Species co-occurrence analysis predicts management outcomes for multiple threats

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Keywords: biodiversity, ecological networks, ecosystem collapse, livestock grazing, habitat clearing, occupancy model, network structure, Noisy Miner *Manorina melanocephala*, robustness, species loss

Article type: Article, Nature Ecology and Evolution

Abstract – 150 words

Main text (excluding introductory paragraph, methods, acknowledgements, references, table and figure legends) – 3431 words

Number of figures – 5

Number of tables – 1

References – 50

Author contributions:

AITT designed the study and performed analyses. DL designed the field monitoring and contributed to field surveys with AITT. AITT and IC developed the conceptual framework. All authors discussed results and wrote the manuscript.

The authors have no competing financial interests.

Mitigating the impacts of global anthropogenic change on species is conservation's greatest challenge. Forecasting the effects of actions to mitigate threats is hampered by incomplete information on species responses. We develop an approach to predict community restructuring under threat management, which combines models of responses to threats with network analyses of species co-occurrence. We discover that contributions by species to network co-occurrence predict their recovery under reduction of multiple threats. Highly-connected species are likely to benefit more from threat management than poorly-connected species. Importantly, we show that information from a few species on co-occurrence and expected responses to alternative threat management actions can be used to train a response model for an entire community. We use a unique management dataset for a threatened bird community to validate our predictions and, in doing so, demonstrate positive feedbacks in occurrence and co-occurrence resulting from shared threat management responses during ecosystem recovery.

Non-random patterns of species co-occurrence form the building blocks of communities [1]. Species co-occurrence results from niche overlap as well as biotic interactions such as competition, mutualism and predation. As a consequence, some taxa coexist more often and some less often than expected by chance [2]. Under global anthropogenic or environmental change, increasing evidence suggests that declines and extinctions of species change the number and magnitude of associations in a community [3,4]. Many of these co-occurrences may be vital to maintaining community structure and function [5]. Similarly, in ecosystems being managed to recover species from the impacts of threatening processes, co-occurrences develop in addition to (or because of) changes to community composition [6]. Understanding the conditions under which species' persistence and coexistence are likely to change is key to designing recovery actions that promote complex functioning communities.

Despite a critical need to account for dependencies such as overlapping ecological niches or species interactions when planning management [7], only a few large-scale predictions of the effects of recovery actions on community structure exist [8,9]. These studies are typically well-studied management systems such as fish communities where the impacts of actions such as harvesting have a long history of research,

and rarely if ever report on whether predictions were validated post-management. In less well-studied systems, research is still building knowledge on the ways that anthropogenic threatening processes drive community structure [10,11]. Those that assess the ability of management strategies to recover communities routinely focus on a subset of individual species or guilds for which the likely benefits of alternative actions can be estimated [7,12,13]. Accurately forecasting the likely responses to reductions in the extent or intensities of threats for all species occurring in realistic, large communities requires an enormous sampling effort across space and time. Waiting for this information to be collected can impede management efforts and even lead to species extinctions if mitigation actions are not delivered in a timely manner . To predict future community structure and composition under alternative management choices in less data-rich systems, new thinking is needed that scales up traditional species-based predictions of biodiversity change to a community-level without the requirement of knowledge on every species' response [4,14,15]. We propose that by using co-occurrence analysis to quantify community assembly in combination with partial information on expected species responses to management, it is possible to predict the future composition and structure of a community after reducing the impacts of cumulative threats.

Coexistence theory provides a useful framework to examine the effects of anthropogenic change and its mitigation on community co-occurrence and structure [16]. Species coexistence depends on a combination of niche and fitness differences and similarities [1,16], and is sensitive to changes in both the environment and species composition of communities. It is known that no two species with the same niche can stably coexist due to competitive exclusion [17]. For stable coexistence, stabilising niche differences between species (e.g. resource partitioning, species-specific natural enemies) must be greater than their relative fitness inequalities (e.g. ability to take up limited resources, shared enemies) [18]. In dynamic and rapidly changing environments impacted by anthropogenic activities, we therefore hypothesise that firstly, species that coexist in the presence of shared enemies or threatening processes share a similar response to the mitigation or elimination of those threats (as niche differences allow them to partition resources and maintain co-occurrence in the recovering landscape). Secondly, species with large fitness inequalities

84 facing the same threatening processes are less likely to coexist in the disturbed landscape, e.g. be spatially
85 segregated due to competitive exclusion by the fitter species and, subsequently, should respond in
86 dissimilar ways to removal of the threat.

87 Linking the individual contributions of species to a co-occurrence network with the vulnerabilities of
88 species to change helps to quantify changes in co-existence and enhance predictions of future community
89 structure [14,19,20]. Co-occurrence network analysis reveals the degree of displacement (negative links) or
90 coexistence (positive links) between species (network "nodes") in a community. Knowledge that a species
91 with many positive co-occurrences is likely to respond positively to management of a threatening process,
92 enables an understanding of how many, and which, additional species might be affected by that
93 management action (i.e. those with which it co-occurs) [20,21]. Loss of a species in an unmanaged site
94 indicates that the current threatening processes have contributed to its local extinction. Loss of a species
95 from sites after management intervention represents a perverse response of the species to threat
96 management due to changed environmental conditions or biotic interactions. According to coexistence
97 theory, we predict that species that previously positively co-occurred with a declining or lost species in
98 the threatened landscape should be more likely to decline or go extinct than other species due to shared
99 environmental requirements. The effects of change in species with high negative co-occurrence are less
100 straightforward to predict. If species A maintained negative co-occurrence with species B through
101 competitive exclusion, we could expect species B to increase if the species with a competitive advantage,
102 here species A, declined [1,16]. If negative co-occurrence was due to non-overlapping niches, species B
103 should be unaffected by species A's decline or extinction.

104 Here we develop an approach to predicting the community-wide consequences of alternative
105 management actions for mitigating multiple threats to biodiversity. Our approach combines traditional
106 species-level knowledge of responses to anthropogenic change [22] with co-occurrence network analyses [19]
107 that determine the structure of the species assemblage. Pioneering explorations of large-scale changes to
108 community assembly using co-occurrence networks focused on single threats such as climate change [19]
109 and therefore failed to address the reality of landscapes facing multiple-threats [23]. Because the threats

faced by communities have both positive and negative impacts and importantly do not result in universal species declines [24], the likely impacts of actions to mitigate multiple threats must be considered simultaneously [13,22].

We present a case study of a bird community in an endangered woodland facing three pervasive threats that have impacts on species around the globe [25]: habitat loss, grazing, and an overabundant native species with community impacts analogous to an invasive competitor. We determine the co-occurrence characteristics of individual species under present levels of the three threats for the entire community (the pre-management community) [26]. We identify probable change in colonisation rates and therefore landscape occupancy of a subset of species for which responses to reducing one or more of the threatening processes can be modelled (see Figure 1). We ask: Do species with similar predicted responses to threat management tend to co-occur and perform similar roles in structuring the threatened community? The answer to this question informs whether species sharing the same patches in a threatened landscape are more likely to respond in an analogous way to recovery actions than species persisting in different patches. If species sharing management responses co-occur, then we should be able to predict the responses of the remainder of the community for which no information is available on likely responses to recovery actions, using information on their shared links with species benefitting or declining from management. Using this knowledge, we make predictions about re-structuring of the entire co-occurrence network after threat reduction (Figure 1). After five years of experimental management of threats to the ecological community, we validate our predictions using networks built from subsets of the community in different stages of recovery (post-management communities that have experienced different threat mitigation actions).

Results

Species co-occurrence and expected responses to threat reduction

The first step of our approach (see *Step 1: Characterising species co-occurrence under threat*; Figure 1) quantified the likelihood and strength of co-occurrence between each of the possible pairwise 3828 co-

136 occurrences in our pre-management bird community of 88 species. We discovered 401 significant positive
137 co-occurrence links between species (range 1 to 35 shared distributions per species) and 166 significant
138 negative links (range 1 to 33 per species; Figure 2). The percentage of significant (i.e. non-random)
139 associations (14.8% of all possible links) and the ratio of more positive than negative links are consistent
140 with studies of ecological and physical networks from around the globe [27].

141 To determine how community structure might change under reduction of one or more threatening
142 processes (see *Step 2: Characterising Individual species colonisation dynamics under threat* in Methods;
143 Figure 1), we modelled each species' likely change in patch colonisation as the interaction between the
144 strength of its pairwise positive or negative co-occurrence links, its individual network co-occurrence
145 characteristics (proportion of positive or negative links with other species that were significant), and the
146 expected change in patch colonisation of each linked predictor species. Less than half of the network (37
147 species) had sufficient detections to predict expected changes in patch colonisation under reduction of
148 one, two or three threatening processes (livestock grazing, tree clearing, and a hyper-aggressive native
149 competitor, the Noisy Miner *Manorina melanocephala*, listed as a Key Threatening Process under the
150 Environment Protection and Biodiversity Act in Australia in 2011 [28]). Patch colonisation probabilities under
151 one, two, three or no threats were modelled using a set of dynamic occupancy models with different
152 threats as predictors, and the difference between colonisation under reduced intensities of threats and
153 current high intensities of threats used to quantify expected change in colonisation per species. Several
154 species maintained high patch colonisation rates even in the face of multiple threats, although average
155 colonisation rates tended towards zero as the number of threatening processes increased
156 (Supplementary Figure 2; see also [22]). We discovered consistent relationships between species' predicted
157 change in colonisation under threat management (calculated as the difference in patch colonisation with
158 and without threats) and co-occurrence, despite variability in species-level impacts of the three processes
159 (Figure 3). For actions mitigating multiple threats (Figure 3a-d), we found that if two species shared a
160 positive link (pairwise co-occurrence strength between species 1 and 2 >0) and species 2 was likely to
161 increase due to colonisation under threat mitigation (change in colonisation >0, predicted only for the 37

species with sufficient data), then species 1 was also predicted to increase. Conversely, if two species shared a positive link and species 2 was more likely to decline under management of multiple threats, then the second species would decline as well. Species pairs with negative links were predicted to behave in the opposite manner; if one was predicted to increase, the other was more likely to decline in colonisation, and vice versa. The strongest effects were observed when all three threats were reduced (Figure 3a).

For two of the three independent mitigation actions, network co-occurrence characteristics of individual species best predicted each species' likely change in patch colonisation (Figure 3e, g). The interaction between pairwise species co-occurrence and predicted patch colonisation change was not significant. When only habitat loss was mitigated, the species most likely to increase in species colonisation positively co-occurred with more species in the pre-management community (i.e. in the presence of all threats) than the species most likely to decline (Figure 3e). If only livestock grazing intensity was mitigated, species that negatively co-occurred with more species in the pre-management community were more likely to decline, whereas species with few negative co-occurrences were more likely to increase (Figure 3g).

Predicting and testing community composition and structure under reduced threats

We tested our predictions of community restructuring under threat management by analysing the change in site occupancy of the study community five years after the onset of management to reduce the intensities of the three major threatening processes. Grazing management involved fencing-off remnants or reducing the intensity of stocking, Noisy Miners were managed through revegetation and natural regeneration of the shrubby understorey [29], and tree loss was managed through preventing clearing and revegetation of dominant *Eucalyptus* species. After five years of management, species richness was significantly lower in sites with few threats mitigated compared with sites where all three threats had been reduced (Table 1). There was a significant linear relationship between predicted change in patch colonisation and observed change in site occupancy. Species with predicted increases in colonisation of

187 managed sites were more likely to increase, and species with predicted declines in colonisation showed
188 declines in site occupancy under management of one or more threats (Figure 4g,h,i).

189 Our modelled predictions relating species' expected change in colonisation rates under threat
190 management to their pairwise co-occurrence characteristics indicated that species with highest positive
191 co-occurrence were most likely to decline without management due to a poor ability to colonise patches
192 (Figure 3). In comparison, species with high negative co-occurrence (those that other species avoid, or
193 that benefit from occurring in unique habitats) had an increased ability to colonise patches and were
194 more likely to increase if threats were not reduced (Figure 3). The dataset collected after five years of
195 management showed high support for our initial modelled predictions. Differences between the bird
196 communities of sites where threats had been substantially reduced and sites with threats remaining at
197 high intensities were strongly related to either declines (in threatened sites; Figure 4f) or colonisation and
198 increased site occupancy (in recovering sites; Figure 4d,e) of the species with the highest positive co-
199 occurrence (Figure 4). In recovering sites managed for multiple threats, species that declined tended to
200 have higher negative co-occurrence (Figure 4d,e).

201 We were also able to predict indirect losses of species from poorly managed sites based on whether they
202 positively or negatively co-occurred with species that responded positively or negatively to management.
203 As hypothesised (see Figure 1), species that consistently co-occurred in the presence of shared
204 threatening processes shared a similar response to threat management (Figure 5). Species pairs with high
205 negative co-occurrence were more likely to respond in dissimilar ways to threat management (Figure 5).
206 These results indicate that coexistence in the threatened landscape (representing shared environmental
207 relationships and threats) directly influenced the ability of a species to respond positively (if it shared
208 patches with another positive responder, or avoided negative responders) or negatively (if it did not share
209 patches with, or avoided, another positive responder) to threat management.

210 Finally, our approach enabled us predict community structure in response to threat management.
211 Communities where few threats were reduced were predicted to have fewer positive links between
212 species (due to loss of highly-connected nodes and increase in species with a negative role in the co-

occurrence network) and lower overall connectance compared with recovering sites where multiple threats had been reduced (and where highly-connected species might persist). We created four co-occurrence networks representing the community under alternative states of threat (reduction of three, two, one or no threats). Network metrics supported our predictions of higher connectance in sites with multiple threats versus no threats managed (Table 1, Figure 4), and resulted in a lower ratio of negative to positive co-occurrence links in mitigated compared with threatened sites. Our models also suggested that communities where more threats had been reduced would be more influenced by a change in positively co-occurring species than sites with little threat reduction (Figures 2 and 3). This prediction was also supported, with communities still undergoing 2-3 threats showing no relationship between site occupancy change and positive co-occurrence (Figure 4f).

Discussion

There is increasing evidence that anthropogenic change not only disrupts occupancy processes such as colonisation and dispersal, but also impacts the direction, frequency and intensity of species associations [10,30,31]. Our analysis provides a foundation for the study of community structure under anthropogenic change, as we discovered that local losses or declines of vulnerable species can signal negative outcomes for the structure of the entire community. We find that who with, and how strongly, a species co-occurs in a threatened community can be used to predict its ability to recover under mitigation of multiple threatening processes, and the effect of its loss or recovery on co-occurring species. Specifically, more connected species have higher vulnerability to cumulative threatening processes and greater impact on change in network structure than poorly connected species. Our results support recent findings from studies of mutualistic networks in which nodes that contribute more to the architecture of a network (in terms of connectedness) have a greater probability of extinction [20]. Evaluating the structure of co-occurrence networks may therefore play an important future role in identifying and conserving critical species links that are key for community function [32].

238 Our findings support our hypothesis and increasing evidence from analyses of ecological networks [33,34]
239 that cumulative threatening processes restructure a community through loss of highly-connected species
240 [3,30]. Ecological network studies have demonstrated the collapse of communities under the influence of
241 certain threatening processes, including catastrophic shifts in aquatic food webs due to nutrient loading
242 and trophic cascades [35], and co-extinction cascades in dispersal networks caused by human over-
243 exploitation of species [23]. These findings have had limited support from co-occurrence networks until
244 now, as previous co-occurrence studies focused on independent rather than cumulative threats [15,19,36]. In
245 our study, there was loss of almost all connectance in sites where all three threatening processes
246 continued unchecked (Figure 4, Table 1). Like the ecological network studies, our findings indicate that we
247 could expect isolation and destabilisation of the community in sites undergoing prolonged and cumulative
248 threats due to reorganisation and restructuring of co-occurrence [35].

249 Our results highlight the benefits of understanding community structure and species associations for
250 predicting the likely effectiveness of management actions aimed at reversing community decline [37].
251 Learning about the roles in the co-occurrence network of species facilitated by, or vulnerable to,
252 alternative threats enabled us to predict, often with considerable confidence, which components of the
253 network were likely to be lost under ongoing cumulative threatening processes (Figure 2). Community-
254 level predictions of threat management outcomes are rare due to the difficulty of incorporating
255 complementarities and species interactions into current optimisation methods [13]. Our study is a first step
256 towards improving existing approaches for prioritising threat mitigation actions. Because species with
257 strong positive co-occurrence in our study were more likely to have a larger positive predicted patch
258 colonisation change under threat mitigation than those with weak positive co-occurrence (Figure 3),
259 targeting threat mitigation towards species with high numbers of, or strongly positive, links is likely to
260 have a disproportionately higher impact on maintaining community structure than targeting species with
261 few connections [32]. We also discovered that threat mitigation has the potential to negatively impact
262 species with negative co-occurrence relationships typical of competitive displacers or weak competitors
263 with unique niches [38]. The finding that mitigating threats has the potential to result in declines in species

that have a negative influence on the occurrence of other species, has further implications for threat management. It suggests that mitigating more than one threat may have synergistic and unexpected outcomes on non-target co-occurring species that go beyond simple additive benefits [24].

Co-occurrence network relationships such as those calculated in this study are derived from spatial associations rather than directly measured biotic interactions. An important next step in co-occurrence research is to investigate the ecological function of key links in networks of spatial associations. For instance, an understanding of the function of lost community links and declining or lost species in our study sites where threats were not reduced is necessary to clarify the mechanisms of the negative outcomes for community structure that occurred because of declines in the most connected species. The most logical explanation is that lost connections represented a functional biotic relationship without which the community destabilised. There are several indications that our co-occurrence network reflects functional relationships between species [39] such as mutualistic behaviour (e.g. mixed-species feeding aggregations that benefit from more efficient foraging and protection from predation [40]). For example, the species with the highest positive degree (e.g. Buff-rumped Thornbill, Grey Fantail, Superb Fairy-wren) are all common members of mixed-species feeding flocks in which mutualistic relationships prevail [41]. Species with strong negative contributions included the Noisy Miner, a listed threatening process known to cause avifaunal disarray through exclusion competition [28] and the Yellow-faced Honeyeater, known to aggressively chase other birds from feeding and nesting locations [42]. However, not all negative co-occurrences indicate negative biotic interactions. Many species with strong negative contributions were birds known to benefit from unique niche space opened up by habitat change (e.g. loss of shrubs due to grazing) due to generalist feeding (e.g. Australian Magpie, Grey Butcherbird) or habitat preferences (e.g. Weebill, Eastern Rosella, Magpie-lark, Striated Pardalote). Loss or degradation of species co-occurrence relationships can forewarn a range of problems, including breakdown of interspecies communication in mixed feeding flocks (that might confer anti-predator advantages and group foraging benefits), and the loss of associated, or change in environmental conditions if an environmental space that previously supported the niches of multiple competing species is no longer able to support either or both taxa.

By demonstrating a tight link between species vulnerability and co-occurrence in the presence of cumulative threatening processes, we predicted a change in community structure when multiple threats were reduced (Figure 4). Increasing intensities of cumulative threatening processes led to colonisation by species with highly negative contributions to the network, declines of species with key connecting roles, loss of positive connections, and negative outcomes that resulted in fundamental changes to co-occurrence network topology [32]. We compared the topology and composition of networks in different states of threat reduction and discovered that both network co-occurrence (connectance) and species-level co-occurrence (positive and negative proportion of significant links) were consistent indicators of the degree of threat still acting on the community. Empirical data on co-occurrence are often easier, cheaper and quicker to collect than quantifying biotic interactions such as in food webs. Despite this, fundamental questions regarding the reorganisation of communities under anthropogenic change have been ignored by an expanding literature that focuses almost exclusively on biodiversity loss or changes to biotic interactions [3,32,35,37]. Our results suggest that analyses of co-occurrence networks have high utility for decision-making under anthropogenic change, as an understanding of the conditions that might lead to altered co-occurrence network structure (here, multiple simultaneous threats) enabled accurate predictions of how communities as a whole would respond to change [21,30]. We anticipate that change in co-occurrence networks will become a valuable empirical indicator of ecosystem resilience and recovery in a changing world [35].

Methods

Framework for predicting future community structure from current co-occurrence

Our approach to predicting community structure after threat management uses information on the structure and strength of links in a co-occurrence network under the influence of multiple threatening processes. We combine species-level predictions of management responses with this pairwise co-occurrence information in a set of models that predict community-wide outcomes of mitigating independent or combined threats. In doing so, we account for two important components of community

316 change: (1) dependencies between co-occurring species due to shared threats and responses to
317 management, and (2) varying contributions of each species to the co-occurrence network. Our approach
318 explicitly accounts for partial information on management responses due to only a subset of known
319 species in a threatened ecosystem. This is typical of most management situations where many species
320 have no known information on threat or management responses due to rarity or low detectability or no
321 available ecological studies.

322 Our framework consists of six steps that rely on pre-management data collected from any typical
323 heterogeneous landscape to make predictions, then post-management data for validation (Figure 1).
324 Initial data on species occurrences and threat intensities are collected across multiple sites representing
325 alternative combinations of *T* threats. We use this "threats present" dataset of sites by species detections
326 to estimate individual species colonisation probabilities and co-occurrence in the disturbed landscape. In
327 Step 1 of our predictive framework, the "threats present" dataset is used to build a single co-occurrence
328 network that quantifies the strength of each significant (non-random) link between every species in the
329 community [27]. In Step 2, the "threats present" dataset is employed in dynamic occupancy models that
330 predict how species will respond (through changes in patch colonisation or extinction rates) to reductions
331 in the intensities of one or more threats (Figure 1). Typically, colonisation probabilities are possible for
332 only a subset of the entire community due to the data intensiveness of modelling occupancy dynamics,
333 whereas co-occurrence can be estimated for the entire community [27]. In Step 3, we combine the partial
334 information dataset on species responses with the complete dataset on co-occurrence to infer responses
335 for species with no existing predictions for threat responses in a set of regression models. In Step 4, using
336 the information from Step 3 on which species are likely to decline versus increase in patches under
337 management and standard co-occurrence network metrics, we forecast the structure and composition of
338 the community when increasing numbers of threats are reduced (Figure 1). In Step 5, we collect new
339 species occurrence data for a "threats managed" dataset where threats have been reduced on treatment
340 sites but not control sites. Sites are now subsetted into four different communities that represent the
341 level of threat reduction achieved: 3 threats remaining (no threat reduction), 2 threats (one threat

342 mitigated), 1 threat (2 threats mitigated) or 0 threats (all three threats mitigated). An alternative
343 approach might be to subset by each individual threat mitigation action; the number of possible grouping
344 will depend on how many sites have been managed and the power of these site groupings to clarify
345 relationships between species. Here we define threat reduction as being achieved when the intensity of a
346 threat in a site after management is below the mean threat intensity in the "threats present" dataset; the
347 method allows alternative definitions of threat reduction and diverse ways of subsetting sites for other
348 contexts. Because network metrics are sensitive to the number of sites with data [27], care must be taken to
349 ensure subsets of data are approximately equal in size. Finally, in Step 6, we test predictions using the
350 "threats managed" dataset to explore whether (a) species' observed changes in colonisation correlates
351 with expected changes (predicted using step 3), (b) whether species' changes in site occupancy over time
352 is related to individual co-occurrence characteristics, and (c) whether the strength of pairwise co-
353 occurrence predicts the similarity in species' responses to management (Figure 1).

354 ***Step 1: Characterising species co-occurrence under threat***

355 To evaluate initial community co-occurrence in the presence of threats, we build a network of species co-
356 occurrence for the initial "threats present" sites by species dataset, with species treated as nodes and site
357 detection (0,1) as observations. We quantify the likelihood and strength of co-occurrence between each
358 pairwise combination of species using probabilistic species co-occurrence analysis [27] with the cooccur
359 package [43]. The probabilistic model of species co-occurrence provides, analytically, the probability (P) that
360 two selected species co-occur at a frequency either less than (P_{lt}) or greater than (P_{gt}) the observed
361 frequency of co-occurrence if the two species were distributed independently of one another among a set
362 of sites [27]. The probabilistic modelling approach has been demonstrated to perform as well as, or better
363 than, traditional analyses of species co-occurrence based on data randomization, reducing the chance of
364 Type I errors whilst also having low Type II error rates [27]. The model calculates p_j, the probability that
365 species 1 and 2 co-occur at j sites, for j = 0 to a given set of S sites. This probability is used to determine
366 the number of significant positive or negative links between species at a given significance level (here α =
367 0.05). The model also calculates an effect size s for each pairwise species association, defined as the
368 absolute difference between observed and expected frequency of co-occurrence [27]. The effect size is

standardised to a value between -1 (complete negative association) and +1 (complete positive association). We include only species pairs with significant links at $\alpha = 0.05$ to determine the strength of co-occurrence between each pair of species, ensuring that values for species pairs with random co-occurrence do not influence the analysis.

We measure three aspects of species' co-occurrence related to the number and strength of their links [19]. In trophic networks, species degree is typically used to calculate the number of links that connect a species *i* to other species in the network. Because positive, negative or random co-occurrence is possible for every species pair in a co-occurrence network, for each species *i*, we instead calculate the total proportion of possible co-occurrence links for each species that are either positive d_i or negative n_i [27] (the difference between $\sum(d_i + n_i)$ and 1 is the proportion of links that are random for that species). Co-occurrence strength s_{ij} is calculated for each pairwise association. Thus, species are characterised by two species-level co-occurrence traits ($d_i + n_i$) and one pairwise co-occurrence trait (s_{ij}) that varies with the number of other species in the network.

Step 2: Characterising species colonisation dynamics under threat

To gain species-level knowledge of responses to threats and their reduction, we require predictions of the probability of species occupying or colonising patches undergoing different combinations of threats. The number of *k*-combinations C_k^T from the total *T* threats acting on the community is:

$$C_k^T = \sum_{0 \le k \le T} \binom{T}{k} = 2^T$$

where C_k^T determines the number of models per species (including a model of zero threats reduced). We use dynamic multi-season, multi-site patch occupancy models to estimate detection probability ρ, probability of a site being occupied during the first survey Ψ, and probability of a site being colonised by the species between sampling sessions Υ. Models are built in a stepwise approach whereby first ρ is estimated with a single predictor from a set of models selected to describe year-specific heterogeneity in detectability (e.g. weather, observers), with the best model selected through the Akaike Information

Criterion (). Patch occupancy Ψ is estimated with $T + y$ models, with T models representing the intensity of each individual threat in the first year plus y null models representing environmental factors (e.g. soil, climate). We retain the single best Ψ predictor selected through the AIC. To explore effects of independent versus cumulative impacts of anthropogenic processes, we then build $C_k^T + z$ models to predict the probability of species colonisation (P) as functions of the intensity of each threat, again with z null models representing environmental factors (e.g. soil, annual biomass) [28,44]. We can then calculate the expected change in colonisation rates of individual species under each threat reduction combination t as:

$$\Delta P(m) = P(m_{Q3}) - P(m_{Q1}).$$

where m_{Q3} is the upper quartile intensity of the threat across all sites and m_{Q1} is the lower quartile intensity of the threat. A positive $\Delta P(m)$ indicates an expected increase in a species' site occupancy rates under reduction of one or more threats, and a negative $\Delta P(m)$ indicates a decline. Taking quartile rather than maximum and minimum values acknowledges that it is rarely possible to eradicate a threatening process, and that threat mitigation outcomes are relative to current baseline conditions. Our approach could also accommodate an alternative change metric.

Step 3: Predicting species responses to threat reduction related to co-occurrence network contributions

To derive empirical relationships between co-occurrence and the species' predicted colonisation rate in the presence of one or more threatening processes, we build generalised linear models with a gaussian distribution. The input dataset is the complete set of possible pairwise co-occurrence links in the community. The response variable is $\Delta Y_i(e,m)$, the expected change in colonisation of species i under threat management strategy m (from a total selection of C_k^T threat reduction choices), and can be negative, zero or positive. Patch colonisation rather than extinction processes are chosen because we expect more positive than negative changes in processes under threat management; the procedure is similar for extinction dynamics. We test five model structures that explore whether the response of species i is related to species with which it coexists most closely (through an interaction between each pair's co-occurrence characteristics and the predicted colonisation of species j; models 1 and 2), or

whether species' responses to management are related only to their ability to coexist in the threatened landscape (models 3, 4 and 5), and select the model with the lowest AIC:

$$\Delta Y_i(e,m) \sim s_{ij} * \Delta P_j\,(m) + d_i + \varepsilon \quad (1)$$

$$\Delta Y_i(e,m) \sim s_{ij} * \Delta P_j\,(m) + n_i + \varepsilon \quad (2)$$

$$\Delta Y_i(e,m) \sim d_i + \varepsilon \quad (3)$$

$$\Delta Y_i(e,m) \sim n_i + \varepsilon \quad (4)$$

$$\Delta Y_i(e,m) \sim s_{ij} + \varepsilon \quad (5)$$

where $\Delta P_j\,(m)$ is the predicted colonisation rate under management strategy m of species j, and d_i and n_i are the proportion of positive and negative links that were significant for species i (these two variables were correlated ($r = 0.30$, $P < 0.01$) and were excluded from the same model models).

Step 4: Forecast future community composition and structure under threat reduction

To test our predictions, we build a second set of co-occurrence networks using the "threats managed" dataset that is subsetted to compare communities in sites that have experienced different reductions in threat intensity. To quantify present and future community structure under management of anthropogenic threats, we use standard network topology measures of network connectance [45,46] and species' degree [26] (defined here as proportions of total possible links to account for varying sizes of networks) to infer the contributions of highly versus poorly connected species to the co-occurrence network. Network connectance is calculated as k/x^2, where k is the total number of significant links in the network and x is the number of species in the network. In interaction networks, high connectance tends to indicate a more complex network with higher stability than networks with low connectance [46], although this has not been tested empirically for co-occurrence networks.

The outputs of the models and the network topology measures are used to make predictions about how the structure of the community might change under threat mitigation (Figure 1). If the most-connected species are the most vulnerable to change under continuing anthropogenic threats (i.e. most likely to be

lost from the community), we expect that communities with the most threats reduced will retain the highest connectance due to retention of highly connected nodes. Communities with the fewest threats reduced are expected to have lower connectance due to loss of nodes with a high contribution to network co-occurrence [37].

Steps 5 and 6: Validate predictions with post-management data

To validate our hypothesis that highly connected species have higher impacts on change in network architecture under threat management than species with low or negative co-occurrence associations, we run two sets of analyses using generalised linear models. The first set of generalised linear models seeks to determine whether our models relating species co-occurrence (negative and positive) and likely change in colonisation under threat management accurately predicted change in site occupancy of each species when threats were managed. The models relate a response variable of the observed change in percentage site occupancy of each species (n = 88) between the "threats present" dataset and the "threats managed" datasets (where 1, 2 or 3 threats had been reduced), to predictors of either (a) the species' predicted change in colonisation under management strategy *m* (fitted values from the best model selected from equations (1) to (5); to test whether predicted colonisation change was related to observed colonisation change), or (b) the species' positive or negative degree (d_i or n_i) in the "threats present" network (to test whether species' individual co-occurrence characteristics predicted threat management response).

In the second validation analysis we determine whether species with significant links to positively co-occurring species in the threatened landscape are more likely to have similar responses to management (i.e. either both increase, or both decline, or both no change five years after management). We build a generalised linear model with a binomial link that has a predictor variable of pairwise species co-occurrence in the "threats present" dataset and a binary response variable that describes whether the species in the pair shared the same direction in response (1) or responded in opposite directions (0).

Dataset

We based our empirical study on repeated annual bird surveys completed between 2011 and 2015 at 97 sites across 29 farms in the critically endangered Box Gum Grassy Woodland ecological community of New South Wales in south-eastern Australia. Sites were woodland patches within a semi-cleared agricultural matrix. Sites were selected to be similar in abiotic conditions, but were expected to show fine-scale differences in biodiversity due to heterogeneity in the intensities of three threatening processes across the landscape: tree clearing, livestock grazing, and a hyper-aggressive species the Noisy Miner *Manorina melanocephala*. The 5-year study was designed to examine the effects of reducing threats to woodland birds through active management of the landscape, with each farm containing at least one control and one treatment site reducing the intensity of grazing, loss of tree cover and Noisy Miner abundance through grazing exclusion (fencing off patches to remove grazing impacts) or Land Stewardship payments (revegetation of sites, which increases tree cover and reduces Noisy Miner impacts through increased shrubby cover[29]). To examine individual species persistence and vulnerability in the presence of threats we subset the monitoring data into a "threats present" dataset comprising the first 3 years of monitoring (acknowledging a 3-year time lag in provision of resources and hence species responses under management [47,48]). This dataset was used to evaluate network co-occurrence and make predictions about changes to community structure under threat reduction. To evaluate individual species persistence and network co-occurrence in sites where threats had been reduced to different levels, we allocated the final two years of monitoring (2014-2015) to the "threats managed" dataset, subset in the following way: (1) zero threats: all threats below mean (53 site-by-year surveys); (2) 1 threat: 2 of 3 threats below mean (55 site-by-year surveys); (3) 2 threats: 1 of 3 threats below mean (52 site-by-year surveys); and (4) 3 threats: all threats above mean (50 site-by-year surveys; to ensure that this dataset had an adequate number of sites to compare with the other categories we included randomly selected sites from the 2-threat dataset).

Each bird survey comprised three 5-minute point interval counts along a 200-metre long permanent transect during spring (breeding season), which was repeated on two separate days in any given year (6 surveys per site per year, total survey effort 2023 surveys due to site access restricting some surveys; see

493 Supplementary Information for details). Detections for all birds seen or heard within a 50-m radius of the
494 three points and the two days were pooled to derive an occupancy dataset that accounted for species
495 detectability per site per year [22]. We detected 131 species of birds across the 5-year study period.

496 We built a network of species co-occurrence for the 3-year "threats present" bird community dataset
497 with species treated as nodes and each year by site survey combination treated as observations. A 3-year
498 dataset ensured that the co-occurrence network represented a discrete unit of time and a relatively static
499 community structure, with timeframes longer than this likely to increase the possibility of species co-
500 occurrences changing due to temporal dynamics [4,6]. We aggregated the 6 surveys at each site per year to
501 derive a site by species matrix in which each unique year by site survey combination was an individual
502 "site"; this allowed for between-year variability in patch detection and therefore co-occurrence due to
503 bird mobility, whilst controlling for detectability. We excluded very rare species detected in <1% of
504 surveys (43 out of 131 species), with 88 species remaining (colonisation rates were predicted for 37 of
505 these). To verify that our results were not driven by the co-occurrence method that we used, we also
506 performed a sensitivity analysis comparing the results of the best model (out of choices (1) to (5) above)
507 using our probabilistic method to the results based on a randomised null model approach to determining
508 significant co-occurrence [49], and found that the responses were analogous.

509 Using the "threats present" dataset, we built multi-season patch occupancy models using the unmarked
510 0.10-6 package in R [50] to describe how species' patch occupancy, colonisation, and extinction rates varied
511 with the presence of one or more threatening processes in a given site . Each point count was considered
512 to be a site visit, and each site had an annual detection history of 6 visits (18 visits throughout 3
513 consecutive years). Due to the inability to build occupancy models for species with too few detections,
514 only species with >1% detection rate across the study period were considered. Of these 88 species,
515 models for only 37 species converged. These species showed a range of ecological characteristics and
516 detectability (Supplementary Table 1). The process followed to build occupancy models is similar to that
517 described in [22].

To model detectability, we fit four models with predictive variables of either year (as a continuous variable accounting for trends or as a categorical covariate accounting for unmeasured year-specific factors), temperature (categorical) or rainfall in the 3 months preceding surveys, plus an intercept-only null model. To model the probability of a site being occupied during the first survey, we used one of the following site-level predictors (within a 250-m buffer): historical grazing regime, percentage native tree cover, abundance of Noisy Miners, soil phosphorus, or mean rainfall. To explore effects of independent versus cumulative impacts of different threatening processes, we modelled the probability of bird colonisation as a function of livestock grazing intensity, tree clearing and Noisy Miner abundance [28,44]. Each of these variables was characterised by a continuous distribution of threat intensity measured at each site in each year; for grazing intensity, this was the paddock dry sheep equivalent for all grazed days (excluding days when pasture was rested) [22], for tree clearing, this was the proportion of the landscape within 250m of the site with woody tree cover (derived from satellite data), and for Noisy Miners, this was the average number of Noisy Miners counted across the 6 surveys per site per year. We ran models with each threatening process as an independent predictor as well as each combination of two threats and finally all three threats. Alternative null threat predictors for colonisation were soil phosphorus (which affects site productivity and vegetation condition) and mean annual biomass of all groundcover (a surrogate for the availability of ground shelter and food resources such as grasses and their seeds). To derive species colonisation probabilities under threat, model predictions for species colonisation under high (75% of the maximum) intensities of threatening processes were calculated and goodness-of-fit was measured through Nagelkerke's R^2. Colonisation predictions for models with no support were set to the null colonisation rate.

Acknowledgements

DBL is supported by an ARC Laureate Fellowship. AITT is funded by the Australian Research Council Centre of Excellence for Environmental Decisions (CEED). The monitoring program was coordinated by D. Florance from The Australian National University (ANU) and approved by the Australian National

University Animal Ethics Committee, and field staff from ANU and volunteers from the Canberra Ornithologists Group assisted with surveys. We thank M Westgate and P Lane for valuable discussions on methodology.

Data availability

The authors declare that the data supporting the findings of this study are available within the paper and its supplementary information files.

Code availability

The R code for the conceptual framework of predicting community responses presented in the current study can be downloaded from the supplementary information files.

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Tables

Table 1. Co-occurrence network metrics for four subsets of a bird metacommunity occurring in endangered box-gum grassy woodland sites in alternative states of threat reduction (see also Supplementary Figure 8).

Community state	Sites	Total species richness	Average ± S.E. species per site	Average ± S.E. % positive links per species (total number)*	Average ± S.E. % negative links per species (total number)*	Ratio negative to positive links	Average ± S.E. number positive links per species	Average ± S.E. number negative links per species	Connectance (total network links/ possible network links)
Initial state ("threats present")	97	88	10.0 ± 0.3	16.4 ± 1.4 (401)	6.1 ± 0.7 (166)	0.4	9.11 ± 0.92	3.77 ± 0.58	0.148
After 4-5 years of management ("threats managed")									
0 threats remaining	30	45	9.7 ± 1.1 [A]	8.2 ± 1.0 [A] (110)	1.3 ± 0.4 (11)	0.1	2.67 ± 0.35 [A]	0.49 ± 0.15 [A]	0.122
1 threat remaining	33	44	7.9 ± 0.9 [B]	8.1 ± 1.0 [A] (40)	0.8 ± 0.3 (4)	0.1	1.82 ± 0.29 [B]	0.18 ± 0.07 [B]	0.047
2 threats remaining	35	38	6.4 ± 1.8 [B]	2.8 ± 0.7 [B] (9)	0.8 ± 0.4 (3)	0.3	0.47 ± 0.10 [C]	0.16 ± 0.07 [B]	0.017
3 threats remaining	30	31	5.8 ± 0.6 [B]	2.5 ± 0.9 [B] (5)	1.0 ± 0.6 (2)	0.4	0.32 ± 0.09 [C]	0.13 ± 0.05 [B]	0.015
Strength of linear trend as threats increase (R^2)			0.10	0.98	0.78		0.92	0.92	0.91

*Model only applied to those species pairs whose expected number of co-occurrences [P(1,2)*N]>1.0 [27]. A significance level of α=0.05 was used to classify species associations.

[A] Significantly different at α=0.05 from communities indicated by B or C (ANOVA).

688 **Figure Legends**

689 **Figure 1. Conceptual model of our framework to predict community response to management.**

690 Showing the six steps to predict community responses to threat mitigation when faced with partial data
691 on species' expected change (e.g. in colonisation or extinction rates) under alternative threat
692 management actions and complete data on pairwise co-occurrence in the threatened landscape.

693 **Figure 2. Co-occurrence network and species-level co-occurrence metrics.**

694 Frequency distributions for (a) positive co-occurrence (percentage of all non-random links that were
695 positive), (b) negative co-occurrence (percentage of all non-random links that were negative); (c) pairwise
696 positive strength; and (d) the entire co-occurrence network of links (blue = positive, i.e. aggregation, red =
697 negative, i.e. avoidance or segregation) between 88 species detected in more than 1% of surveys across a
698 threatened (pre-management) landscape. For species codes see Supplementary Table 1.

699 **Figure 3. Model predictions of species' responses after five years of threat management.**

700 Interaction between the strength of pairwise co-occurrence for each species pair and the likely change in
701 each of 37 predictor species' patch colonisation rates under a given set of threat management actions,
702 with the predicted change of species 1 modified by whether species 2 is expected to decline, increase or
703 not change its colonisation of the landscape under management. Sites are aggregated according to the
704 level of threat reduction, either (a) all three threats (R^2 = 0.20), (b) two threats (habitat loss and grazing;
705 R^2 = 0.07), (c) two threats (overabundant miners and grazing; R^2 = 0.24), (d) two threats (overabundant
706 miners and habitat loss; R^2 = 0.11), (e) one threat (habitat loss; R^2 = 0.28), (f) one threat (overabundant
707 miners R^2 = 0.28), (g) one threat (grazing; R^2 = 0.12). All relationships are predicted from generalised linear
708 models (see Supplementary Table 6).

709 **Figure 4. Validation of predicted changes in bird community after five years of managing multiple**
710 **threatening processes.**

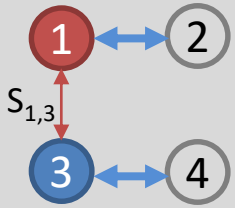
Structure and composition of the co-occurrence network of 88 species after (a) all three threats, (b) two threats or (c) only one threat is reduced (blue line= positive co-occurrence, red line = negative co-occurrence, shading = 95% confidence interval). Metrics of species-level co-occurrence when threats present (see Figure 2; threats = livestock grazing, overabundant native competitor, habitat loss) predict observed changes in site occupancy of the 88 species after five years of reducing (d) all three threats (33 sites; positive: $y = 0.58x - 13.99$, $P < 0.01$, $R^2 = 0.22$; negative: $y = -0.60x - 0.78$, $P = 0.02$, $R^2 = 0.07$), (e) two threats (35 sites; positive: $y = 0.19x - 10.69$, $P = 0.02$, $R^2 = 0.07$; negative: $y = -0.32x - 5.58$, $P = 0.03$, $R^2 = 0.05$), (f) only one of the three threats (29 sites; negative: $y = -0.32x - 8.01$, $P = 0.01$; $R^2 = 0.07$; model for positive co-occurrence not significant). Co-occurrence is measured as the percentage of all possible links for a species that were either positive (blue) or negative (red) versus random (not significant). Expected changes in species' colonisation rates also predict observed changes in site occupancy under management of (g) three threats ($P = 0.01$; $R^2 = 0.20$), (h) two threats ($P = 0.01$; $R^2 = 0.10$) and (i) only one of the three threats ($P = 0.01$; $R^2 = 0.07$). All relationships are predicted from generalised linear models (see Supplementary Table 7), and shading represents 95% confidence intervals. See Supplementary Table 1 for species codes.

Figure 5. Relationship between "threats present" pairwise co-occurrence of 88 species and the similarity in species' responses to five years of threat management.

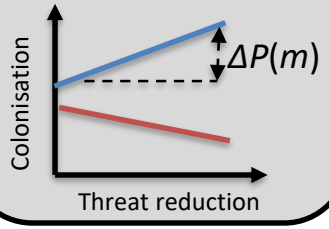
Species pairs with strong positive connections are more likely to have similar responses (e.g. both increase, both decline) than pairs with strong negative connections that are more likely to respond in opposite ways (generalised linear model; $y = -76.08x - 0.07$, $P < 0.01$; $R^2 = 0.12$). A different response between species is when one species increases and the other either does not or declines, or vice versa. Shading represents 95% confidence intervals.

"Threats present" dataset

Step 1: Characterise all species' pairwise co-occurrence s_{ij} under threat

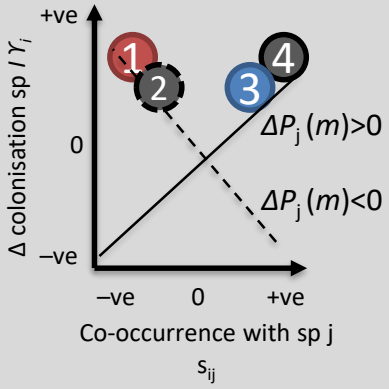


Step 2: Characterise responses $\Delta P(m)$ to threat reduction for subset of species



Step 3: Predict all species' responses to threat reduction by combining information on co-occurrence and expected change for species pairs

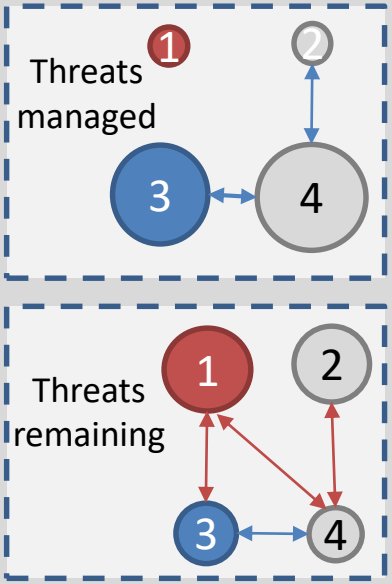
$\Delta Y_i(e,m) \sim s_{ij} * \Delta P_j(m)$



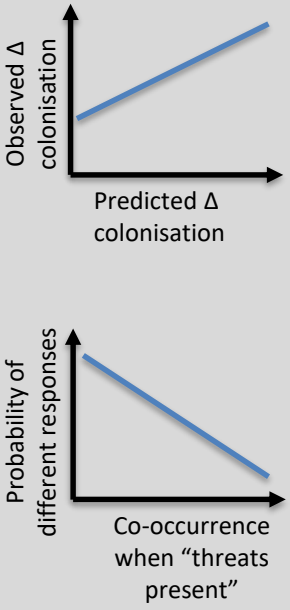
Step 4: Forecast future community composition and network structure (individual species losses/gains, effect of feedbacks on network)

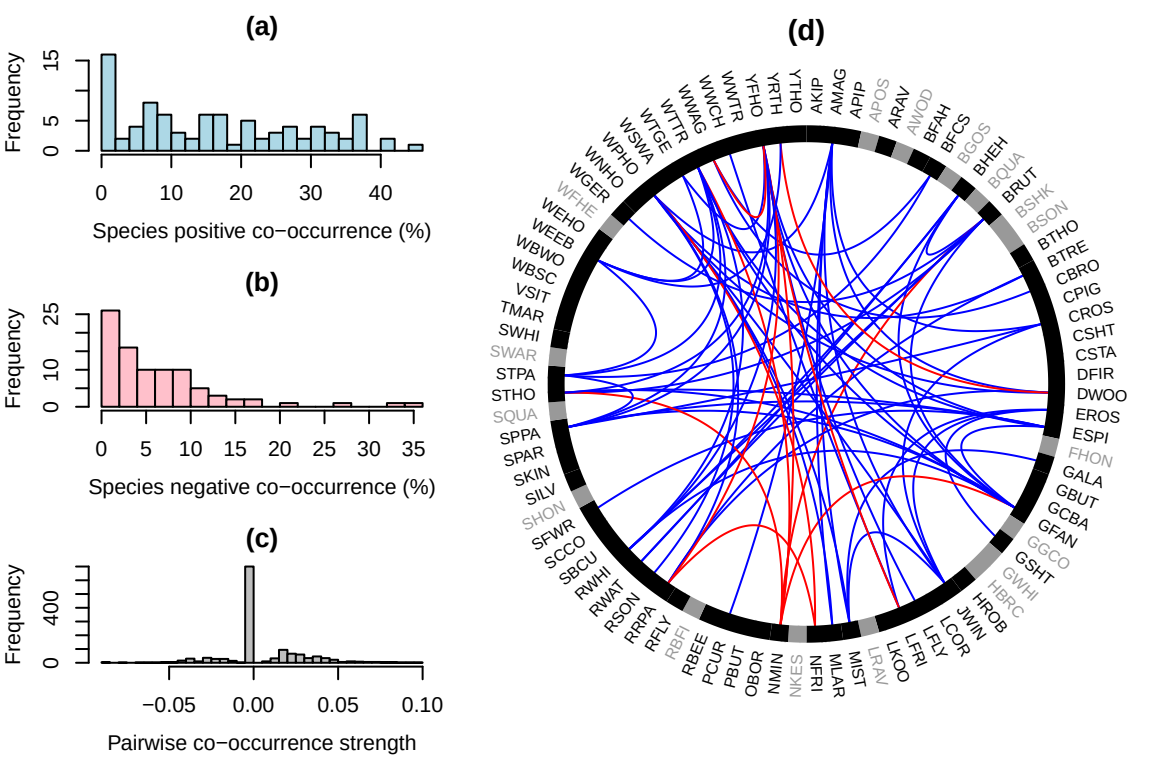
"Threats managed" dataset

Step 5: Threat management reduces intensity and number of threats to species in some sites

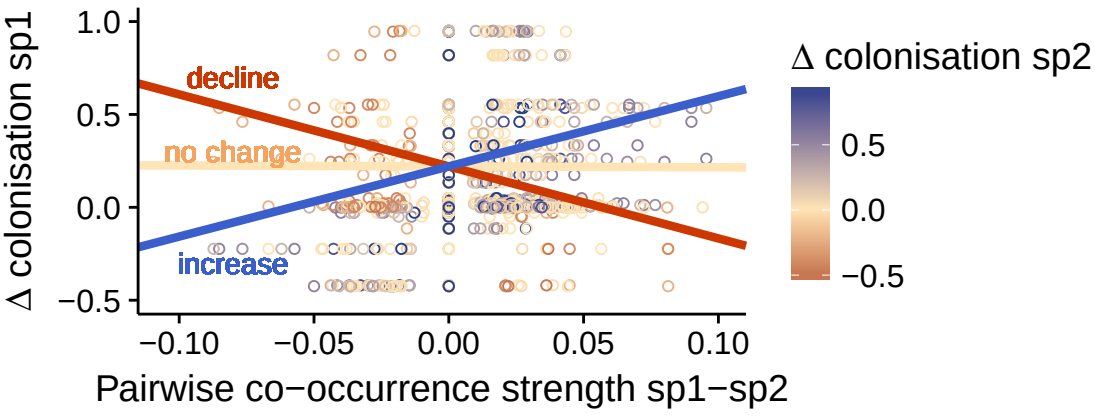


Step 6: Validate predictions with post-management data

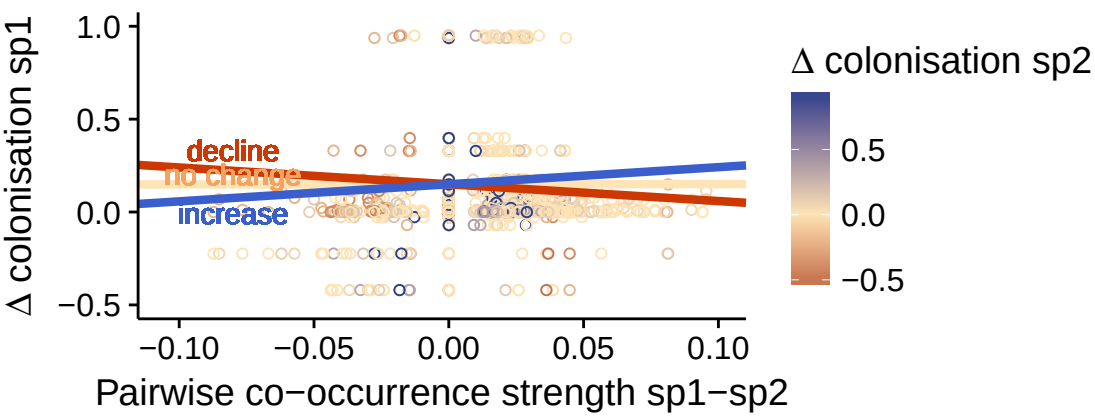



(a)
Frequency
0
5
15
0
10
20
30
40
Species positive co−occurrence (%)
(b)
Frequency
0
10
25
0
5
10
15
20
25
30
35
Species negative co−occurrence (%)
(c)
Frequency
0
400
−0.05
0.00
0.05
0.10
Pairwise co−occurrence strength
(d)
YTHO
AKIP
AMAG
APIP
APOS
ARAV
AWOD
BFAH
BFCS
BGOS
BHEH
BQUA
BRUT
BSHK
BSON
BTHO
BTRE
CBRO
CPIG
CROS
CSHT
CSTA
DFIR
DWOO
EROS
ESPI
FHON
GALA
GBUT
GCBA
GFAN
GGCO
GSHT
GWHI
HBRC
HROB
JWIN
LCOR
LFLY
LFRI
LKOO
LRAV
MIST
MLAR
NFRI
NKES
NMIN
OBOR
PBUT
PCUR
RBEE
RBFI
RFLY
RRPA
RSON
RWAT
RWHI
SBCU
SCCO
SFWR
SHON
SILV
SKIN
SPAR
SPPA
SQUA
STHO
STPA
SWAR
SWHI
TMAR
VSIT
WBSC
WBWO
WEEB
WEHO
WFHE
WGER
WNHO
WPHO
WSWA
WTGE
WTTR
WWAG
WWCH
WWTR
YFHO
YRTH

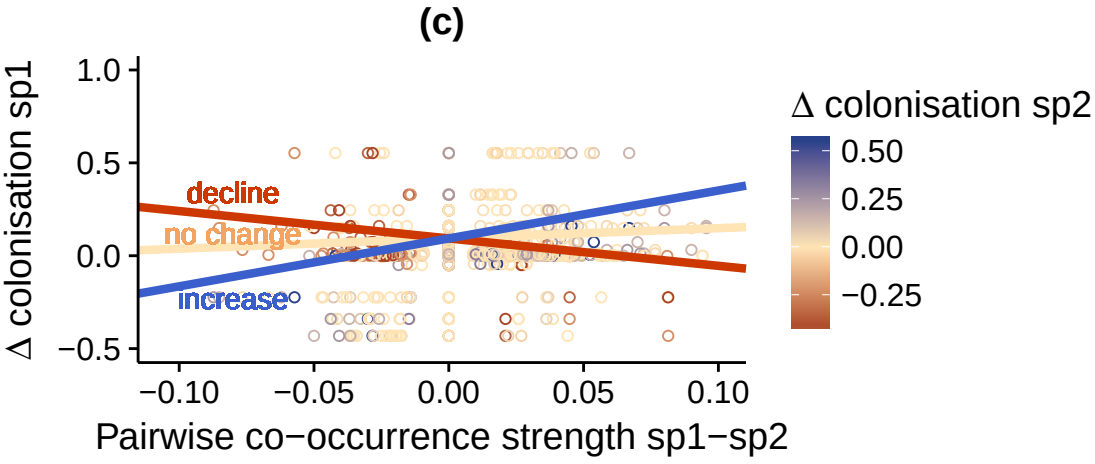
(a)


Δ colonisation sp1
1.0
0.5
0.0
−0.5
decline
no change
increase
−0.10
−0.05
0.00
0.05
0.10
Pairwise co−occurrence strength sp1−sp2
Δ colonisation sp2
0.5
0.0
−0.5

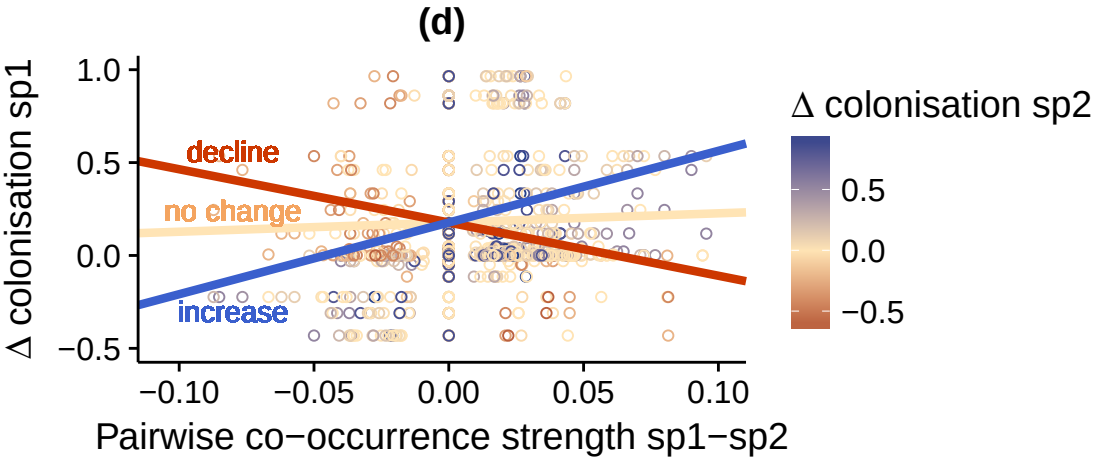
(b)


Δ colonisation sp1
1.0
0.5
0.0
−0.5
decline
no change
increase
−0.10
−0.05
0.00
0.05
0.10
Pairwise co−occurrence strength sp1−sp2
Δ colonisation sp2
0.5
0.0
−0.5

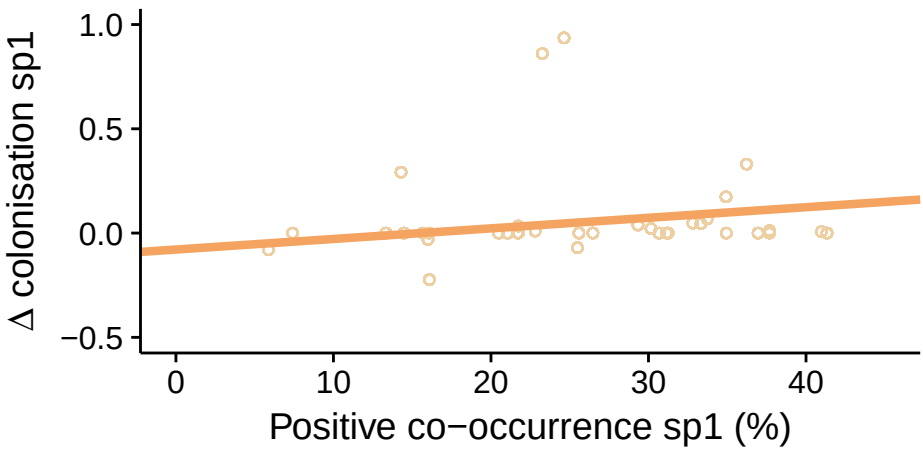
(c)


Δ colonisation sp1
1.0
0.5
0.0
−0.5
decline
no change
increase
−0.10
−0.05
0.00
0.05
0.10
Pairwise co−occurrence strength sp1−sp2
Δ colonisation sp2
0.50
0.25
0.00
−0.25

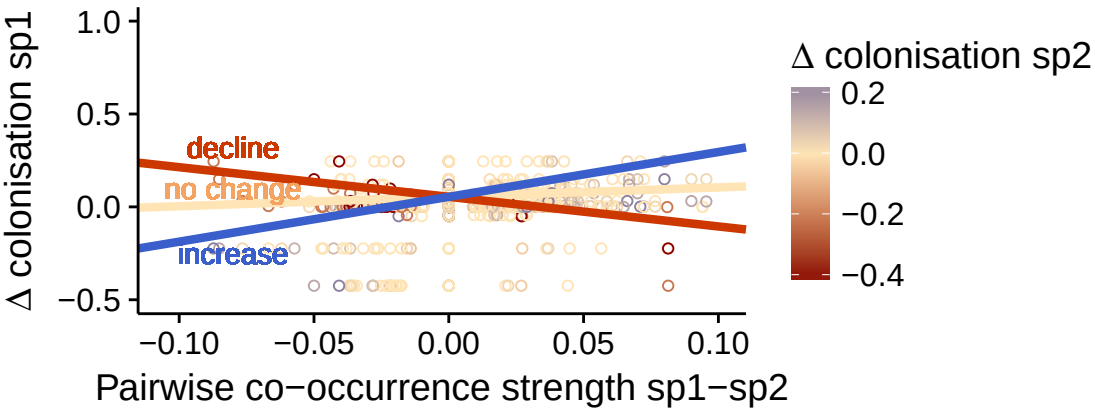
(d)


Δ colonisation sp1
1.0
0.5
0.0
−0.5
decline
no change
increase
−0.10
−0.05
0.00
0.05
0.10
Pairwise co−occurrence strength sp1−sp2
Δ colonisation sp2
0.5
0.0
−0.5

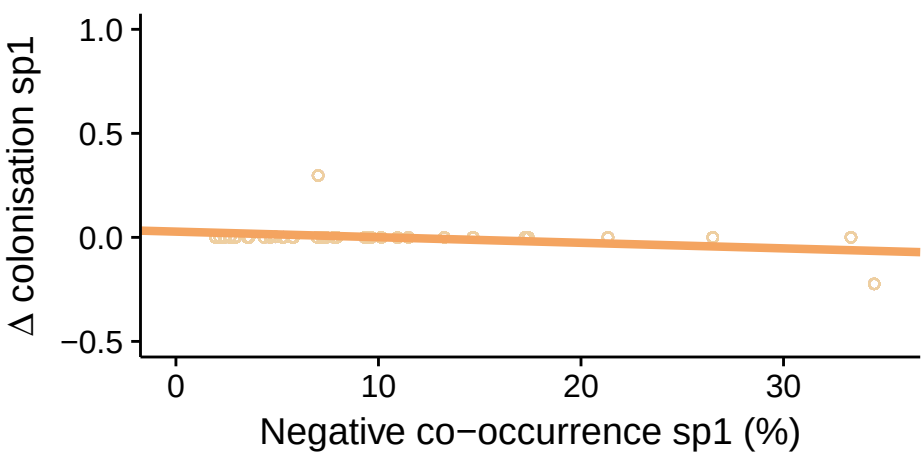
(e)

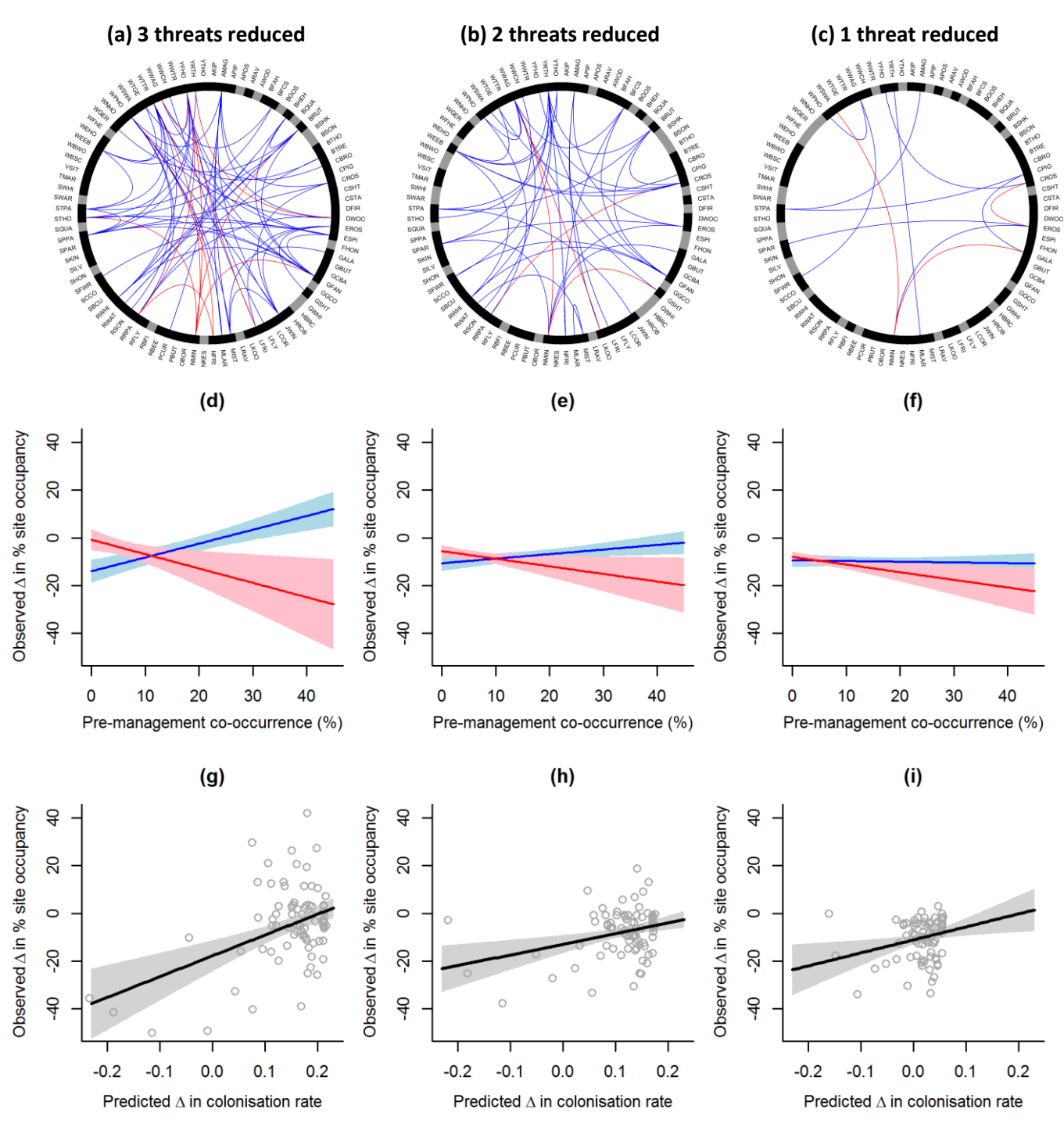

Δ colonisation sp1
1.0
0.5
0.0
−0.5
0
10
20
30
40
Positive co−occurrence sp1 (%)

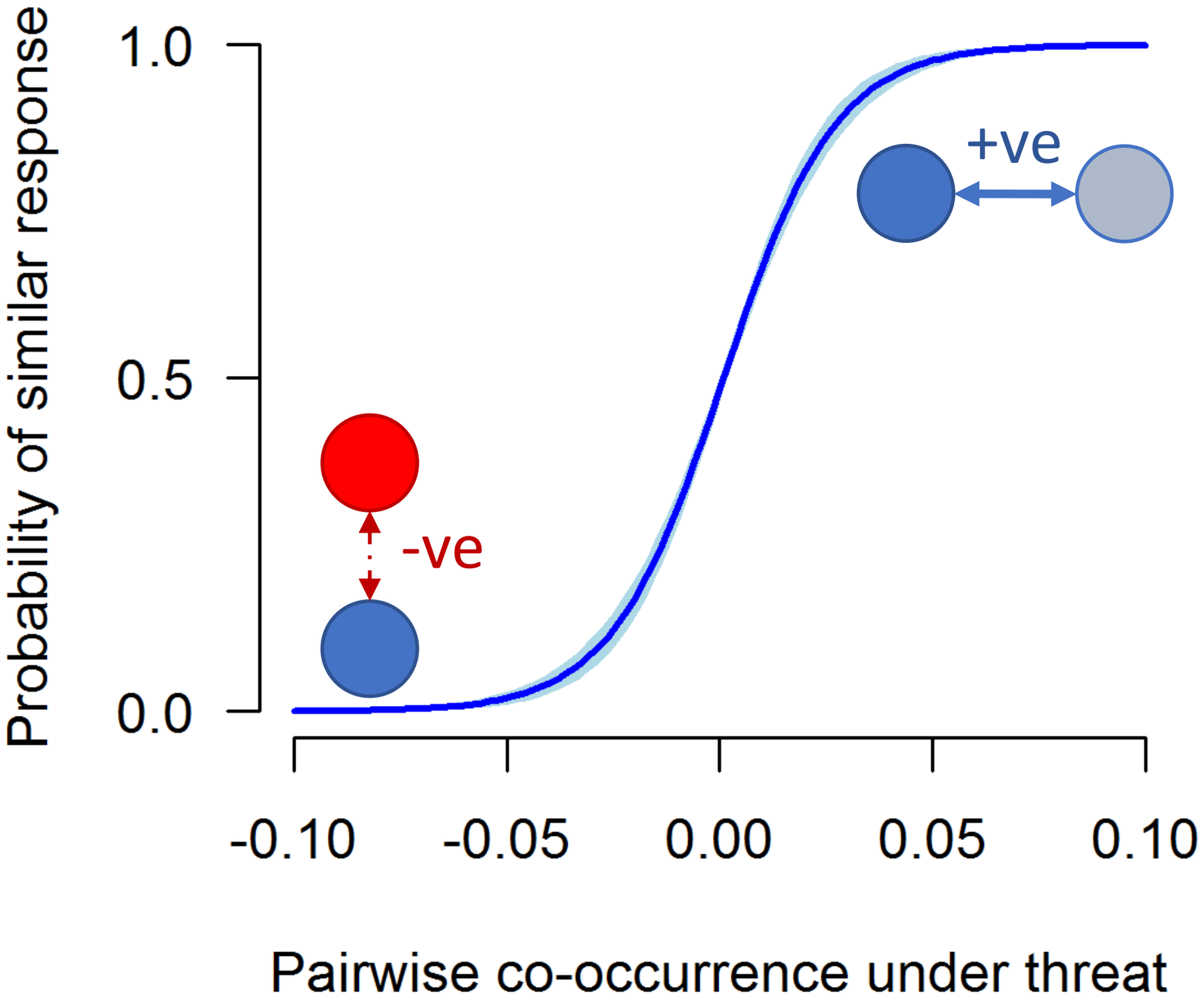
(f)


Δ colonisation sp1
1.0
0.5
0.0
−0.5
decline
no change
increase
−0.10
−0.05
0.00
0.05
0.10
Pairwise co−occurrence strength sp1−sp2
Δ colonisation sp2
0.2
0.0
−0.2
−0.4

(g)


Δ colonisation sp1
1.0
0.5
0.0
−0.5
0
10
20
30
Negative co−occurrence sp1 (%)


(a) 3 threats reduced
(b) 2 threats reduced
(c) 1 threat reduced
(d)
(e)
(f)
(g)
(h)
(i)
Observed Δ in % site occupancy
Pre-management co-occurrence (%)
Predicted Δ in colonisation rate


Probability of similar response
1.0
0.5
0.0
+ve
-ve
-0.10
-0.05
0.00
0.05
0.10
Pairwise co-occurrence under threat