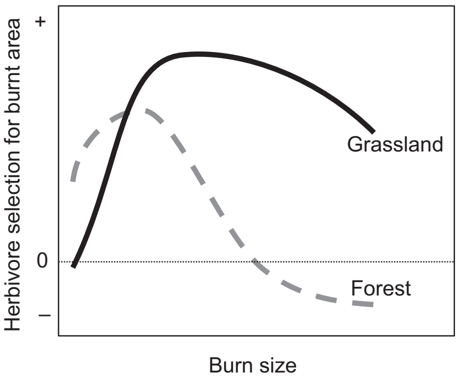

Fig. 4 Generalized relationships between burn size, and the extent to which herbivores select for the burnt area, demonstrating how chain interactions may vary with disturbance properties such as spatial scale, and between ecosystems (Fuhlendorf *et al*., 2009). Selection for burnt areas also varies between herbivore species (Sensenig *et al*., 2010), and under certain conditions, herbivores may select against burnt areas (e.g. if dense postfire regrowth hinders herbivore movements, Wan *et al*., 2014).

Studies of interaction modifications are also often limited in their ability to inform changes to management practices. This is because most studies are based on factorial experiments using binary treatments (i.e. 2 × 2 factorial designs). When the effects of disturbances, and their interactions, are nonlinear, the key points of interest from a management perspective are the points at which changes in one disturbance will have very large (e.g. points of inflection), or very small (e.g. beyond thresholds), effects on the variable of interest (Groffman *et al*., 2006)(Fig. 5a). Knowledge of the existence of these points, and their approximate values, would allow managers to identify: when management is most likely, or least likely to be successful; what level of management is required to achieve an outcome; or how management should differ in the presence of other disturbances (Groffman *et al*., 2006). However, factorial studies employing binary contrasts cannot detect these points (Fig. 5) and cannot be generalised beyond the levels chosen for study (Inouye, 2001), and hence are of limited use for predicting the outcome of changes to management.

Factorial experiments employing binary comparisons are also problematic because whether they detect synergisms or antagonisms can be entirely dependent on the levels chosen for study (Fig. 5; Dunne, 2010), but the management implications of synergisms and antagonisms are very different. Synergistic interactions can

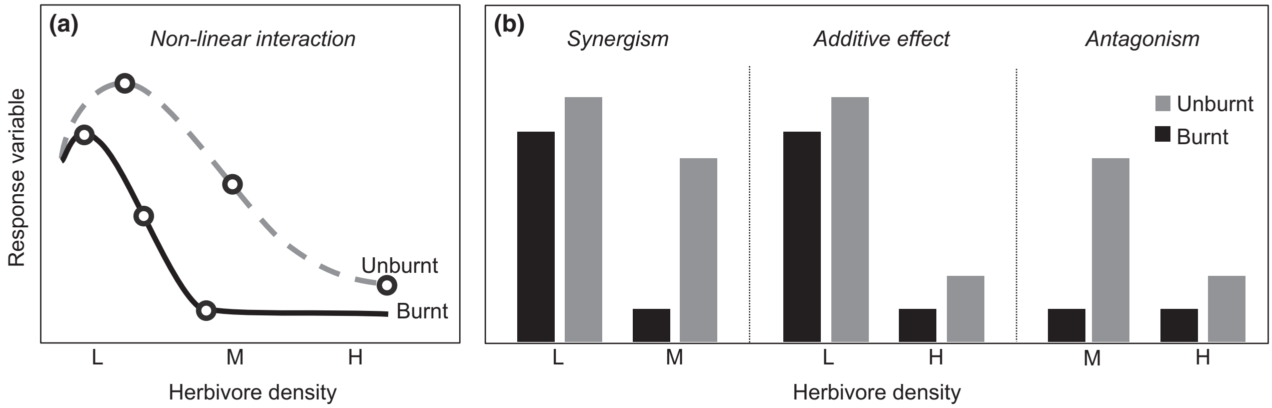

Fig. 5 When interactive effects are nonlinear, differences in interpretation can occur when examining disturbances as continuous or factorial treatments. (a) An hypothetical, nonlinear, interaction modification between fire and herbivory, showing the key points of management interest (turning points, shifts in marginal rates and limits; open circles) and how these vary across different levels of fire and herbivore density (L, low density; M, moderate density; H, high density). (b) The likely results of factorial studies in the same study system, showing how the experimental results will vary depending on the treatment levels chosen for comparison (L vs. M, synergism; L vs. H, additive effects; M vs. H, antagonism).

accelerate biodiversity decline, but synergisms may be more likely to respond to management, as managing one disturbance can mitigate the effects of both (Brown *et al.*, 2013; Piggott *et al.*, 2015). By contrast, mitigating the effects of antagonistic interactions usually requires both disturbances to be managed concurrently (Didham *et al.*, 2007; Brown *et al.*, 2013). Therefore, if the results of factorial studies are used to inform management, but the underlying relationships are nonlinear, unintended outcomes are likely to result.

As an example, Fig. 5a presents a hypothetical nonlinear interaction between fire and herbivory. In this example, a factorial study would detect; (1) a synergism if the herbivore densities compared were low and moderate; (2) no interaction if herbivore densities were low and high; and (3) an antagonism if herbivore densities were moderate and high (Fig. 5). If a factorial study compared low and high herbivore densities, the authors would likely conclude that fire and grazing were not interacting, and that reducing grazing intensity is likely to be the most effective action to increase the response variable. As can be seen in Fig. 5a, even if herbivore density were halved in this situation, there would be little change in the response variable in burnt environments, resulting in a waste of limited conservation resources. As field experiments tend to employ extreme treatments, with large effect sizes (Foster *et al.*, 2014), and synergisms are more likely to be detected when individual effect sizes are small (Folt *et al.*, 1999; Piggott *et al.*, 2015), factorial experiments may also under-estimate the occurrence of synergisms in natural ecosystems. Clearly, single-level factorial studies can miss a large (and potentially important) part of the picture if used to study nonlinear interactions. Therefore, researchers who aim to inform more efficient and effective management of terrestrial ecosystems through disturbance interaction studies should consider whether nonlinear effects are likely, and if so, explore alternatives to factorial designs which include a gradient of biologically and management-relevant treatment levels.

Bridging the gap to improve management applications

There is a lack of integration of theory into the design and interpretation of disturbance interaction experiments. We have demonstrated this by reviewing recent studies of fire–grazing interactions. We have also shown that this lack of integration means that interaction experiments, despite often being motivated by management problems, fall short of their potential in effectively informing the management of multiple disturbances. Land managers, faced with complex systems, competing demands and a mandate for transparent decision-making, often rely on system and management models to inform management practices (Underwood, 1995; Williams, 2011). A core role of experimental studies should therefore be to improve our understanding of the relationships on which such models are based (Underwood, 1995). As we have argued in this study, to do this requires experimental studies of disturbance interactions to more effectively, and broadly, engage with the theoretical literature. Closing the gap between the theoretical and experimental literature on disturbance interactions is not straightforward – interactions are complex, multiscale processes which can be difficult to manipulate experimentally. However, there are some adjustments that could be made to the design and interpretation of disturbance interaction studies which would both improve links with theory and generate more useful information for the management of multiple disturbances. While we have focussed on studies of terrestrial disturbance interactions in this study, similar experimental designs are used to study many other types of interactions, in a range of ecosystems. The problems and solutions presented below will therefore be relevant to the study of many kinds of ecological interactions.

Study design

Focus on testing the key relationships and interaction pathways identified in theoretical models as important for management

Most studies report the net effects of an experimentally manipulated interaction (Fig. 2), but it is difficult to generalise the results of such studies, and they often do not test the key relationships that make up management models. It is not always feasible, or desirable, to test all interaction pathways in a single study. However, future studies of disturbance interactions should explicitly identify the interaction pathway(s) being tested, and ensure that the study is conducted at an appropriate spatial and temporal scale. Such experimental tests of theoretically important relationships and pathways would allow theoretical models to be verified, which could then be used to inform decisions at management-relevant scales (Inouye, 2001; Belovsky *et al*., 2004; Cottingham *et al*., 2005; Denny & Benedetti-Cecchi, 2012).

Quantify variation in disturbances/stressors, as well as their ecological effects

Few experimental studies measure or analyse disturbances as continuous variables. However, environmental variation, and/or chain interactions mean that even if disturbance treatments are experimentally imposed, disturbance intensity/extent is likely to vary within treatments (i.e. between replicates). If measured, this variation can be used to a researchers' advantage, as by pairing this quantitative measure of disturbance directly with responses, researchers will be able to separately quantify chain and modification effects and test for nonlinear effects (Oliver & Morecroft, 2014).

Spread replicates across gradients, rather than pooling within treatments

Many studies are based on the additive model of interactions, and employ factorial designs, where single levels are replicated multiple times. However, as demonstrated in Fig. 5, factorial designs are inappropriate if interactions are nonlinear, as the results may be subjective (dependent on the treatment levels selected by researchers) and therefore misleading. Alternative regression-based study designs, where replicates are instead spread across a gradient of levels of a factor (e.g. stocking densities/fire sizes), would be better able to detect and describe nonlinear effects (Cottingham *et al*., 2005). It would not be feasible to test all combinations of two disturbance gradients in a single study. However, a gradient could be achieved for a single disturbance without a substantial increase in research effort compared with a factorial design. For example, a study with 24 sites in a factorial design would have six replicates for each of four treatment combinations (i.e. a 2 × 2 design). The same number of sites, if employed a regression-based design, could be spread across 12 different levels of one disturbance, and the two levels of the second disturbance (i.e. a 12 × 2 design).

Extend gradients outside their current 'natural' range

Most of the reviewed studies used binary comparisons of treatments in their experiments (e.g. burnt/unburnt or patch burnt/uniformly burnt), which are usually at 'moderate' or average levels of disturbance size or intensity. However, chain interactions with other disturbances, or with external global change drivers such as climate, have the potential to generate conditions, and levels of variation, that are outside the current natural range (Thornton *et al*., 2014; Kayler *et al*., 2015). Studies which test responses to conditions both within, and beyond current natural limits are therefore necessary to highlight potential thresholds or state-changes that are currently unlikely, but that may occur with these novel combinations of conditions (Belovsky *et al*., 2004; Kayler *et al*., 2015). For such studies, simulation and modelling tools will be useful for informing how far outside current ranges treatment gradients should extend (Kayler *et al*., 2015).

Interpretation

Clearly define the interaction being tested

Many studies do not clearly define which aspect of an interaction they are testing (Fig. 2). This makes it difficult for readers to interpret results. Clearly defining which pathway/aspect of an interaction is being tested, and ensuring that the design and analyses used actually test this component of the interaction, will allow the study to be interpreted within a broader context.

Frame and interpret studies in a broad theoretical context

Many studies of disturbance interactions focus their discussion and interpretation solely on the specific interaction being studied (e.g. most of the reviewed papers focussed exclusively on the fire–grazing literature in framing their studies). However, theoretical studies of interactions are often more generalised, or are focussed on other interactions or ecosystems, and so go unacknowledged in studies that are very specific in approach. Exploring and testing ideas developed from studies of different types of interactions and different systems is key to bridging the gap between theory and experimental studies (Peters *et al*., 2011; Buma, 2015).

Discuss results in the context of existing theoretical models

System models and management models are frequently used to inform management decisions. Yet many relationships in such models have not been experimentally verified (Knapp *et al*., 2011). Interpreting results in the context of existing theoretical models, and discussing whether results support theoretical pathways is key to improving these models, and hence management decisions.

Conclusions

Managing ecological interactions is a key challenge to biodiversity conservation, and one that is becoming increasingly important as global change drives rapid shifts in threats, abiotic conditions, and disturbance regimes (Brook *et al*., 2008; Turner, 2010). This challenge also presents an opportunity, through which a detailed, mechanistic understanding of ecological interactions can be used to develop novel solutions for biodiversity conservation. For example, failure to account for interactions between habitat modification and invasive species can cause invasive control programmes to be ineffective, or even harmful for native species (Norbury *et al*., 2013). However, a mechanistic understanding of habitat-predator interactions is now being used to develop management interventions that may be both more efficient and effective than lethal control for protecting wildlife from introduced predators (Didham *et al*., 2007; Doherty *et al*., 2015).

Carefully executed empirical studies, which are well integrated with theory, are essential for developing the detailed understanding that these novel solutions require. For example, novel strategies to conserve frogs that are threatened by the disease Chytridiomycosis have been identified, not from solution-focussed studies, but from well-designed empirical studies, grounded in theory, that investigated the multiple interacting processes affecting disease prevalence and impacts (Scheele *et al*., 2014; Heard *et al*., 2015). The suggestions we have presented for the design and interpretation of disturbance interaction studies aim to guide research that will provide a similar understanding for managing multiple stressors. By gaining a deeper, mechanistic understanding of interactions, such studies will be able to provide context-specific information to guide management while also testing and refining theoretical models, which can then be translated to other processes and ecosystems.

Many studies of disturbance interactions aim to improve the management of ecosystems. However, studies which focus on specific management problems and fail to integrate relevant theory are often limited in their broader management applications. There are many studies of ecological interactions that are well integrated with the theoretical literature (Mandle & Ticktin, 2012; Kimuyu *et al*., 2014), but such studies remain the exception, rather than the rule. Until this trend is reversed, disturbance interaction experiments will continue to fall short of their potential in informing effective ecological management.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of the 50 fire-grazing studies reviewed.