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Author for correspondence:

Karen Ikin
 e-mail: karen.ikin@anu.edu.au

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Avian functional responses to landscape recovery

Karen Ikin^{1,2}, Philip S. Barton¹, Wade Blanchard¹, Mason Crane^{1,3}, John Stein¹ and David B. Lindenmayer^{1,2,3,4}

¹Fenner School of Environment and Society, ²ARC Centre of Excellence for Environmental Decisions, ³Sustainable Farms, and ⁴National Environmental Science Program Threatened Species Hub, The Australian National University, Frank Fenner Building 141, Linnaeus Way, Acton ACT 2601, Australia

KI, 0000-0001-9179-080X

Restoring native vegetation in agricultural landscapes can reverse biodiversity declines via species gains. Depending on whether the traits of colonizers are complementary or redundant to the assemblage, species gains can increase the efficiency or stability of ecological functions, yet detecting these processes is not straightforward. We propose a new conceptual model to identify potential changes to complementarity and redundancy in response to landscape change via relative changes in taxonomic and functional richness. We applied our model to a 14-year study of birds across an extensive agricultural region. We found compelling evidence that high levels of landscape-scale tree cover and patch-scale restoration were significant determinants of functional change in the overall bird assemblage. This was true for every one of the six traits investigated individually, indicating increased trait-specific functional complementarity and redundancy in the assemblage. Applying our conceptual model to species diversity data provided new insights into how the return of vertebrates to restored landscapes may affect ecological function.

1. Introduction

Globally, the most spatially extensive form of land use is agriculture, with croplands and pasture accounting for nearly 40% of the world's land surface [1]. Landscape change in agricultural regions is commonly perceived as adversely impacting biodiversity. For instance, a recent analysis of threatening processes identified over 60% of IUCN Red List threatened and near-threatened species imperiled by agricultural expansion and intensification [2]. Yet agricultural landscape change is heterogeneous, and some regions, particularly in high-income countries, are in fact undergoing landscape recovery through a reduction in cropland and pasture, and an increase in native vegetation cover [3]. This 'positive' landscape change is occurring through restoration processes of farm abandonment, facilitating the establishment of secondary, regrowth vegetation [4], as well as active revegetation, via restoration plantings [5]. An important goal of active restoration is to return biodiversity to degraded lands, and evaluation of restoration success is typically focused on the responses of species and taxonomic groups [6,7]. Recently, the consideration of ecological function in restoration has been proposed [8–10]. A pivotal question is: how does the recovery of vegetation cover affect the recovery of ecological function brought about by the return of biodiversity?

Current understanding of changes to species-mediated ecological function within agricultural landscapes is based largely on small-scale field experiments or simulations [11–13], and relatively few studies test predictions in larger-scale 'real-world' systems [14–16]. However, undertaking the direct measurement of an array of ecological functions at scales relevant to management and conservation is hugely difficult. An alternative approach often taken is to examine changes to the functional diversity of species assemblages [17–24]. Gradients associated with landscape recovery create new environmental filters [19,25], leading to both losses and gains of species [26]. Species remaining or colonizing after landscape recovery may perform similar functions to the prior assemblage,

resulting in stability or increased redundancy in the ecological functions the assemblage performs [27,28]. Alternatively, colonizing species may perform different functions, creating increased functional complementarity within an assemblage [29–31]. Furthermore, colonizing species might replace other species, and bring either similar or different functions. Yet detecting whether colonizing species bring redundant or complementary ecological functions to an assemblage is not straightforward, and is an important barrier to interpreting changes to ecological function brought about by biotic responses to restoration.

We propose a new conceptual model to identify potential changes to functional redundancy and complementarity from easily calculated metrics of species diversity (figure 1). In doing so, we build on previous work on the effects of disturbance on the taxonomic–functional richness relationship that show that the slope and shape of this relationship may shift in landscapes undergoing change [17,25,33–38]. For instance, increased disturbance intensity can lead to species with disturbance-tolerant traits dominating an assemblage, with subsequently lower functional richness than expected from taxonomic richness. This contrasts with less disturbed communities where the distribution of traits may be more uniform and the relationship between taxonomic and functional richness more straightforward [35]. Furthermore, landscape change can cause turnover in assemblage composition, leading to changes in functional diversity but not changes to the number of species in assemblages [39]. Consequently, the theoretical understanding that altered species diversity with landscape change may result in similar effects on ecological function [17,35,40–42], with the attendant implication that taxonomic richness can be used as a proxy for functional responses, may not apply. Our conceptualization is an important advance on these understandings, as it uses the recognition that landscape change may affect either, both or neither of taxonomic and functional richness to infer a range of functional responses to landscape recovery. That is, in landscapes undergoing change, we propose that the consequent relative changes in taxonomic and functional richness can indicate corresponding changes to complementarity and redundancy in the ecological functions the assemblage performs.

We demonstrate the value of our new conceptual model with a 14-year study involving 6528 surveys of 122 terrestrial bird species (electronic supplementary material, table S1) across an extensive agricultural region of Australia (electronic supplementary material, figure S1). We focused on six ecological traits of birds that relate to ecological function (table 1) [43]. Using these data, we addressed two questions. (i) How are taxonomic and functional richness related to the type and scale of landscape recovery (i.e. secondary regrowth versus restoration plantings; in the patch versus surrounding landscape)? (ii) Which traits drive patterns of observed functional responses? We examine the implications of our findings for functional redundancy and complementarity in the context of our conceptual model.

Relatively few studies have examined how vertebrate functional diversity (as opposed to that of plants or insects) changes in response to landscape change [17,19,34,44], although there has been a recent increase in such research [20,45–49]. Moreover, most studies have explored only adverse impacts of landscape change (e.g. habitat loss and fragmentation), and there is a paucity of studies examining functional responses to ‘positive’ landscape recovery following restoration [50,51].

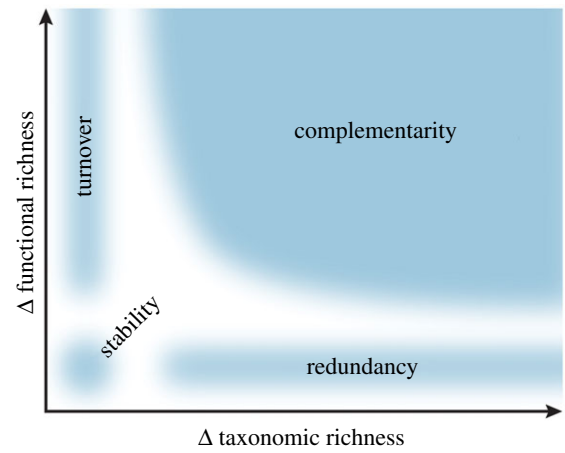


Figure 1. Predicted responses of taxonomic and functional richness to landscape change, and the consequences for ecological function. The relative change in the easily calculated diversity metrics, taxonomic and functional richness, underpins our new conceptual model. Where both taxonomic richness and functional richness increase with a landscape attribute (e.g. vegetation cover), species gained contribute complementary functions to the assemblage [29–31]. Functional complementarity is related to the efficiency in the performance of ecological function [32]. Where only taxonomic richness increases, species gained contribute redundant functions [27,28]. Functional redundancy is related to stability in the performance of ecological function [32]. Where only functional richness increases, functional turnover (from species with redundant traits to species with complementary traits) is occurring. Where both are unchanged, the assemblage is stable. It is also possible to have a loss of functional richness with increasing taxonomic richness (i.e. turnover from complementary to redundant traits) [33]. (Online version in colour.)

There are, therefore, relatively few insights into how the return of vertebrates to restored agricultural landscapes may affect ecological function. By applying our new conceptual model to our empirical data, we identified how landscape recovery affected trait-specific complementary and redundancy among bird species. This enabled us to evaluate the extent and mechanisms of restored functional richness, including implications for the efficiency and stability of ecological function [32], through the changes in diversity of avian functional traits.

2. Material and methods

(a) Study design and data collection

Our study was located in the southwest Slopes bioregion, New South Wales, Australia (electronic supplementary material, figure S1). The study design consisted of 17 agricultural landscapes, each with two farms where we placed four 2 ha sites (136 sites in total) in vegetated patches of old-growth woodland, regrowth woodland and restoration plantings. These sites were established in 2001 as part of the long-term Southwest Slopes Restoration Study, which aims to investigate fauna responses to remnant native vegetation and vegetation plantings in agricultural landscapes [52,53]. Old-growth woodland (greater than 220 years old) was composed of temperate box-gum *Eucalyptus* woodland and was of degraded condition due to agricultural practices. Regrowth (majority older than 1990) included *Eucalyptus* woodland regenerating naturally from germinating seeds and stems that had resprouted from living trees following disturbance, such as clearing or fire. Extensive restoration plantings had been

Table 1. Ecological traits of birds that are predicted to relate to their effect on ecological function. Every bird species was assigned to a guild within each trait.

ecological trait	guilds	link to ecological function
primary diet	insects; nectar; seeds; varied; vertebrates; mistletoe	insectivores and omnivores may contribute positively to invertebrate pest control. Nectarivores may contribute positively to pollination; granivores may contribute negatively to crop consumption; omnivores may contribute positively to carcass and waste disposal
foraging substrate	ground; understorey; canopy; aerial	understorey foraging species are mostly insectivores, which may contribute positively to invertebrate pest control; canopy foraging species are mostly insectivores and nectarivores, which may contribute positively to pollination
feeding aggregation	flocking; non-flocking	flocking species may have high localized impact on services such as pest control and pollination
nesting aggregation	colonial; non-colonial	colonial nesting species may concentrate nutrients within small areas
seasonal movements	local dispersal; nomadic; partial migrant; total migrant	local dispersers may concentrate nutrients within small areas; nomadic and migratory species may influence large-scale cycling of nutrients and services such as pest control and pollination over large regions
body mass	5.7 g–1.8 kg (median 35.2 g) very small: <20 g; small: 20–90 g; large: >90 g	relates to morphological and life-history traits that may dictate species' effects on ecological function; for example, larger bodied birds with higher metabolic rates may consume more pest species

established over the last 30 years, and were composed generally of *Eucalyptus* and *Acacia* species.

We collected bird presence/absence data during six point counts in each site in October and November (spring) of 2002, 2004, 2006, 2008, 2009, 2011, 2013 and 2015 (6528 surveys). We followed a strict survey protocol designed to reduce biases in false-negative errors [54] and observer heterogeneity [55]. Morning point counts were conducted at the 0 m, 100 m and 200 m points of a permanent transect, repeated by a different observer on a second morning. All terrestrial birds seen or heard within 50 m of the point during 5 min were recorded; species recorded during any of the six point counts were recorded as present in the site for that year.

For each bird survey year, we measured the percentage of tree cover in a 500 m radius circle centred on the 100 m transect point, using Landsat satellite imagery of annual forest extent [56] (<http://wald.anu.edu.au/australias-environment-explorer-data-description-and-download/>). This product does not adequately represent plantings or regeneration less than 2 m high or vegetation with less than 20% canopy cover, and thus underestimates increases in tree cover through time. For this reason, we focused on spatial differences in tree cover between sites to define recovery at the landscape scale. We used the natural logarithm of the percentage surrounding tree cover in subsequent analyses.

(b) Taxonomic and functional richness calculations

We considered six traits related to ecological function (table 1) [43,57]:

- (i) *primary diet* and (ii) *foraging substrate*, which relate to functions such as pest insect control (e.g. by insectivores, understorey foragers), seed dispersal (e.g. by granivores) and pollination (e.g. by nectarivores, canopy foragers);
- (iii) *feeding aggregation*, which relates to the localized impact of functions (e.g. by flocking species);
- (iv) *nesting aggregation* and (v) *seasonal movements*, which relate to nutrient cycling over small (e.g. by colonial nesting species) and large (e.g. by migratory species) regions; and
- (vi) *body size*, which relates to a range of morphological and life-history traits that dictate effects on ecological function.

Using a published database of Australian bird information [58], supplemented by BirdLife Australia species summaries (<http://birdlife.org.au/>), we assigned every species to a discrete guild within each categorical trait, and its mean (ln) body mass for the continuous body size trait (electronic supplementary material, table S1).

For each site in each year ($n = 1088$ site by year combinations), we calculated taxonomic richness as the number of species present. For guilds that were sufficiently species-rich (more than five species assigned to the guild), we calculated guild richness as the taxonomic richness of species in each guild present. For the body size trait, we divided species into three 'guilds' (very small: less than 20 g; small: 20–90 g; large: greater than 90 g) to calculate guild richness.

We calculated seven measures of functional richness, using the *FD* package [59,60] in the R statistical program [61], which uses trait diversity as a proxy for functional diversity. The first measure used all six ecological traits to calculate the functional richness of the assemblage. From our species-trait matrix, we used the *dbFD* function to compute a Gower dissimilarity matrix with a square root correction to create a species–species distance matrix. The function then performed a principal coordinates analysis on this corrected matrix, and used the resulting axes to find the minimum convex hull that included all species. Functional richness was then calculated as the volume of this convex hull (i.e. the amount of functional space occupied by the bird assemblage) [62]. The additional six measures focused on the functional richness of each of the six individual ecological traits. To do this, we either summed the number of guilds present within each of the categorical traits (primary diet, foraging substrate, feeding aggregation, nesting aggregation and seasonal movements), or calculated the range of values for the continuous trait (body size).

(c) Statistical analyses

For the following analyses, we used linear mixed models in the *lme4* package [63], fitted with year, and site nested in farm nested in landscape as random variables to account for temporal and spatial dependencies in the data. We standardized all variables prior to analyses (mean = 0, s.d. = 1).

To find the relationship between taxonomic richness and functional richness, we modelled functional richness against linear (untransformed) taxonomic richness and nonlinear

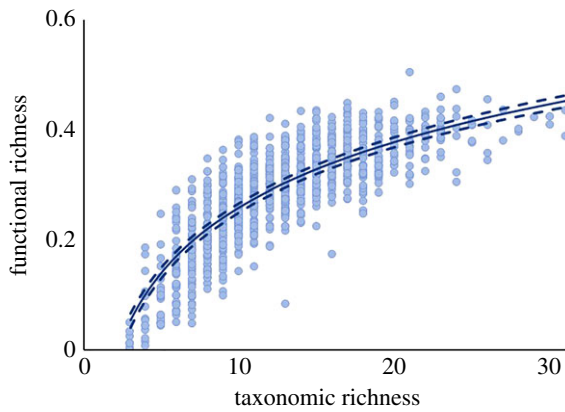


Figure 2. Relationship between taxonomic richness and functional richness. Solid line shows model prediction, dashed lines show 95% prediction intervals. Points show raw data. (Online version in colour.)

(quadratic or logarithmic) transformations of taxonomic richness. We compared these three models based on their Akaike information criterion (AIC) values (using the *AICcmodavg* package [64]) to select the model with the lowest AIC. We calculated conditional R^2 values (using the *r.squaredGLMM* function in the *MuMIn* package [65]) to assess model fit (i.e. the proportion of variance explained by the full model).

To investigate the response of taxonomic (guild) richness and functional richness to landscape recovery, we modelled each measure against patch type (i.e. whether the site was in a patch of old-growth woodland, regrowth or planting) and the percentage of tree cover in the surrounding landscape. We initially fitted the interaction of patch type and percentage tree cover, but dropped the interaction term after finding no evidence of an interaction between these two variables (electronic supplementary material, table S2). We used model diagnostic plots to confirm model assumptions and calculated the conditional R^2 to assess model fit.

3. Results

We found a positive nonlinear (logarithmic) relationship between bird taxonomic richness and functional richness (figure 2; electronic supplementary material, table S3). However, taxonomic and functional richness responded differently to landscape recovery (figure 3; electronic supplementary material, table S4). First, we found that taxonomic richness did not significantly differ between patch types (figure 3a), while functional richness was significantly higher in plantings compared with old growth and regrowth (figure 3b). Second, we found that both taxonomic and functional richness increased with increasing tree cover within 500 m (figure 3; electronic supplementary material, table S4).

We found that idiosyncratic responses of the individual traits underpinned these patterns in the assemblage (figure 4). For nearly all traits (with the exception of the nesting aggregation trait), regrowth had similar functional richness (i.e. a similar number of guilds present) and similar guild richness to old-growth woodland. With the exception of the foraging substrate trait, plantings and old growth had similar functional richness of the different traits. By contrast, guild richness differed between plantings and old growth, with plantings having more insectivores, nectarivores, understory foragers, non-flocking species, non-colonial nesters, partial migrants and very small species, and fewer granivores, omnivores, colonial nesters and large species. Trait responses differed with

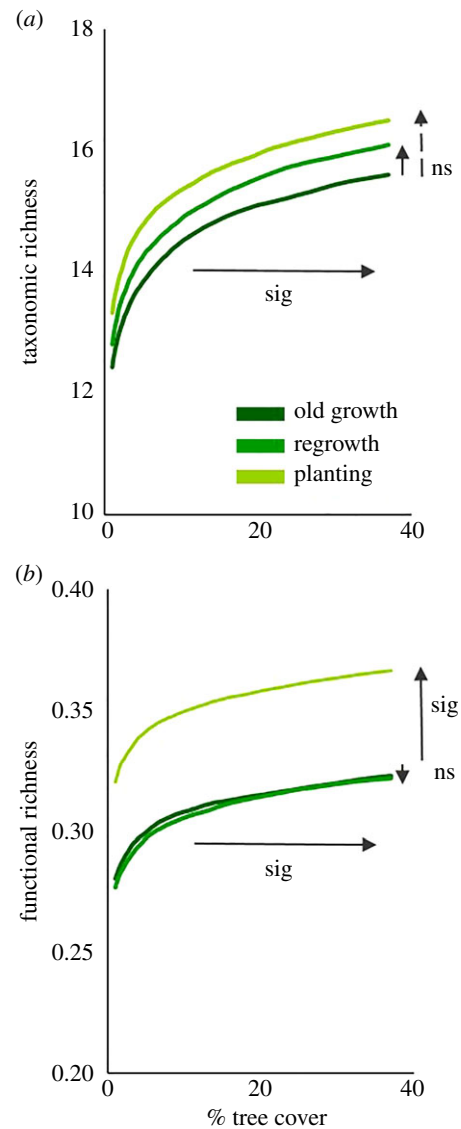


Figure 3. Relationships between taxonomic and functional richness and two aspects of landscape recovery: patch type (old growth, regrowth and planting) and landscape-scale vegetation cover. Solid line shows model prediction, dashed lines show 95% prediction intervals. Arrows indicate whether taxonomic and functional richness was significantly related ($p < 0.05$; 'sig') or not (ns) to the explanatory variables. (Online version in colour.)

increasing tree cover in the landscape (figure 4). Functional richness of the primary diet, foraging substrate and body mass traits increased with landscape tree cover. Furthermore, there was increased richness of all guilds, with the exception of granivores, which declined with increasing tree cover, and ground foragers, colonial nesters, nomadic species, and small and large species, which were not related to tree cover.

4. Discussion

While forest is cleared at a rate of five million hectares globally per year [66], some agricultural regions are gaining native vegetation cover via secondary regrowth and restoration plantings [4,5]. Innovative techniques are needed to better understand biodiversity responses to this positive landscape change. This is a particular imperative given that processes of species gain are not simply the reverse of species loss [26]. Our new conceptual model, based on relative changes in taxonomic and functional richness with landscape change, revealed novel insights into how landscape recovery

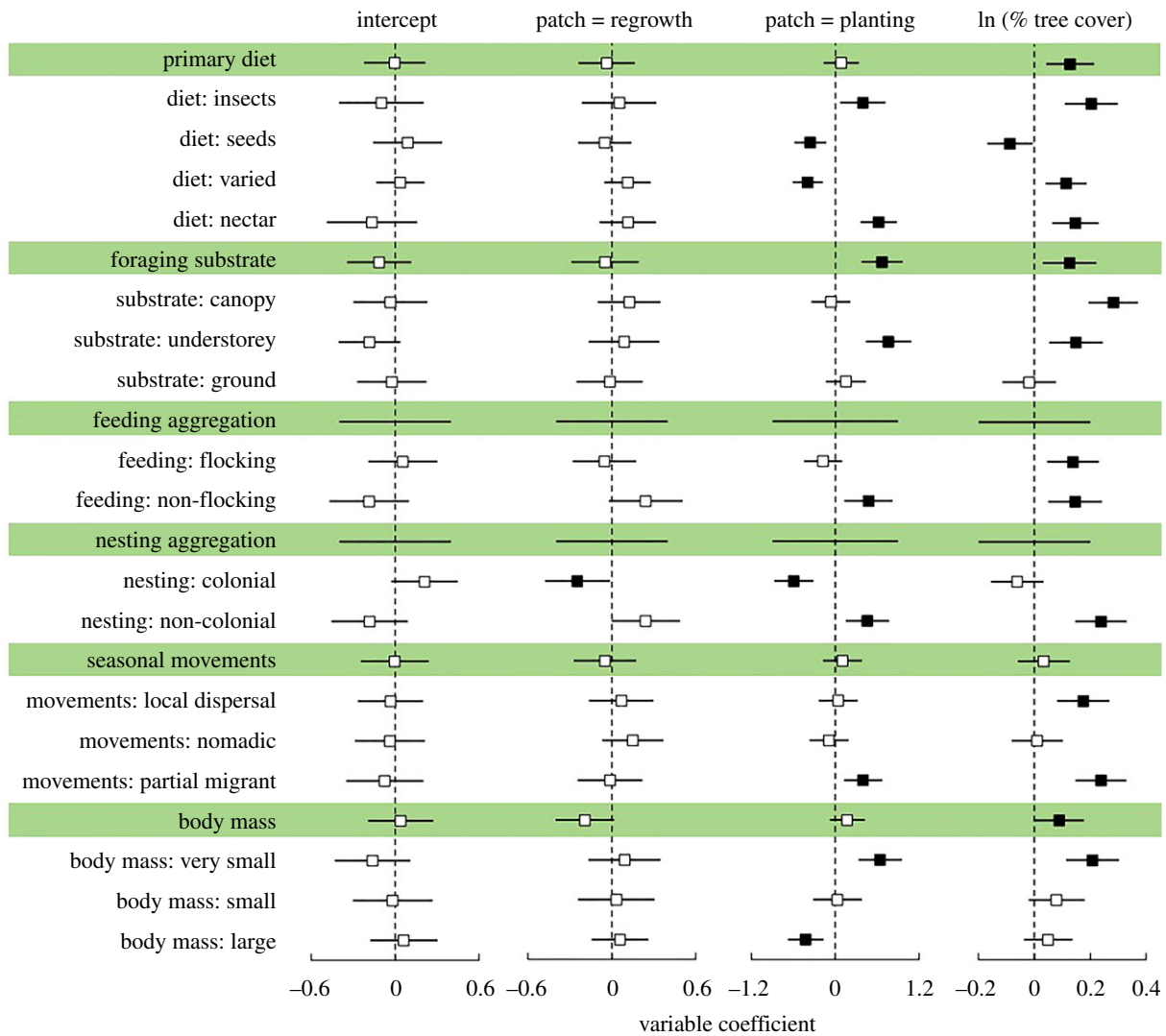


Figure 4. Standardized explanatory variable coefficients for individual trait functional richness (shaded) and guild richness (not shaded). Error bars are 95% confidence intervals, and black points indicate that these confidence intervals did not cross zero, i.e. that functional or guild richness was significantly related ($p < 0.05$) to the explanatory variable. Functional richness of the feeding and nesting aggregation traits was not modelled because nearly all sites had both guilds present. (Online version in colour.)

influences the functional responses of species assemblages. We discovered increasing trait-specific functional complementarity and functional redundancy of birds with increasing landscape-scale tree cover and establishment of restoration plantings, thus identifying how biodiversity recovery is occurring in a large modified landscape. Based on our findings, we can evaluate the extent and mechanisms of restored ecological function to which landscape recovery may lead.

We found clear evidence that landscape recovery is increasing aspects of functional complementarity and redundancy among avian assemblages in our degraded agricultural landscape. However, we uncovered unexpected differences in how the scale and type of landscape recovery influenced these functional changes. Recovery at the landscape scale, as indicated spatially by the amount of tree cover surrounding studied patches, was a significant determinant of functional change for the overall bird assemblage and for every trait investigated. For example, applying our conceptual model to our finding of a positive effect of tree cover on both taxonomic and functional richness indicates higher functional complementarity in landscapes with more vegetation cover. The increased permeability of these landscapes probably underpins the functional responses that we detected: landscapes

with high tree cover facilitate movement of species, particularly for mobile taxa such as birds that are able to cross small gaps to use patches as connected areas of habitat [67]. Our findings show that conservation and management actions to restore native vegetation in agricultural landscapes can therefore have a widespread positive effect on avian functional diversity.

Increased tree cover in a landscape increased both the number of guilds and guild richness within the primary diet and foraging substrate traits, as patches were colonized by species belonging to guilds not already present, thus indicating under our conceptual model increased functional complementarity. These findings suggest that positive landscape change via ecological restoration can improve the *efficiency* in the performance of ecological functions [32]. As communities gain new and functionally distinct species (observed as increases in both taxonomic and functional richness), the assemblage may be better able to perform new ecological functions [29–31]. In our study, patches surrounded by higher tree cover gained insectivores and nectarivores, and canopy and understorey foragers, and thus gained functions associated with these guilds, such as potential suppression of insect populations, seed dispersal and pollination [57]. Landscape recovery, therefore, by increasing the number of species

performing ecological functions, improves the efficiency of how these functions are performed.

We found that patches in landscapes with high tree cover were colonized by species belonging to already-present guilds within the feeding and nesting aggregation, movements and body size traits, thus indicating under our conceptual model increased functional redundancy. These findings suggest that landscape recovery improves the *stability* of ecological functions [32]. As patches gain new but functionally similar species (observed as increases in taxonomic richness only), the assemblage becomes more able to perform its current ecological functions [27,28]. In our study, landscapes with high tree cover gained species related to where ecological functions are delivered, such as flocking species that may have a highly localized impact on services such as pest control and pollination, and local dispersers that may contribute to cycling nutrients within small areas [43]. As a result, with landscape recovery, these functions are more likely to be maintained even if individual species populations vary.

When compared with landscape-scale effects, we found that the effects of recovery at the patch scale (i.e. secondary regrowth and restoration plantings) on the bird assemblage were greater in magnitude but influenced fewer aspects of functional change. It was unexpected that the functional differences between regrowth and old-growth patches were not more apparent, as our conceptual model indicated only lower functional redundancy within the nesting aggregation trait in the regrowth bird assemblage. Previous studies of taxonomic change have found that regrowth woodland is particularly valuable habitat for woodland birds, especially when remnant old growth is heavily degraded due to agricultural practices [68,69]. By contrast, we found that the bird assemblage in plantings, compared with old-growth patches, was more functionally diverse for a similar number of species, with our conceptual model indicating higher functional complementarity within the foraging substrate trait and higher functional redundancy within the primary diet, feeding and nesting aggregation, movements and body size traits. Although lacking in several important habitat resources such as large old trees and coarse woody debris [69], plantings have high structural complexity that provides a diversity of habitat resources for insectivores and nectarivores, understorey foragers, and small-bodied species. Thus, the establishment of restoration plantings in agricultural landscapes improves both the efficiency and stability in the performance of related functions like pollination and possibly also suppression of insect populations.

Our application of fundamental ecological theory and the development of our new conceptual model provides a potent novel approach to infer potential changes in ecological function based on easily accessible data. This is crucial for investigating and evaluating ecosystem processes at landscape scales

relevant to on-ground action, where the direct measurement of an array of ecological functions may not be feasible [12,13]. For instance, many environmental monitoring programmes already collect sufficient species diversity data to implement our conceptual model; typically, these programmes would not have the capacity to expand monitoring to include ecological function. However, although our model is founded on a well-established understanding of biodiversity-ecosystem functioning [17,19–24], we propose that an important research advance would be to relate our conceptual model of functional complementarity and redundancy to a quantified measure of ecological function (e.g. pollination or insect predation rate). Studies such as the Biodiversity Exploratory project [14] and European FunDivEUROPE project [16] showcase how this may be achieved at large scales.

In conclusion, we have discovered that investigating vertebrate taxonomic and functional richness, and differentiating between functional redundancy and functional complementarity, can give new insight into how landscape recovery can affect ecological function. By investigating independent taxonomic and functional richness responses to the scale and type of landscape recovery, we discovered potential trait-specific increases in functional complementarity and redundancy. Increased tree cover at the landscape scale was a significant determinant of functional change for the overall bird assemblage and for every one of the six traits investigated individually. Bird assemblages in restoration plantings had strong functional differences to assemblages in old-growth woodland patches. Applying our conceptual model, these findings indicate that landscape recovery enhanced trait complementarity and redundancy, with flow-on improvements in the efficiency and stability of ecological function provided by some traits. Our findings thus provide guidance on the consequences of agricultural restoration for biodiversity by demonstrating how the conservation and management of native vegetation, at patch and landscape scales, can lead to strikingly different functional attributes of the bird assemblage.

Data accessibility. Data available from the Dryad Digital Repository at: <https://doi.org/10.5061/dryad.d6k0804> [70].

Authors' contributions. K.I., P.S.B. and D.B.L. designed the study. M.C. managed the collection of the bird data. J.S. calculated the tree cover data. K.I. and W.B. conducted the analyses. K.I., P.S.B. and D.B.L. led the writing of the manuscript with input from W.B., M.C. and J.S.

Competing interests. We declare we have no competing interests.

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