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Species co-occurrence networks show reptile community reorganization under agricultural transformation

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Agricultural transformation represents one of the greatest threats to biodiversity, causing degradation and loss of habitat, leading to changes in the richness and composition of communities. These changes in richness and composition may, in turn, lead to altered species co-occurrence, but our knowledge of this remains limited. We used a novel co-occurrence network approach to examine the impact of agricultural transformation on reptile community structure within two large ($> 172\ 000\ \text{km}^2$; 224 sites) agricultural regions in southeastern Australia. We contrasted assemblages from sites surrounded by intact and modified landscapes and tested four key hypotheses that agricultural transformation leads to (H1) declines in species richness, (H2) altered assemblages, (H3) declines in overall co-occurrence, and (H4) complex restructuring of pairwise associations. We found that modified landscapes differed in composition but not richness compared with intact sites. Modified landscapes were also characterized by differences in co-occurrence network structure; with species sharing fewer sites with each other (reduced co-occurrence connectance), fewer highly-connected species (truncation of the frequency distribution of co-occurrence degree) and increased modularity of co-occurrence networks. Critically, overall loss of co-occurrence was underpinned by complex changes to the number and distribution of pair-wise co-occurrence links, with 41-44% of species also gaining associations with other species. Change in co-occurrence was not correlated with changes in occupancy, nor by functional trait membership, allowing a novel classification of species susceptibility to agricultural transformation. Our study reveals the value of using co-occurrence analysis to uncover impacts of agricultural transformation that may be masked in conventional studies of species richness and community composition.

Introduction

Agricultural transformation is a major driver of biodiversity decline (Sala et al. 2000, Tscharntke et al. 2005, Newbold et al. 2015). This process, driven by the replacement of natural environments with human-modified landscapes such as agricultural fields, impacts > 50% of all ice-free land (Hooke 2012) – an area set to increase as global demand for agriculture increases (Alexandratos and Bruinsma 2012, Tscharntke et al.

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2012a, b). Studies of the impacts of agricultural transformation on biodiversity routinely identify loss of local-scale (α) and landscape-scale (γ) diversity (Fig. 1 A; Liu et al. 2014, Newbold et al. 2015) as well as changes in community composition (β) (Fig. 1B; Karp et al. 2012, Solar et al. 2016). However, other more subtle changes to the way biota coexist and interact are likely (Bascompte 2010, Poisot et al. 2015), even before discernable changes in richness or composition occur (Tylianakis et al. 2007, Morriën et al. 2017). For example, agricultural transformation may lead to changes in the occupancy of species among sites, thus altering coexistence among species, even though overall richness might not change. Identifying nuanced changes in the structure of a community could provide an important opportunity to anticipate negative consequences to biodiversity before species are lost or communities irreversibly restructured.

One approach to characterizing more subtle changes to communities is through quantifying species co-occurrence.



Figure 1. Conceptual diagram describing known and anticipated effects of agricultural transformation. (A) Species richness decline. (B) Community composition change. (C) Loss of co-occurrence as measured by a range of network metrics (connectance, link distribution and modularity). (D) Restructuring of pairwise associations between species without changes to total network co-occurrence. Increasing line darkness represents increasing co-occurrence strength (i.e. likelihood of co-occurrence). Grey polygons represent species associations (with increasing modularity under agricultural transformation).

Co-occurrence has long been used to examine community structure (Gotelli and McCabe 2002) by describing how species within a community coexist. Species co-occurrence is often represented by a network of nodes (species) linked by vectors (edges) of varying strength corresponding to the frequency of paired species presence at a site (Newman et al. 2001, Araújo et al. 2011). Several processes could be responsible for species associations, such as shared environmental requirements, ecological interactions or other higher order processes (e.g. two species sharing a common predator). Our understanding of co-occurrence networks is founded mainly on studies examining biotic interaction theory like food webs (Berlow et al. 2009) or plant-pollinator networks (Burkle et al. 2013). These biotic interaction studies have demonstrated a number of useful ways to summarize complex network topology into network metrics that can be used to track community change over time, or across different regions (Urban and Keitt 2008, Tylianakis et al. 2010). For example, network 'connectance' - the proportion of realized interactions from the pool of all possible interactions between the species of a network (May 1973) - is considered an important indicator of community complexity (Gilbert 2009, Tylianakis et al. 2010). Similarly, measuring the distribution of species associations can reveal the nature of community change, for example from one composed mainly of many species with few links and a few species with many links, to one with randomly distributed or truncated link distributions (Thébault and Fontaine 2010, Tylianakis et al. 2010). These advancements in co-occurrence theory have prompted an interest in co-occurrence networks to evaluate impacts of anthropogenic processes like climate or land-use change on community structure (Araújo et al. 2011, Burkle et al. 2013, Poisot et al. 2015, Morriën et al. 2017). Such studies have provided promising opportunities to identify community assembly processes.

Some challenges, however, surround the use of network metrics for interpreting anthropogenic impacts with cooccurrence networks. One challenge is that the structure (topology) of different types of networks varies (Thébault and Fontaine 2010), and so interpreting what each network means in the context of different threats remains problematic (Cazelles et al. 2016). For example, biotic interaction networks, which are built from (or imply) interactions between species, will differ with co-occurrence networks which are built from shared site occupancy without implying any direct interaction. Another challenge is that network metrics summarize ecological communities assuming a universal response of all species within that network to environmental changes (Burkle et al. 2013). However, environmental and anthropogenic changes rarely act evenly across all species in a community. For example, anthropogenic impacts of livestock grazing have revealed differential species-specific impacts for woodland reptile and bird communities within the same study region (Kay et al. 2016a, Tulloch et al. 2016a). Subsequently, we know far less about how structural changes in the networks occur, preventing most studies from providing useful guidance to conservation managers interested in identifying how and what aspects of the community to manage for.

A finer-scale understanding of co-occurrence among species may improve predictions of how and why communities respond to anthropogenic processes like agricultural transformation (Veech 2013, 2014, Blois et al. 2014, Borthagaray et al. 2014). If a species declines in abundance or distribution in a landscape (a common symptom of agricultural transformation), we might expect habitat availability for other similar species to increase (MacArthur and Levins 1964, Levin 1970), potentially influencing species co-occurrence in a number of ways. For example, consider a community of co-occurring arboreal mammals that share the same habitat such as trees in a forest. Agricultural transformation (i.e. deforestation) would cause a loss of the amount or quality of tree habitats, such that some species lose a critical resource (e.g. tree cavities) but others do not. This loss of resources could reduce the co-occurrence of species within the community (Fig. 1C), an effect that has been documented through universal change in single network metrics previously (Burkle et al. 2013). However, agricultural transformation may lead to restructuring of the community without noticeable change in cooccurrence (Fig. 1D; Thébault and Fontaine 2010). Loss of trees may cause extinctions from the site and hence lose connections with unaffected species (Fig. 1D a-b). Alternatively, tree loss may cause the affected species to switch resources to another tree or refugial site (possible if they are generalists). This, in turn, could lead to coexistence with previously non co-occurring species within the ecosystem (Fig. 1D a-c), or increased (strengthened) coexistence between previously co-occurring species (Fig. 1D a-d), either by shifting in habitat-use requirements or partitioning use of the resource. The type of outcome will vary for each species, depending on their ability to share the available niche (Connor and Simberloff 1979). These kinds of changes are important to decipher but this is not possible from simple species richness or species composition analyses.

Previous studies suggest that agricultural transformation will lead to (H1) reductions in species richness (Fig. 1A; Ruffell et al. 2017) and (H2) changes in species composition (Fig. 1B; Solar et al. 2016). However, recent advances in co-occurrence theory suggest that agricultural transformation may also lead to (H3) a change in co-occurrence reflected across the entire network, with declines in connectance and changes in the distribution of co-occurrence among species (Fig. 1C; Tylianakis et al. 2010, Araújo et al. 2011, Blois et al. 2014). This may in turn lead to greater segregation of the community, and hence increased modularity of the network (Valdovinos et al. 2009, Garay-Narváez et al. 2014). For instance, human impacts can be advantageous for certain members of a community due to presence of certain functional traits or characteristics which result in these sub-communities becoming less associated with other members of the community (Sebastián-González et al. 2015, Takemoto et al. 2016). Additionally, we may expect (H4) species-specific responses that lead to restructuring of species-pair associations within the network, rather than

a network-wide response, such that some species-pairs lose associations while others gain associations (Fig. 1D). Characterizing species by their potential to lose, gain or restructure co-occurrence links provides a powerful opportunity to identify components of the community that are more at risk from anthropogenic change and could benefit most from targeted management (Arita and Peres-Neto 2016). Furthermore, because changes to network connectance could be a result of factors such as lower site occupancy across the landscape (Tylianakis et al. 2010), or particular functional trait associations (e.g. habitat guild, body size, taxonomy), these factors should be examined.

Here, we combine co-occurrence network analysis with traditional community richness and compositional analyses to explore the above hypotheses (H1-H4) that species cooccurrence may reveal overlooked effects of agricultural transformation. We gathered a large-scale (224 sites spanning > 172 000 km²) empirical dataset of species occupancy and agricultural transformation within a critically endangered woodland ecosystem of south-eastern Australia. We focused on characterizing differences in the reptile community (42 species) across sites classified by the level of agricultural transformation for two distinct agro-climatic regions. Reptiles are particularly vulnerable to agricultural transformation due to their relatively low mobility and high reliance on groundcover habitats (Fischer et al. 2004, Jellinek et al. 2004, Schutz and Driscoll 2008, Brown et al. 2011). Despite this, few studies document the impacts of agricultural transformation or other threats on reptile communities (Bland and Böhm 2016) and so we used this group to address the following four questions: 1) does species richness decline under agricultural transformation? (H1; Fig. 1A); 2) does the community composition change under agricultural transformation? (H2; Fig. 1B); 3) does agricultural transformation lead to a change in species co-occurrence reflected across the entire network (in terms of network connectance, degree distribution and network modularity)? (H3; Fig. 1C), and 4) does agricultural transformation lead to alteration of individual species-pair associations within the network that may be masked in network-wide measures of co-occurrence? (H4; Fig. 1D).

Methods

Datasets

We surveyed reptiles between 2011 and 2014 across 224 woodland patches spanning 99 farms within the critically endangered Box Gum Grassy Woodland ecological community of south-eastern Australia (172 000 km², Supplementary material Appendix 1 Fig. A1). We grouped sites into two broad agro-climatic systems (Kay et al. 2016b) that were expected to host different assemblages (Supplementary material Appendix 1): a winter-rainfall mixed grazing and cropping system (Tablelands region, 147 sites), and a low-rainfall cropping system (Western region, 77 sites).

Each reptile survey consisted of a time-constrained and area-constrained (20 min \times 0.8 ha) active search of natural habitat and inspection of artificial refuge arrays within each site (Kay et al. 2016b; Supplementary material Appendix 1). We conducted five surveys with a total effort of 1120 site-visits over spring (September 2011, 2012, 2014) and autumn (March 2012, 2014) to maximize sampling of the assemblage, recording 59 species in total. Occupancy for all reptiles was combined into a single site-visit by species matrix. We removed species with <1% occupancy across each landscape (17 out of 59 species) leaving 42 species for analysis. For most species abundance was low at the site level (1–2 individuals) so we converted abundances to presence–absence to reduce the influence of highly abundant species.

Fertilization and cultivation are major drivers of agricultural transformation (Emmerson et al. 2016). These activities have immense impact on the structure and type of ground layer vegetation and other resources necessary to reptiles (Brown et al. 2011, Jellinek et al. 2014 and references within). To quantify agricultural transformation throughout our study area, we interviewed farmers to determine the area of the landscape within 0.5 km radius of each site that had been fertilized or cultivated in the past 15 yr (Supplementary material Appendix 1). We considered this distance appropriate because 1) reptiles are highly sensitive to immediate surrounding vegetation due to high habitat specificity, often have small home ranges and limited dispersal (Schutz and Driscoll 2008), and 2) larger (> 1 km) distances would sometimes confound site-level effects within farms.

Thresholds defining ecosystem vulnerability have been recently developed in a review of global ecosystem health for the IUCN Red List of ecosystems (Keith et al. 2013, Bland et al. 2016). Natural ecosystems modified by present and ongoing agricultural activities, such as cultivation and fertilizer enrichment, are vulnerable to collapse when reduced in extent by > 30% (Keith et al. 2013). Subsequently, we defined sites as intact as those with $\geq 70\%$ cover unmodified by these activities within the 500 m buffer (supporting communities potentially less prone to collapse) and sites with > 30% modified cover (i.e. fertilized or cultivated within 15 yr) as modified (and supporting communities potentially more prone to collapse). We repeated our analyses using a range of threshold values to explore the sensitivity of our results (Supplementary material Appendix 7).

Species richness and community composition

We examined differences in species richness within intact and modified landscapes for each region separately using generalized linear mixed models (GLMM) with Poisson distribution (log link). Because our analyses focused on whole assemblages at the site level, we pooled observations within sites and across time to compile an assemblage at every site. For each subset of sites within intact and modified landscapes, we modelled richness as the response variable, with the proportion of agricultural transformation as a continuous predictor and site as a random effect. We tested for spatial dependence in the model residuals using a Moran's I test (Cliff and Ord 1981) to ensure that sites within farms were sufficiently spaced to meet assumption of independence, and found no evidence of spatial autocorrelation in either region ($p_r = 0.454$; $p_w = 0.318$).

We explored differences in assemblage composition between intact and modified landscapes for both the Western and Tablelands regions using multi-response permutation procedure (MRPP; Mielke et al. 2007) in PC-Ord ver. 6 (McCune and Mefford 2011); a nonparametric multivariate test of differences between groups. We determined statistical significance using 9999 permutations of the species data among sites and calculated pairwise site differences using the Bray–Curtis dissimilarity metric using the 'vegan' package (ver. 2.3.3; Oksanen et al. 2015) for R ver. 3.3.1. We visualized assemblage differences among agricultural transformation categories using principal coordinates analysis ordinations (PCoA; McCune and Mefford 2011).

Constructing networks of species co-occurrence

We used the approach of Lane et al. (2014), as adopted in Tulloch et al. (2016b), to build species co-occurrence networks for reptiles surveyed in intact and modified landscapes in both regions. We calculated the co-occurrence between each pair of species using the 'sppairs' package (ver. 1.0; Westgate and Lane 2015) in R ver. 3.3.1. The strength of co-occurrence (frequency of paired species presence at a site) was quantified from the slope (coefficient) of a logistic generalized linear mixed model for each pair of species, where species A was the response and species B the predictor (Lane et al. 2014, Tulloch et al. 2016b). We fitted site as a random effect to account for temporal dependency due to repeated observations across years, and excluded pairwise co-occurrence relationships that were not statistically significant at $\alpha = 0.05$ (Araújo et al. 2011). To fit the models we initially used the pooled species by site presence-absence dataset applied in the richness and compositional analyses. Due to low reptile occupancy at each site, the models failed to converge when run using the 224 sites. Therefore, we treated each of the survey repetitions as unique events to generate sufficient power to run co-occurrence models, generating each of the four networks by inputting a presence/absence dataset of species by sitevisit (1120 site-visits in total).

Because the large number of pairwise models considered inflates the chance of spurious results and over-estimation of the number of significant connections, we also conducted a parallel study of co-occurrence significance using the probabilistic approach described by Veech (2013). Whilst there were some differences in the strength of co-occurrence of individual species, the overall patterns of relationships between landscape transformation and co-occurrence metrics did not change (Supplementary material Appendix 5). This is most likely due to the fact that with the large amount of data from our surveys, individual pairwise co-occurrences were very likely to be statistically significant even if adjusted for multiplicity (Lane et al. 2014).

Sampling intensity is known to influence some network indices (Goldwasser and Roughgarden 1997, Nielsen and Bascompte 2007, Dormann et al. 2009). We accounted for differences in sampling effort between intact and modified landscape types by randomly selecting an equal subset of sites within each agro-climatic region (equal to the minimum number of sites present in intact or modified treatments for each region; Western = 25 sites, Tablelands = 57sites), and generating 100 random networks. We calculated the mean strength of all significant co-occurrence relationships between each species pair across each of the 100 random networks to create the final species-by-species cooccurrence matrix for the intact and modified landscape in each region (4 meta-networks in total). Where mean values equaled zero, we included rather than omitted them to ensure underestimation rather than overestimation of strength values. The temporal extent of data used to build networks was relatively short (4 yr; 2011-2014) and therefore we did not account for the temporal dynamics known to influence in co-occurrence at longer time-scale dynamics (i.e. community succession) (Poisot et al. 2015, Tulloch et al. 2016b).

Network co-occurrence metrics

We examined several complimentary and universally applied network metrics to quantify the impacts of agricultural transformation on reptile species co-occurrence (Tylianakis et al. 2010). First, we quantified the degree (number of positive co-occurrence relationships; Dunne et al. 2002, Tylianakis et al. 2010) for each species, and summed them to obtain the total number of positive cooccurrence links, k, for each network. Because degree is sensitive to the number of species in each network and to sampling effort (Goldwasser and Roughgarden 1997, Nielsen and Bascompte 2007, Dormann et al. 2009), we used network connectance as a measure that accounts for network size, k/n², where n is the number of network nodes (sensu Gilbert 2009).

Second, we examined whether there was change between intact and modified landscapes in the distribution of cooccurrence measures (degree and strength) (Dunne et al. 2002, Tylianakis et al. 2010, Araújo et al. 2011). We did this by characterizing the architecture of each network by examining the frequency distribution of species degree and strength (sensu Tylianakis et al. 2010).

Third, we examined whether the modularity of cooccurrence networks differed under agricultural transformation. Because human impacts can lead to greater segregation of ecological communities (sensu Sebastián-González et al. 2015, Takemoto et al. 2016), we examined whether cooccurrence networks in modified landscapes exhibited more modular structure than those in intact landscapes. To characterize differences in modularity, we quantified and plotted the modularity of each network using the igraph package (ver. 1.0.1; Csárdi and Nepusz 2006) in R ver. 3.3.1, using the 'modularity' function to find network modules. We considered networks with modularity values of > 0.4 as having a modular structure, following Newman (2006).

Pairwise associations

We examined species pairwise associations to reveal effects of agricultural transformation on community restructuring that could be masked by network metrics. For each association, we classified change in each link between intact and modified communities as either lost (significant positive co-occurrence to no co-occurrence), gained (no positive co-occurrence to significant positive co-occurrence) or stable (positive cooccurrence link maintained). Of the three classifications here, we considered only lost or gained links to represent changes in network structure.

There is a range of conditions that might result in restructured associations (MacArthur and Levins 1964, Levin 1970, Connor and Simberloff 1979). Species may lose or gain connections due to changes in spatial occupancy (even if overall populations are stable), or population asynchrony among species pairs. To test whether co-occurrence changes were simply related to species' occupancy of the landscape, we constructed simple linear models relating each species' change in occupancy to changes in co-occurrence (in terms of species link density – the relative number of significant links that a species had from all possible links – as well as mean strength). Doing so allowed us to determine if the species becoming rarer in the landscape were the ones losing co-occurrence, and vice versa, and to classify species as having: 1) both increased co-occurrence and prevalence ('increaser'); 2) reduced co-occurrence but greater prevalence ('pioneer'); 3) both reduced co-occurrence and prevalence ('decliner'), and; 4) greater co-occurrence but reduced prevalence ('refugial').

Finally, we examined whether co-occurrence differed among particular functional groups, and if this could be used to predict how a network might restructure under modification (Borthagaray et al. 2014). We examined the proportion of each species' susceptibility classification ('increaser', 'pioneer', 'decliner', 'refugial') within key functional groups considered important for reptiles. We included microhabitat guild (terrestrial, saxicolous, fossorial, arboreal and semiarboreal, following Michael et al. 2015), body size (large $[\geq 50 \text{ cm}]$, medium [10–50 cm], small [<10 cm]; Borthagaray et al. 2014), taxonomic guild (following Wilson and Swan 2013), habitat specialization (specialist, generalist following Michael et al. 2015) and dietary guild (following Wilson and Swan 2013). We then explored whether assigned susceptibility classifications differed among these functional groups.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3j7f6> (Kay et al. 2017).

Results

Community richness and composition

Our analyses included 2869 individuals from 42 reptile species (Supplementary material Appendix 2). Individual species occupancy was lower in modified landscapes for 24 (62%) and 21 (78%) species in the Western and Tablelands communities, and higher for 15 (38%) and 8 (30%) species respectively. Species richness per site was not significantly different across landscapes in either region (Table 1, GLMM; $p_w = 0.749$; $p_t = 0.484$; Supplementary material Appendix 3 Fig. A5, Table A3).

We found a significant difference in the composition of reptile communities between intact and modified landscapes in both regions (MRPP; $p_w = 0.019$; $p_t < 0.001$; Supplementary material Appendix 3 Fig. A6, Table A4).

Network co-occurrence metrics

Co-occurrence networks from modified landscapes revealed lower degree and lower average links per species compared with intact landscapes (Table 1). We found connectance was lower for sites in modified landscapes in both regions,

Table 1. Summary statistics of 1) site-level agricultural transformation attributes, 2) reptile richness and composition variables, and 3) co-occurrence network variables for both intact (>70% unmodified) and modified (<70% unmodified) sites across the two agro-climatic regions within the study area.

	Western region		Tablelands region	
	intact	modified	intact	modified
Site characteristics				
Number of sites	52	25	90	57
Mean percentage of modified landscape within 500 m buffer (\pm SD)	4.8 (8.3)	64.5 (22.2)	9.4 (10.1)	58.3 (19.7)
Reptile richness and composition				
Species richness (mean/site)	39 (4.58)	27 (4.36)	27 (3.63)	24 (3.40)
Number (%) of species increasing in occupancy	15 (38%)		8 (30%)	
Number (%) of species declining in occupancy	24 (62%)		21 (78%)	
Co-occurrence networks				
Total positive links per network	200	51	162	22
Links per species	5.13	1.89	6.00	0.92
Connectance (no. links/spp. ²)	0.13	0.07	0.22	0.04
Network modularity index	0.21	0.54	0.17	0.52

indicating that reduction in the number of co-occurrences occurred independently of differences in network size (Table 1).

The distributions of both degree and strength were considerably different between intact and modified landscapes (Supplementary material Appendix 4 Fig. A7). Modified landscapes had a truncated degree distribution, with the loss of well-connected nodes.

Networks in modified landscapes were considerably more modular than in intact landscapes (Table 1; Supplementary material Appendix 6). Values > 0.4 suggest that the network has a modular structure (Newman 2006).

Pairwise associations

Relatively few species associations were constant across landscapes, with the vast majority restructuring (92% and 96% of links in Western and Tablelands respectively) mostly through losing rather than gaining connections (Table 2). The majority of pairwise associations (75% and 91% of restructured links) were either lost or gained by species that persisted across landscape types (Table 2), with a smaller percentage permanently lost due to a loss of one or both species (25% and 8% of restructured links). Few species gained associations due to the presence of a species in modified but not intact landscapes (0% and 1% of links in Western and Tablelands respectively; Table 2).

Almost all pairwise associations changed in strength (98% for both regions; Table 2). This change was mostly attributed to a loss (79% and 88% of all restructured links in Western and Tablelands respectively) – and to a lesser extent gain (21% and 12%) – in associations, rather than a change in strength of maintained associations (Table 2). Where pairwise associations were maintained in intact and modified land-scapes, these nearly always had higher strength in modified landscapes (Table 2).

In total, 17 (44%) and 12 (41%) species gained at least one association for both the Western and Tablelands regions, with 6 species in each region (15% and 22%)

establishing completely novel co-occurrences (e.g. *Egernia* cunninghamiana Fig. 2). No species that had multiple co-occurrence connections in intact landscapes maintained all co-occurrences in modified landscapes. Six (16%) and 9 (31%) species from the Western and Tablelands lost all existing connections (e.g. *Parasuta dwyeri* Fig. 2B) under agricultural transformation. There was little consistency between regions in the species that established, lost or maintained connections (Fig. 2).

Changes in co-occurrence (in terms of link density) were not correlated with changes in occupancy in the Tablelands $(p_r = 0.828)$ but were positively associated in the Western region ($p_w < 0.001$; Fig. 3, Supplementary material Appendix 4 Table A6). The majority of species had both lower link density and occupancy under agricultural transformation (i.e. met our definition of 'decliners'; 52% and 66% of species in Western and Tablelands respectively), with only 1-2 species decreasing in occupancy but increasing in link density ('refugial', Fig. 3). Other species either increased in both occupancy and link density with others ('increaser', 16% and 4% of Western and Tablelands respectively) or increased in occupancy while decreasing in link density ('pioneers',16% of Western and 19% of Tablelands community). There were no significant relationships between changes in species occupancy and changes in co-occurrence strength in either region ($p_w = 0.248$, $p_t = 0.874$; Supplementary material Appendix 4 Fig. A8).

Grouping co-occurrence effects by species functional groups (i.e. microhabitat guild, body size, habitat specialization, taxonomic guild, and dietary guild) did not reveal any functional groups that might be used to predict the sensitivity of a species' co-occurrence relationships to agricultural transformation (Supplementary material Appendix 4 Fig. A9).

Discussion

In this study we tested hypotheses (Fig. 1) regarding the well-established impact of agricultural transformation on

Table 2. Summary of the changes in individual species pairwise co-occurrence link dynamics (degree and strength) between sites within intact and modified landscapes for the two study regions. Changes in degree and strength are classified as either lost, gained or changed (restructured) under agricultural transformation.

Pairwise species co-occurrences	Western		Tablelands	
	n	% links	n	% links
Change in pairwise species co-occurrence connections (degree)				
Stable (or no link)	20	8%	8	4%
Links restructured	218	92%	170	96%
 Links lost (because species lost from modified landscape) 	54	25%	13	8%
 Links gained (because species gain in modified landscape) 	0	0%	2	1%
 Links lost (species present across both landscapes) 	130	60%	143	83%
 Links gained (species present across both landscapes) 	34	15%	14	8%
Change in pairwise species co-occurrence strength				
Stable (or no strength)	4	2%	4	2%
Strength changed	234	98%	176	98%
 Decreased strength (because the link was removed) 	182	78%	154	88%
 Increased strength (because the link was formed) 	34	15%	14	8%
 Decreased strength (of an existing link) 	2	1%	0	0%
– Increased strength (of an existing link)	16	7%	8	5%



Figure 2. Species co-occurrence networks derived from reptile communities in sites within intact and modified landscapes across the (A) Western and (B) Tablelands study regions. Nodes represent species present (with > 1% occupancy) in each landscape. Vectors between nodes represent significant positive co-occurrence relationships, with vector strength proportional to line darkness (lightest grey = low strength, black = high strength). Species codes represent first two letters of the genus and last three letters of species name. Greyed names represent species absent (locally extinct) from landscape type.

(H1) species richness and (H2) composition, and a less explored response in species co-occurrence (H3) across the entire network, and (H4) individual species-pair associations within the network. Our first hypothesis that agricultural transformation would result in reduced mean site-level richness was not upheld. However, we found agricultural transformation significantly altered species composition of reptile communities in woodland remnants, supporting our second hypothesis. Similarly, our third hypothesis that overall declines in species co-occurrence are reflected across the entire network by a decline in network connectance, change in degree distribution as well as increased modularity was upheld. Finally, we found that overall loss of co-occurrence was not due to an even loss across all species, supporting our fourth hypothesis, and instead changes were complex and involved gains and switches in species co-occurrence. Our study demonstrates how examination of co-occurrence can reveal new insights into the impact of agricultural transformation on biodiversity, providing a different perspective to traditional richness and compositional approaches. Our



Figure 3. (A) Relationships (plus significance values) between change in occupancy and change in average co-occurrence link density (links/ species²) for species within intact and modified landscapes for each case study region. Dots represent individual species (codes represent the first two letters of the genus and second three letters for the species names). Hollow circles represent species no longer present in modified landscapes. (B) Relevant quadrants superimposed onto network structure, with color codes representing plot quadrants; species that increase in occupancy and increase in connectance ('Increaser', blue), species that increase in occupancy but decrease in occupancy but increase in connectance ('Refugial', green), species that decrease in occupancy and connectance ('Decliner', red), and species that do not deviate either in occupancy or connectance (black).

findings provide a novel set of information that can feed back into conservation decisions capable of identifying impacts before species are lost and communities irreversibly change.

Loss of species richness and changes in community composition as a result of agricultural transformation is well documented (Liu et al. 2014, Newbold et al. 2015, Ruffell et al. 2017), albeit less so for reptiles than other taxonomic groups (Trimble and van Aarde 2012). Our results support hypotheses for compositional change, but departed from expectations of reduced site-level richness and join others (Tylianakis et al. 2007) in highlighting apparent challenges with using simple diversity metrics like richness to quantify impacts of anthropogenic change on biodiversity. One problem with relying on detecting change in species richness is that effects generally occur over long time-periods (decades/ centuries) (Helm et al. 2006). Similarly, changes in richness may already be manifest in extant populations long exposed to anthropogenic impacts making observable differences

impossible to detect (e.g. prior-filtering of sites; Brown et al. 2011, Jellinek et al. 2014). A second problem is that detecting statistical change in richness will be challenging for some groups with inherently low site-level diversity (like reptiles). This is because models quantifying the loss of a single species from a starting point of only 2-3 species (as in our study) requires a far greater number of replicates than models from a starting point of 15-20 species. The absence of change in richness observed in our study, which represents one of the largest investigations of the effects of any anthropogenic threat on reptiles to date (1120 visits of 224 sites over 4 yr), underscores the difficulty in obtaining sufficiently large datasets capable of detecting changes in richness. Despite many conservation efforts to track and manage changes in diversity (Lindenmayer and Fischer 2006), increasing evidence suggests that other important changes are occurring to community structure due to anthropogenic change (Dornelas et al. 2014). Our data support this by identifying the role of anthropogenic-related assemblage restructuring in the absence of species loss.

Examining co-occurrence proved useful for identifying other aspects of changes in community composition under agricultural transformation. Network analysis revealed a lower connectance, fewer well-associated species with loss of weak links, and increased network modularity under agricultural transformation (Table 1, Fig. 2; Supplementary material Appendix 6). Characterizing these changes in network structure allowed us to detect changes in species distributions that we might anticipate under agricultural transformation. Loss of connectance, and increased modularity of networks, may drive reduction of resilience or function under the target threat (Gilbert 2009, Thébault and Fontaine 2010, Heleno et al. 2012, Fournier et al. 2016). Similarly, fewer well associated species suggest a loss of keystone species critical to the functioning of ecosystems (Fournier et al. 2016, Tulloch et al. 2016b). These interpretations are consistent with studies examining co-occurrence response to other anthropogenic threats (Araújo et al. 2011, Morriën et al. 2017), but are largely founded on what we know from biotic interaction networks (Thébault and Fontaine 2010). Caution is, however, required in the interpretation of cooccurrence network analysis (Tylianakis et al. 2010, Cazelles et al. 2016). For example, even if network metrics are useful for a general description of co-occurrence, they are not necessarily useful for identifying the causes of change in co-occurrence due to the difficulty of replicating networks (especially for vertebrates that require a high degree of sampling effort) to achieve sufficient power for statistical analysis (but see Horner-Devine et al. 2007 for an example of replicated vertebrate co-occurrence networks using a meta-analysis). For this reason, most co-occurrence network analysis to date has focused more on genetic and microbial communities where replication of communities is easier (Williams et al. 2014, Li et al. 2015). In addition, the standard statistical machinery available for richness and composition analyses is not well developed and as readily available for comparing networks (although methods to model the likelihood of different sets

of predictors in explaining patterns in community structure are increasing, see for example Peres-Neto et al. 2006). A critical next step is to understand the functional implications of differences in co-occurrence network topology, as well as the development of standardized statistical approaches for comparing multiple networks of species co-occurrence and relating differences to environmental or landscape change.

Our examination of pairwise connections appear very useful for providing detailed insight into how communities may respond to agricultural transformation (Veech 2013, Arita and Peres-Neto 2016). Nearly all pairwise connections restructured (i.e. were lost or gained), with a considerably high number of species (41-44%) demonstrating ability to gain new associations (e.g. Nebulifera robusta, Fig. 2A). Although restructured associations may in some cases be random and not ecologically meaningful, developing knowledge about how many and what type of species exhibit ability for restructuring associations can help reveal a species' unique vulnerability to the target threat. For example, species-level restructuring did not conform to any functional grouping in this study (Supplementary material Appendix 4 Fig. A9). Despite growing interest in the role of functional traits on summarizing outcomes (Lindenmayer et al. 2015, Thompson et al. 2016), our results clearly show that there is no relation between the role of the species (i.e. 'decliner', 'refugial', 'increaser' and 'pioneer') and any of their known properties (e.g. microhabitat, size, family, feeding guild etc). Ergo, addressing threats like agricultural transformation cannot rely on broad/universal responses at the whole community level, which is often the lens of examination (Burkle et al. 2013). Instead, approaches capable of identifying specieslevel responses, such as co-occurrence analysis, may significantly advance our ability to address such threats.

Implications for management

Our observation that changes to co-occurrence within the community are not universal (Fig. 3) represents a novel and useful opportunity to inform biodiversiy conservation management in the context of anthropogenic changes. For example, consider a group of organisms for which information is limited but that are vital to some ecosystem functions (e.g. an insect pollinator). Identifying components of the communities more or less vulnerable to a particular threat allows us to act before damage is done through irreversible species loss and reduced ecosystem functioning (Gilbert 2009, Heleno et al. 2012). Combining knowledge of occupancy with cooccurrence enabled us to characterize species by their distinctive response to agricultural transformation. We identified species that have become less common and also exhibit lower co-occurrence (i.e. reduced link density) under agricultural transformation (Fig. 3 bottom left quadrant). These 'decliner' species are more vulnerable to stochastic climatic and environmental threats (Lindenmayer and Fischer 2006) and could represent a 'red flag' for possible local extinction risk to managers. Conservation strategies protecting species-rich sites would likely miss the remnant patches for these species and so fail to adequately protect them. Instead, targeted species management strategies would be better. Species declining in occupancy but gaining co-occurrence (Fig. 3 top left quadrant) represent another possible 'at risk' group. This is because increased co-occurrence among particular sets of species could indicate groups being forced into refugia with other species that are declining (Tylianakis et al. 2010). Alternatively, it could indicate the invasion of one species' habitat by another species leading to transient co-occurrence. Importantly, our study also has identified species that may respond neutrally or even positively to agricultural transformation. Species that are increasing and losing co-occurrence (Fig. 3 bottom right quadrant) most likely represent those dispersing into novel unoccupied environments (because of loss of another species or change in environmental conditions), and may not require urgent management. Furthermore, species that are increasing in both co-occurrence and occupancy (Fig. 3 top right quadrant) represent those expanding their distributions into occupied sites. Determining whether the expansion of these species under agricultural transformation represents a beneficial (e.g. restoration of a species with important functional role or conservation listing) or negative (e.g. domination by an aggressive competitor) ecological outcome is important for guiding management for these species. For some groups (e.g. reptiles) this will likely require gathering additional ecological data to ascertain (Bland and Böhm 2016, Tingley et al. 2016).

Our approach reveals change in species associations under agricultural transformation but there remains a clear need for deeper ecological inference (Cazelles et al. 2016, Fournier et al. 2016). Increasingly, studies are finding nonrandom changes in co-occurrence networks in response to environmental changes (Tulloch et al. 2016b, Morriën et al. 2017). Burkle et al. (2013) showed that both interactions and co-occurrence changed over time under anthropogenic influences, while Morriën et al. (2017) found co-occurrence networks of soil micro organisms changed under land restoration. Only some of these studies have been able to explicitly link interactions such as competition or mutualism with the changes in co-occurrence. We stress that the patterns found in our study, as well as in others, require deeper understanding of the driver of association change. For example, our measure of transformation (proportion of surrounding area either fertilized or cultivated) combined a subset of possible, interacting threats to biodiversity that blur the precise mechanism of change. To better understand the drivers of association change, we suggest that researchers studying interaction networks work alongside community ecologists studying cooccurrence to understand how changes in species interactions might be explained by co-occurrence networks, and in turn, whether co-occurrence networks adequately describe community function and change in resilience.

Our study highlights the value of co-occurrence networks to identify the impacts of agricultural transformation on biodiversity. Importantly, our study also presents several potential research opportunities to advance the usage of co-occurrence networks. First, our study is based on a simplified binary classification of agricultural transformation. However, our approach may be readily transferred to categorical classifications of land-use, or even continuous data, where sufficient co-occurrence data exists. Although reptiles represent a key component of biodiversity (Bland and Böhm 2016), they differ in α , β , and γ diversity to other vertebrate groups (Gaston 2000). Replication of our approach for other α -diverse taxonomic groups would provide generality to our findings, and help determine the extent to which co-occurrence networks reliably reveal community restructuring. Second, experimental tests aiming to tease apart underpinning processes driving co-occurrence (e.g. competition, resource availability) should be conducted to help develop a stronger ecological understanding of these differences. Importantly, our analyses focussed on positive co-occurrence associations and could be repeated for negative associations if managers are interested in investigating the effects of particular threats suspected to result in species avoidance (e.g. predators or invasive competitors). Third, our study deliberately used a measure of agricultural transformation that comprised multiple threatening actions facing in-situ communities (e.g. fertilization, habitat removal, invasive species), motivated by an increasing need for holistic strategies that address multiple threats (Tulloch et al. 2016b). A useful next step would be to isolate the independent effects of the various processes to further refine management recommendations. Fourth, species co-occurrence may be influenced by temporal dynamics (such as community succession) over extended timeframes (Poisot et al. 2015, Tulloch et al. 2016b). We limited the temporal extent of our data (to 4 yr) to reduce this influence, however a better understanding of how temporal dynamics influence cooccurrence and particularly species co-occurrence restructure is needed. Long-term monitoring studies would prove useful for examining these important aspects.

Conclusion

Agricultural transformation is a global driver of biodiversity decline in agro-ecosystems (Sala et al. 2000). Previous examinations of its impact on biodiversity have largely focused on identifying changes in species richness and community composition. Our large-scale examination of species co-occurrence networks builds on this work to give more comprehensive insight into the impact of agricultural transformation on biodiversity that is not possible in conventional studies of species richness and community composition. In particular, agricultural transformation led to complex changes in species associations, with many species gaining and losing association with other species rather than a uniform loss throughout the community. Considering co-occurrence at the species-level in conjunction with species occupancy allowed stratification of assemblages by their distinctive response to the threat of agricultural transformation. This allowed us to identify those species at most risk of future decline as well as those for which targeted monitoring is required. Wider examination

of species co-occurrence networks to expose the ecological impacts of a range of other pervasive anthropogenic threats (e.g. climate change) is needed.

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Supplementary material (Appendix ECOG-03079 at <www. ecography.org/appendix/ecog-03079>). Appendix 1–7.

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