Tree decline and the future of Australian farmland biodiversity

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Farmland biodiversity is greatly enhanced by the presence of trees. However, farmland trees are declining worldwide, including in North America, Central America, and parts of southern Europe. We show that tree decline and its likely consequences are particularly severe in Australia's temperate agricultural zone, which is a threatened ecoregion. Using field data on trees, remotely sensed imagery, and a demographic model for trees, we predict that by 2100, the number of trees on an average farm will contract to two-thirds of its present level. Statistical habitat models suggest that this tree decline will negatively affect many currently common animal species, with predicted declines in birds and bats of up to 50% by 2100. Declines were predicted for 24 of 32 bird species modeled and for all of six bat species modeled. Widespread declines in trees, birds, and bats may lead to a reduction in economically important ecosystem services such as shade provision for livestock and pest control. Moreover, many other species for which we have no empirical data also depend on trees, suggesting that fundamental changes in ecosystem functioning are likely. We conclude that Australia's temperate agricultural zone has crossed a threshold and no longer functions as a self-sustaining woodland ecosystem. A regime shift is occurring, with a woodland system deteriorating into a treeless pasture system. Management options exist to reverse tree decline, but new policy settings are required to encourage their widespread adoption.

countryside biogeography | grassy box woodlands | ranchland | regime shift | scattered trees

The future of farmland biodiversity is a major concern around the world (1–3). Farmland biodiversity is valuable in its own right, but also because it provides ecosystem services that are of direct benefit to agricultural production. For example, birds and bats control insect pests (4–6), and trees provide shade for livestock (7, 8). Scattered trees occurring throughout the farmland matrix are prominent features of agricultural landscapes around the world, including in southern Europe (9, 10), North America (11, 12), Central America (13–15), and Australia (16). Farmland trees often represent relicts of largely cleared forest or woodland ecosystems (17, 18) and are believed to play important roles in maintaining ecosystem function and farmland biodiversity (7, 13, 16).

Southeastern Australia's temperate agricultural zone is part of a threatened ecoregion (19) where farmland trees are declining rapidly. In cropping landscapes, trees are cleared to make way for agricultural machinery (20, 21). In livestock grazing landscapes, trees are declining because of a combination of natural or accelerated tree mortality coupled with widespread recruitment failure (22). The decline of scattered trees is increasingly recognized as a threat to biodiversity and associated ecosystem services, both in the academic literature (7, 17, 20, 22–24) and increasingly in conservation policy (25).

Scattered trees are declining not only in Australia, but declines also have been observed or predicted in Africa (26), Central America (27), North America (12), and Europe (10, 28–30), with grazing and agriculture typically playing important roles. Despite the global significance of tree decline in agricultural landscapes,

spatially, and temporally explicit analyses of tree decline and its likely consequences remain rare (17, 31). Key questions are as follows: (i) What will happen to tree cover in different parts of the landscape, and over what timeframe? (ii) Which animal species will be negatively affected by tree decline, and which will be positively affected? (iii) What will be the future distribution patterns of affected animal species relative to their current distribution?

We investigated these questions in a 1 million-ha area in the Upper Lachlan Catchment of New South Wales (Fig. S1). Before European settlement in the 1800s, the region was dominated by grassy box woodlands in the valleys and dry forest on the hilltops (dominant tree species include *Eucalyptus melliodora*, *E. albens*, *E. macrorhyncha*, and *E. polyanthemos*). The area is now dominated by livestock grazing. Tree cover has been reduced to ≈15%, and one-third of remaining tree cover occurs in patches smaller than 1 ha or as scattered paddock trees (32). Larger patches remain primarily on hilltops, because settlers preferentially cleared the more productive soils in the valleys (32, 33). Remnant tree cover is important because it enhances water infiltration, offers shade for livestock, and provides habitat and connectivity for native species (7).

We used three sources of primary field data in our analysis, originating from 126 sites distributed over 33 large farms: (i) data on the density and diameters of trees; (ii) presence/absence data on birds; and (iii) activity data on bats. We also drew on a validated 10-m–resolution map of tree cover for the region (32) and on a published demographic model for trees that predicts future tree densities on the basis of specified mortality and recruitment rates at a given site (17). The unique combination of extensive field data on two fundamentally different animal taxa, remotely sensed data, and a demographic model for trees enabled us to obtain new, spatially explicit insights into likely biodiversity changes in the future.

There were five steps to our analysis (Fig. S2). First, we calibrated the demographic model for trees by applying four combinations of plausible mortality and recruitment rates to tree data from grazed sites and ungrazed remnant patches. Although many factors determine whether tree density at a given site will increase or decrease, it is widely accepted in our study region that the best examples of functioning woodlands are ungrazed remnant patches where livestock grazing is excluded (34, 35). Tree recruitment, in particular, is significantly higher in ungrazed patches (22, 36), and recruitment rates in ungrazed patches provide the best available estimates of natural recruitment rates. On this basis, we reasoned that a realistic

demographic model would predict relatively stable tree densities in ungrazed patches. Second, we applied the calibrated demographic model to grazed sites throughout the region and used regression modeling to find landscape-scale predictors of modeled future tree densities. Third, drawing on these landscape-scale predictors, we produced landscape-scale maps of predicted tree densities at four time steps into the future (24, 48, 96, and 192 y) and compared these with a map of present tree density. Fourth, we used our field data to develop original habitat models for 32 bird species and six bat species, with particular emphasis on their response to tree density. Fifth, we separately applied these habitat models to maps of present tree density and modeled future tree density, thus generating predictions of the future distribution of birds and bats.

Results

Calibration of Demographic Model for Trees. Of four alternative model parameterizations, all predicted relatively stable numbers of trees in ungrazed patches (Fig. S3) and all predicted tree decline in grazed sites (Fig. S3). We concluded from this first part of our analysis that: (*i*) the demographic model produced ecologically plausible results and (*ii*) the precise parameterization of the demographic model was secondary, because all scenarios showed broadly similar patterns in tree decline for grazed areas (Fig. S3). In subsequent steps, we focused on the scenario that produced the most stable predictions for tree numbers in ungrazed woodland sites, because we presumed this scenario to be ecologically most plausible (see Fig. S3 for details).

Landscape-Scale Predictors of Future Tree Density. We separately modeled tree density into the future at all grazed sites and tested which landscape-scale variables were correlated with predicted patterns of decline. We found that the declines predicted for a given site were significantly related to its current tree density and its pasture type [R^2_{adj} (24 y) = 0.95; R^2_{adj} (96 y) = 0.84; see Table S1 for details]. Relative to the current tree density at a given site, tree density was predicted to decline fastest where trees occurred at low density and in introduced, rather than native or mixed, pastures (Table S1).

Landscape-Scale Trends in Tree Cover. We applied the relationships with pasture type and current tree density (Table S1) to predict future tree density across all grazed pastures on 32 farms. We compared current tree density with predicted tree density at four time steps into the future (24, 48, 96, and 192 y). Predictions showed a steady expansion in the amount of treeless land (Fig. 1, Fig. 2*A*, and Table S2). For example, the proportion of land on an average farm with tree densities of <1 tree per 2 ha was predicted to expand from ≈20% at present to nearly 40% in 96 y (Fig. 2*A*). Concurrently, areas of dense tree cover were predicted to contract. For example, at present 30% of an average farm has tree densities of ≥25 trees per 2 ha, but this proportion was predicted to decline to 20% by the end of this century (Fig. 2*A*). Major changes were evident when the actual number of trees was considered. At present, an average farm supports 20,000 trees per 1,000 ha of grazing land,
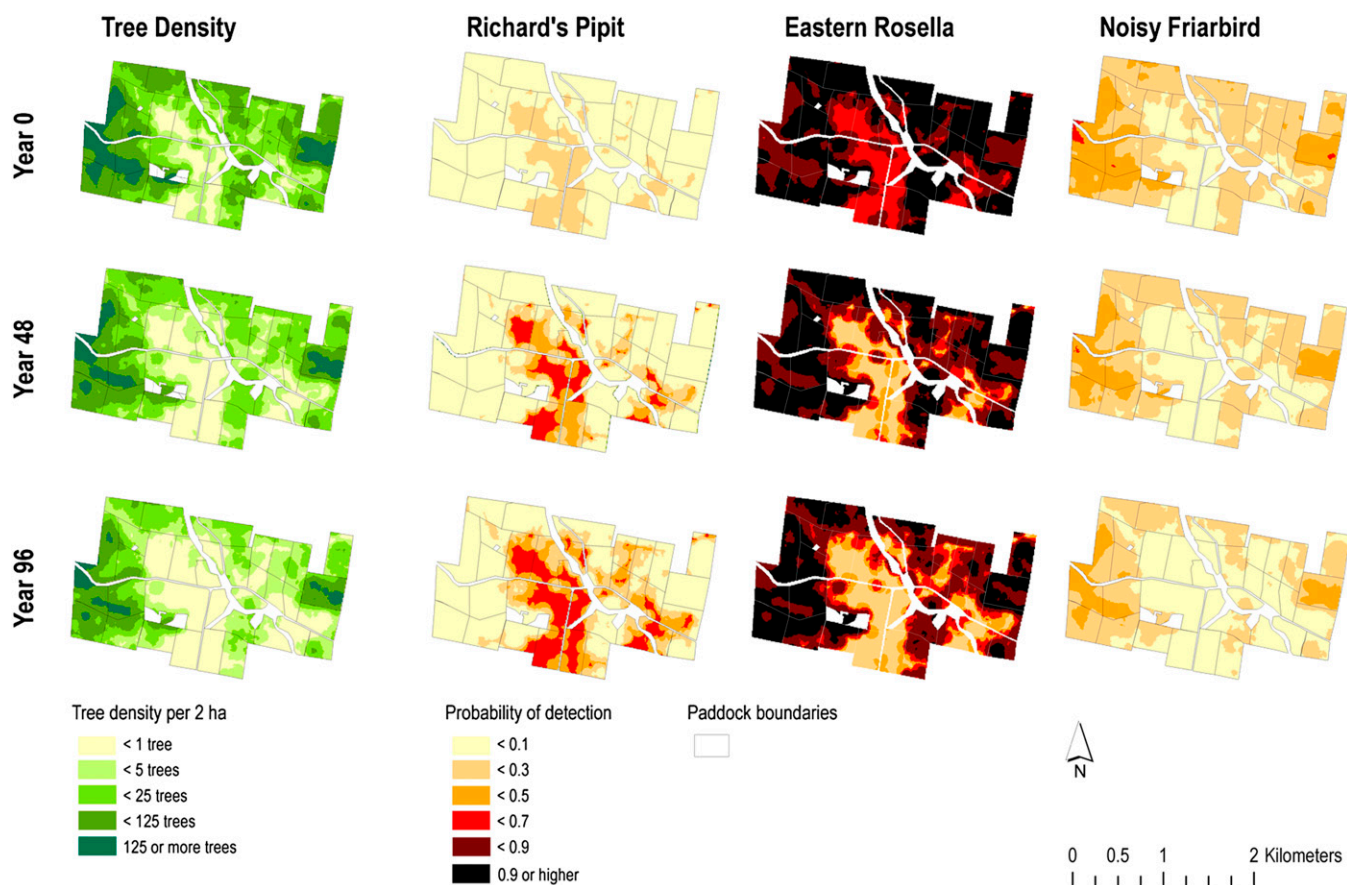
Fig. 1. Predicted changes in tree density and three species of birds on one of the farms modeled. Richard's pipit had a negative response to tree cover, the eastern rosella had a quadratic response to tree cover, and the noisy friarbird had a positive response to tree cover (for details and scientific names, see Table S3). All maps are based on models derived from original empirical data. Similar maps were produced for 32 farms for tree density, 32 bird species, and 6 bat species at 5 time steps. Robust interpretation should focus on the average patterns predicted across all farms (Fig. 2); the above example for a specific farm is for illustration purposes only.
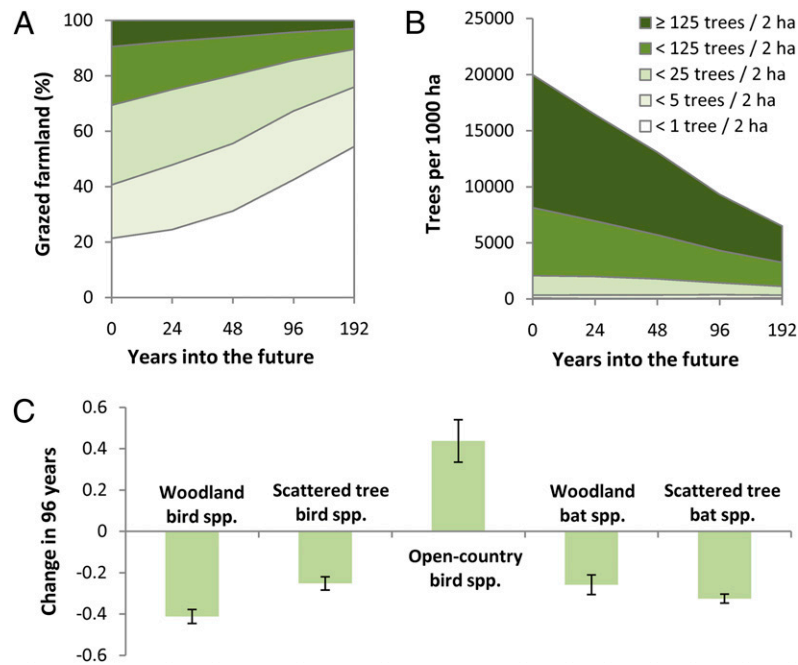
Fig. 2. Predicted changes in the amount of an average farm occupied by tree cover at different densities (*A*), the number of trees on an average farm occurring at different densities (*B*), and the number of bird detections and the level of bat activity on an average farm (*C*). For *A* and *B*, data are the predicted means across 32 farms, scaled for each farm to 1,000 ha of grazed land. A numerical summary including SEMs is given in Table S2. For *C*, species are classified according to their response to tree cover (negative response = open-country species; quadratic response = scattered tree species; positive response = woodland species; Table S3 and S4). Bars summarize predicted mean changes (±SE) within a given group of species. For details on individual species, see Table S5.

but this number was predicted to decline to 13,000 trees within 48 y (Fig. 2*B* and Table S2).

Habitat Models for Birds and Bats. Of the 32 most widespread bird species, 5 did not respond to tree density, 3 responded negatively, and 11 responded positively. The remaining 13 species peaked at intermediate tree densities, with 12 species peaking at densities between 6 and 61 trees per 2 ha, and 1 species peaking at 157 trees per 2 ha (Table S3; see Fig. 2 for an overview of current tree densities). Three bat species responded positively to tree density, and three peaked at intermediate levels of tree density (Table S4).

Landscape-Scale Trends for Birds and Bats. A comparison of expected current and future detection numbers suggested declines for 24 of 32 bird species (Figs. 1 and 2*C*). Predicted declines ranged from 4 to 35% within 48 y, and from 6 to 53% within 96 y (Table S5). All six bat species were predicted to decline with the ongoing loss of trees, by up to 22% within 48 y, and by up to 37% within 96 y (Table S5). The only species predicted to increase were the three bird species that responded negatively to tree cover (Fig. 2*C* and Tables S3 and S5).

Discussion

We demonstrated without ambiguity that southeastern Australian grazing landscapes are on a trajectory of ongoing degradation, and we were able to give an indication of likely minimum effects on biodiversity over specified time periods. Our predictions for tree decline in grazed areas are consistent with previous demographic modeling of farmland trees from around the world (17), suggesting the phenomenon we document is unlikely to be unique to Australia. For example, in the United States, tree recruitment in oak savannas (*Quercus* spp.) is widely believed to be below replacement levels (11, 12). Although the reasons for this recruitment failure are sometimes unclear (37), like in Australia, tree recruitment is particularly low on private land (12), and birds are among the animals predicted to be negatively affected by ongoing tree decline (11). In

Europe, anthropogenic systems with scattered oak trees are facing a similar situation, with insufficient recruitment reported in Spanish dehesas (9, 10) and wood pastures in the United Kingdom (29, 30) and Romania (28). Some tropical systems also experience a broadly similar situation. In Central America, remnant rainforest trees scattered through cattle pastures are common (15, 18, 27). However, tree recruitment is often below replacement levels (but see ref. 15), and possible large-scale losses of trees (18, 27) would have negative effects on a range of ecosystem processes, including a loss of functional connectivity for forest birds (38). Finally, of particular concern are intensifying landscapes in poor tropical countries such as Madagascar, where traditional practices have maintained trees for centuries, but modern agricultural practices threaten their persistence (39).

Patterns of Decline. Relative to the current number of trees, tree decline was predicted to be most rapid where trees occurred at low densities and in introduced pastures (Table S1). This prediction is consistent with existing empirical work, which has shown that trees are oldest where they occur at low densities (22), and that regeneration is least likely in introduced pastures where soil nutrient levels are unnaturally high (22, 23, 40). Despite the high vulnerability of individual trees in areas of low density, in absolute terms, a larger number of trees was predicted to be lost from areas of high tree density (Fig. 2*B*). Changes in tree cover therefore are spatially heterogeneous, with relative and absolute rates of decline differing between areas of high and low tree density.

Tree decline, in turn, will cause the decline of many currently common species of birds and bats, because most of them depend on the resources provided by farmland trees (13, 16, 41, 42). Predicted declines were most rapid for small insectivorous bird species dependent on woodland patches, such as the rufous whistler *Pachycephala rufiventris* or striated thornbill *Acanthiza lineata* (Table S5 and Fig. 2*C*). The decline of small insectivorous woodland birds already is a major concern in Australia (43–45), and our data suggest that ongoing tree decline may be one of the

underlying drivers. Modeled declines were less pronounced for some other species, such as granivorous parrots (e.g., eastern rosella *Platycercus eximius* and galah *Eolophus roseicapillus*; Table S5). These species forage in grazing pastures but depend on mature scattered trees for nesting. Because scattered trees are widely believed to be declining (17, 20, 22), it was somewhat surprising that predicted declines for granivorous parrots were lower than for woodland insectivores. However, the spatially explicit nature of our models pointed toward a plausible explanation. Although scattered trees are disappearing from grazed pastures, new areas of scattered trees are being generated in areas currently occupied by woodland patches, which are slowly degrading and "thinning out" because of a lack of tree recruitment (Fig. 1). The result is that the proportion of grazing land covered by scattered trees may actually remain relatively constant for some time into the future, whereas the proportion of land with denser tree cover will steadily decline (Fig. 2*A*).

The only species predicted to increase on the basis of their response to tree cover were grassland specialists, such as Richard's pipit *Anthus novaeseelandiae* (Fig. 1 and Table S5). Notably, predictions for these species may be overly optimistic, because other factors related to land use intensity may negatively affect them. Increasingly intensive use of grasslands in the European Union, for example, is associated with the decline of grassland birds (46, 47), and similar trends may exist in Australia (48, 49).

Patterns in the predicted declines of bat species broadly mirrored those of birds (Fig. 2*C*), but no species was predicted to benefit from ongoing tree decline (Table S5). Both species adapted to forage in relatively open areas (e.g., *Tadarida australis*), and those foraging in cluttered vegetation (e.g., *Nyctophilus* spp.) were predicted to decline. Trees are vitally important for bats because they aid echolocation and orientation (50), and also attract insect prey (42). We acknowledge that our habitat models for bats only accounted for foraging habitat and not for the availability of suitable roost trees with cavities. Given the presence of many old trees, roost sites at present probably are not a limiting resource, especially considering that bats can move several kilometers between roosting and foraging habitat (51). However, ongoing tree decline may limit the availability of roost trees in the future.

Uncertainties. Our findings should not be interpreted as precise predictions of what the future will hold at any specific location or time in the future. However, throughout the modeling process, we made conservative assumptions, suggesting that actual declines under status quo management are likely to be at least of the magnitude predicted here. Most importantly, we did not consider potential threshold or cumulative effects at the level of individual species or the ecosystem as a whole (52). Ongoing habitat loss may cause the spatial isolation of populations (53), thereby disrupting metapopulation dynamics or creating sink habitat (54). Because we did not consider population dynamics explicitly, our models are likely to underestimate actual declines. Full population viability analyses would be desirable, but a lack of suitable data means such analyses would be feasible only for a small subset of species (24). Moreover, all of the species modeled were common species (for which there were adequate data), and many uncommon species depend more strongly on large areas of intact woodland than the species we modeled (55–58). On this basis, our predictions should be interpreted as conservative estimates of expected minimum declines for a given species or group of species.

Consequences of Declines. The three groups of organisms we considered (trees, birds, bats) are of conservation interest in their own right but also provide important ecosystem services. In addition to many indirect benefits (such as habitat provision for other organisms), trees offer direct benefits to graziers, including shade provision for livestock (8), improved water infiltration (59), and at intermediate densities, improved pasture growth and profitability (60, 61). Moreover, recent work in our study area demonstrated that many graziers have a strong emotional attachment to scattered paddock trees (62), suggesting they are culturally important (63).

Birds and bats also have been shown to provide economically valuable ecosystem services in other parts of the world (5, 6, 64, 65). In our study region, the nature and magnitude of such benefits has not been quantified to date. However, potential benefits include pest control services by both birds and bats (66, 67), and pollination services by some species of birds, especially the honeyeaters and some parrot species (68, 69).

In combination, our analyses provide evidence that a regime shift is underway in southeastern Australian grazing systems. A regime shift occurs when a system crosses a threshold and is governed by a different set of processes and feedbacks (70, 71). Current ecological processes, in particular with respect to tree regeneration and mortality, are unable to sustain the system in its current condition. Ongoing tree decline will cause a cascade of changes through the system. Multiple interacting changes in species and ecosystem processes, in turn, suggest that the ecosystem as a whole eventually will be characterized by a new set of feedbacks and emergent properties: That is, we are witnessing how a woodland ecosystem is in the process of degrading into a treeless pasture system. Controlling variables underlying the regime shift are livestock grazing pressure and nutrient enrichment, both of which inhibit natural tree regeneration (22, 23, 40).

Management Options. Tree decline is an urgent and large-scale problem in southeastern Australia (24), which is already considered a threatened ecoregion because of its high level of landscape modification (19). Undesired regime shifts have been documented in a variety of ecosystems, including lakes, reefs, and rangelands (70, 71). Many regime shifts are rapid and only noticed once it is too late to reverse them (72). The situation we documented here is different and, thus, offers a unique opportunity to stem and reverse ecosystem degradation. Because trees are long-lived, it will take many decades before a treeless state is realized across the landscape (27). In the meantime, remnant trees provide an ecological memory (73) of the previous, self-sustaining woodland state. Although trees are still scattered throughout the landscape, they provide restoration nuclei that can be used to facilitate the return of the system to a self-sustaining state (7, 22, 23, 74). Several management actions can be taken to support the return of the system to a state where trees can reproduce, including the adoption of rotational grazing with prolonged rest periods, and the reduction of fertilizer use (22, 23).

Because the ecological benefits of changes in grazing management may not be immediate, other measures may be needed to perpetuate tree cover in the short term. Our work strongly supports the practice of livestock exclusion from woodland patches, which is already used by many farmers and has been supported through a range of government programs (36). Tree regeneration is greatly enhanced in ungrazed woodland patches (22), and the continued existence of woodland patches is important for many species of conservation concern, such as small insectivorous birds (see above and Fig. 1*C*). It also may be desirable to undertake management activities that maintain scattered trees throughout the pastures, for example by planting individual trees with protective guards, or by direct-seeding pastures and excluding livestock until the trees can withstand grazing (22, 75). Many farmers in the region are concerned about tree decline, and a considerable number are receptive to the possible solutions outlined here (62). However, public investment to assist farmers in their desire to maintain trees is limited, and arguably insufficient, to bring about the regional-scale changes in land management that are necessary to prevent ongoing tree decline. Reversing the regime shift documented here thus hinges on new policy initiatives that support those farmers wanting to maintain trees.

Methods

A methods overview is presented in Fig. S2.

Study area and design. We studied a 1,000,000-ha area in the Upper Lachlan Catchment of New South Wales. We worked on 33 farms (ranging in size from 236 to 3,036 ha; median 900 ha). The main land use types were livestock grazing [80 ± 4% per farm (mean ± SE)], cropping (6 ± 3%), and land set aside for conservation or restoration purposes (8 ± 2%). We established 126 2-ha survey sites. Sites were initially stratified as open paddock sites, scattered tree sites, grazed woodlands, and ungrazed woodlands, thereby spanning the full range of existing tree densities [see Fischer et al. (22) for details; note that tree density was ultimately analyzed as a continuum]. In addition, sites covered the full range of grazing regimes in the study area, both with respect to stocking rate and extent of livestock rotation, which were held independent by strategically choosing farms practicing different grazing regimes. We note that grazing by native marsupials and the European rabbit (*Oryctolagus cuniculus*) occurred throughout the study area but was assumed constant across all sites; the "ungrazed" status of sites thus referred to commercial livestock grazing only. The overarching goal of the project was to investigate regional-scale patterns of tree regeneration and assess the implications of widespread regeneration failure for future tree cover and tree-dependent animals (such as birds and bats). The experimental design is explained in detail by Fischer et al. (22).

Demographic Model. We quantified the number and diameter distribution of trees at each of the 126 sites. We used a published demographic model to predict the number of trees into the future (17). The model used specified time periods in which individual trees belonging to different age cohorts experience a specified rate of mortality and in which a specified number of new trees is recruited to the site. The demographic model was applied separately to each site, and we recorded the initial number of trees as well as the predicted number after 24, 48, 96, and 192 y. Further details on the demographic model and the calibration of recruitment and mortality rates are provided in SI Methods.

Spatial Extrapolation of Demographic Model. We were interested in predicting trends in tree density not only at the sites where we had measured trees, but more generally across the case farms. For this analysis, we focused on grazed areas only because we assumed that ungrazed locations would maintain their tree cover into the future (Fig. S3). We did not consider areas cropped within the last 6 y.

Regression modeling. For all grazed 2-ha sites, we tabulated the number of trees predicted by the demographic model at 24, 48, 96, and 192 y in the future. We treated those predictions as response variables in regression analyses and modeled them as a function of the current number of trees, pasture type (native, mixed, introduced), easting, northing, years since last fertilizer application, geological substrate, topographic wetness index (32), stocking rate, and number of days grazed per year. Numbers of trees were natural-log transformed because they were highly skewed. We treated the response variable (future number of trees) as a continuous, rather than count, variable because the demographic model produced noninteger tree numbers as output. We used multiple regression to predict the (log-transformed) number of future trees as a function of the other variables, including meaningful two-way interactions. We initially used a linear mixed model and included a random effect for "farm," but its variance component was small relative to the residual variance, so we reverted to conventional multiple regression. We eliminated nonsignificant variables by using backward selection, a simple method that we considered appropriate to our objectives, and that tends to result in relatively small models (76).

Mapping of future tree cover. For 32 farms, we mapped all paddocks, including their attributes used in regression modeling, at a 10-m resolution. We also mapped the density of trees within 2 ha for every 10 × 10 m pixel based on a highly significant relationship between remotely sensed percent tree cover and tree density on the ground (Table S6 and ref. 22). We then applied the

regression equations predicting the future number of trees to each pixel, thereby generating a continuous map of the predicted future number of trees within 2 ha of any given pixel. That value was divided by 200 to give the expected future number of trees in any given pixel, based on its 2-ha surrounds (200 pixels = 2 ha, the size of a survey site). Summary statistics describing temporal changes in tree density maps were generated for each farm. First, for every time step, we calculated the proportion of farmland in different tree density classes for every farm. Second, we calculated the expected number of trees in a given density class by adding the expected tree numbers calculated for individual pixels. For every farm, tree numbers were scaled to 1,000 ha of grazed farmland, so that tree numbers on farms of different sizes could be compared in a meaningful way.

Bird and Bat Distribution Models. The methods used to collect and analyze data on birds and bats are described in detail in SI Methods. A summary is presented here.

Birds were surveyed at 108 grazed sites spanning the full range of grazing conditions and tree densities in the study area. At each site, two observers (J.F. and J.S.) conducted two 20-min 2-ha active searches (49), where the presence of all birds heard or seen within the site was documented. Each observer recorded birds at every site once in spring 2007 and again in spring 2008, generally on mornings without strong wind or rain. Thus, the dataset of bird presence/absence was based on a total of 80 min of survey effort for each site.

Bats were surveyed at 80 sites, which were a subset of the sites used for bird surveys. Each site was surveyed by using Anabat detectors (Titley Electronics), with two detectors per site, for a total of four nights in November/December 2008, and then again in February/March 2009, resulting in a total of 16 detector nights of data recorded from each site. This survey protocol was based on a published pilot study, which showed that activity levels could be accurately estimated with this amount of effort (77). Anabat files were analyzed by using Anascheme software as outlined by Fischer et al. (77), Law and Chidel (78), and Adams et al. (79). We calculated the nightly median number of passes for each species at each site as an index of typical activity.

For both birds and bats, we used generalized linear mixed modeling to identify significant predictors of the presence (birds) or activity (bats) of individual species. For birds, 32 bird species present at >15% of grazed sites were individually modeled. For bats, the six most widespread species were modeled. For both groups of species, we were particularly interested in the effect of tree density, which we fitted both as a linear and quadratic term. The resulting regression models were used to predict bird occurrence and bat activity across the grazed areas of each farm, for each of the five time steps (0, 24, 48, 96, and 192 y into the future), drawing on the predicted tree layers applying to a given time step.

Summary statistics describing temporal changes in bird detection probabilities and bat activity were generated for each farm. For a given bird species, the sum of cell-level detection probabilities was considered its expected count of detections on a given farm. For a given bat species, the sum of expected cell-level activity levels was considered its expected farm-level activity level. Expected detections (for birds) and activity levels (for bats) were scaled to 1,000 ha of grazed farmland to enable meaningful comparison across farms of different sizes. The expected percent decline for a given species was calculated for each farm by dividing its predicted change in the number of detections by its current number of detections.

1. Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: Is habitat heterogeneity the key? *Trends Ecol Evol* 18:182–188.
2. Daily GC (2001) Ecological forecasts. *Nature* 411:245.
3. Green RE, Cornell SJ, Scharlemann JPW, Balmford A (2005) Farming and the fate of wild nature. *Science* 307:550–555.
4. Koh LP (2008) Birds defend oil palms from herbivorous insects. *Ecol Appl* 18:821–825.
5. Cleveland CJ, et al. (2006) Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. *Front Ecol Environ* 5:238–243.
6. Williams-Guillén K, Perfecto I, Vandermeer J (2008) Bats limit insects in a neotropical agroforestry system. *Science* 320:70.
7. Manning AD, Fischer J, Lindenmayer DB (2006) Scattered trees are keystone structures - Implications for conservation. *Biol Conserv* 132:311–321.
8. Bird PR, et al. (1992) The role of shelter in Australia for protecting soils, plants and livestock. *Agrofor Syst* 20:59–86.
9. Plieninger T, Schaar M (2008) Modification of land cover in a traditional agroforestry system in Spain: Processes of tree expansion and regression. *Ecol Soc* 13:25.
10. Pulido FJ, Diaz M, de Trucios SJH (2001) Size structure and regeneration of Spanish holm oak Quercus ilex forests and dehesas: Effects of agroforestry use on their long-term sustainability. *For Ecol Manage* 146:1–13.

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11. DeMars CA, Rosenberg DK, Fontaine JB (2010) Multi-scale factors affecting bird use of isolated remnant oak trees in agro-ecosystems. *Biol Conserv* 143:1485–1492.

12. Zavaleta ES, Hulvey KB, Fulfrost B (2007) Regional patterns of recruitment success and failure in two endemic California oaks. *Divers Distrib* 13:735–745.

13. Harvey CA, et al. (2006) Patterns of animal diversity in different forms of tree cover in agricultural landscapes. *Ecol Appl* 16:1986–1999.

14. Luck GW, Daily GC (2003) Tropical countryside bird assemblages: Richness, composition, and foraging differ by landscape context. *Ecol Appl* 13:235–247.

15. Esquivel MJ, Harvey CA, Finegan B, Casanoves F, Skarpe C (2008) Effects of pasture management on the natural regeneration of neotropical trees. *J Appl Ecol* 45: 371–380.

16. Haslem A, Bennett AF (2008) Birds in agricultural mosaics: The influence of landscape pattern and countryside heterogeneity. *Ecol Appl* 18:185–196.

17. Gibbons P, et al. (2008) The future of scattered trees in agricultural landscapes. *Conserv Biol* 22:1309–1319.

18. Janzen DH (1986) The Future of Tropical Ecology. *Annu Rev Ecol Syst* 17:305–324.

19. Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecol Lett* 8:23–29.

20. Ozolins A, Brack C, Freudenberger D (2001) Abundance and decline of isolated trees in the agricultural landscapes of central New South Wales, Australia. *Pac Conserv Biol* 7:195–203.

21. Maron M, Fitzsimons JA (2007) Agricultural intensification and loss of matrix habitat over 23 years in the West Wimmera, south-eastern Australia. *Biol Conserv* 135: 587–593.

22. Fischer J, et al. (2009) Reversing a tree regeneration crisis in an endangered ecoregion. *Proc Natl Acad Sci USA* 106:10386–10391.

23. Dorrough J, Moxham C (2005) Eucalypt establishment in agricultural landscapes and implications for landscape-scale restoration. *Biol Conserv* 123:55–66.

24. Vesk PA, Mac Nally R (2006) The clock is ticking—Revegetation and habitat for birds and arboreal mammals in rural landscapes of southern Australia. *Agric Ecosyst Environ* 112:356–366.

25. Gibbons P, et al. (2009) An operational method to assess impacts of land clearing on terrestrial biodiversity. *Ecol Indic* 9:26–40.

26. Barnes RFW (1983) Effects of elephant browsing on woodlands in a Tanzanian National Park: Measurements, models and management. *J Appl Ecol* 20:521–539.

27. Janzen DH (2001) Latent extinction - the living dead. *Encyclopedia of Biodiversity*, ed Levin SA (Academic Press, San Diego), Vol 3, pp 689–699.

28. Moga CI, Hartel T, Öllerer K (2009) Ancient oak wood-pasture as a habitat for the endangered tree pipit Anthus trivialis. *Biologia* 64:1011–1015.

29. Pigott CD (1983) Regeneration of oak-birch woodland following exclusion of sheep. *J Ecol* 71:629–646.

30. Mountford EP, Peterken GF, Edwards PJ, Manners JG (1999) Long-term change in growth, mortality and regeneration of trees in Denny Wood, an old-growth wood-pasture in the New Forest (UK). *Perspect Plant Ecol Evol Syst* 2:223–272.

31. Maron M, Dunn P, McAlpine CA, Apan A (2010) Can offsets really compensate for habitat removal? The case of the endangered red-tailed black-cockatoo. *J Appl Ecol* 47:348–355.

32. Fischer J, et al. (2010) Towards landscape-wide conservation outcomes in Australia's temperate grazing region. *Front Ecol Environ* 8:69–74.

33. Gibbons P, Boak M (2002) The value of paddock trees for regional conservation in an agricultural landscape. *Ecol Manage Restor* 3:205–210.

34. Gibbons P, et al. (2008) Rapidly quantifying reference conditions in modified landscapes. *Biol Conserv* 141:2483–2493.

35. Prober S, Thiele K (1995) Conservation of the grassy White Box woodlands: Relative contributions of size and disturbance to floristic composition and diversity of remnants. *Aust J Bot* 43:349–366.

36. Spooner PG, Briggs SV (2008) Woodlands on farms in southern New South Wales: A longer-term assessment of vegetation changes after fencing. *Ecol Manage Restor* 9: 33–41.

37. Tyler CM, Kuhn B, Davis FW (2006) Demography and recruitment limitations of three oak species in California. *Q Rev Biol* 81:127–152.

38. Gillies CS, St. Clair CC (2010) Functional responses in habitat selection by tropical birds moving through fragmented forest. *J Appl Ecol* 47:182–190.

39. Martin EA, Ratsimisetra L, Laloë F, Carrière SM (2009) Conservation value for birds of traditionally managed isolated trees in an agricultural landscape of Madagascar. *Biodivers Conserv* 18:2719–2742.

40. Semple WS, Koen TB (2003) Effect of pasture type on regeneration of eucalypts in the woodland zone of south-eastern Australia. *Cunninghamia* 8:76–84.

41. Law BS, Chidel M, Turner G (2000) The use by wildlife of paddock trees in farmland. *Pac Conserv Biol* 6:130–143.

42. Lumsden LF, Bennett AF (2005) Scattered trees in rural landscapes: Foraging habitat for insectivorous bats in south-eastern Australia. *Biol Conserv* 122:205–222.

43. Ford HA, Barrett GW, Saunders DA, Recher HF (2001) Why have birds in the woodlands of Southern Australia declined? *Biol Conserv* 97:71–88.

44. Recher HF (1999) The state of Australia's avifauna: A personal opinion and prediction for the new millennium. *Aust Zool* 31:11–29.

45. Barrett GW, et al. (2007) Comparison of atlas data to determine the conservation status of bird species in New South Wales, with an emphasis on woodland-dependent species. *Aust Zool* 34:37–77.

46. Batáry P, Báldi A, Erdős S (2007) Grassland versus non-grassland bird abundance and diversity in managed grasslands: Local, landscape and regional scale effects. *Biodivers Conserv* 16:871–881.

47. Stoate C, et al. (2009) Ecological impacts of early 21st century agricultural change in Europe—a review. *J Environ Manage* 91:22–46.

48. Attwood SJ, et al. (2009) Declining birds in Australian agricultural landscapes may benefit from aspects of the European agri-environment model. *Biol Conserv* 142: 1981–1991.

49. Barrett G, Silcocks A, Barry S, Cunningham R, Poulter R (2003) *The New Atlas of Australian Birds* (R Australasian Ornithol Union, Victoria, Australia).

50. Kalko EKV, Schnitzler HU (1993) Plasticity in echolocation signals of European pipistrelle bats in search flight—implications for habitat use and prey detection. *Behav Ecol Sociobiol* 33:415–428.

51. Lumsden LF, Bennett AF, Silins JE (2002) Location of roosts of the lesser long-eared bat Nyctophilus geoffroyi and Gould's wattled bat Chalinolobus gouldii in a fragmented landscape in south-eastern Australia. *Biol Conserv* 106:237–249.

52. Lindenmayer DB, Fischer J (2006) *Habitat fragmentation and landscape change* (Island, Washington, DC).

53. Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst* 34:487–515.

54. Pulliam HR (1988) Sources, sinks and population regulation. *Am Nat* 132:652–661.

55. Martin TG, McIntyre S (2007) Impacts of livestock grazing and tree clearing on birds of woodland and riparian habitats. *Conserv Biol* 21:504–514.

56. Watson J, Freudenberger D, Paull D (2001) An assessment of the focal-species approach for conserving birds in variegated landscapes in southeastern Australia. *Conserv Biol* 15:1364–1373.

57. Radford JQ, Bennett AF (2007) The relative importance of landscape properties for woodland birds in agricultural environments. *J Appl Ecol* 44:737–747.

58. Seddon JA, Briggs SV, Doyle SJ (2003) Relationships between bird species and characteristics of woodland remnants in central New South Wales. *Pac Conserv Biol* 9: 95–119.

59. Eldridge DJ, Freudenberger D (2005) Ecosystem wicks: Woodland trees enhance water infiltration in a fragmented agricultural landscape in eastern Australia. *Austral Ecol* 30:336–347.

60. Williams DG, et al. (1999) *Effects of Trees on Native Pasture Production* (Rural Industries Res Dev Corp Publication No 99/165, Canberra, Australia).

61. Walpole SC (1999) Assessment of the economic and ecological impacts of remnant vegetation on pasture productivity. *Pac Conserv Biol* 5:28–35.

62. Sherren K, Fischer J, Price R (2010) Using photography to elicit grazier values and management practices relating to tree survival and recruitment. *Land Use policy* 27: 1056–1067.

63. Seabrook L, McAlpine C, Fensham R (2008) What influences farmers to keep trees? A case study from the Brigalow Belt, Queensland, Australia. *Landsc Urban Plan* 84:266–281.

64. Sekercioglu CH (2006) Increasing awareness of avian ecological function. *Trends Ecol Evol* 21:464–471.

65. Sekercioğlu CH, Daily GC, Ehrlich PR (2004) Ecosystem consequences of bird declines. *Proc Natl Acad Sci USA* 101:18042–18047.

66. Kirk DA, Evenden MA, Mineau P (1997) Past and current attempts to evaluate the role of birds as predators of insect pests in temperate agriculture. *Curr Ornithol* 13: 175–269.

67. Lumsden LF, Bennett AF (1999) The conservation of insectivorous bats in rural landscapes of northern Victoria. *People and Nature Conservation*, eds Bennett AF, Backhouse G, Clark T (Trans R Zool Soc of New South Wales, Sydney), pp 142–148.

68. Southerton SG, Birt P, Porter J, Ford HA (2004) Review of gene movement by bats and birds and its potential significance for eucalypt plantation forestry. *Aust For* 67:44–53.

69. Paton DC (2000) Disruption of bird-plant pollination systems in southern Australia. *Conserv Biol* 14:1232–1234.

70. Folke C, et al. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annu Rev Ecol Evol Syst* 35:557–581.

71. Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413:591–596.

72. Walker B, Meyers JA (2004) Thresholds in ecological and social-ecological systems: A developing database. *Ecol Soc* 9:3.

73. Bengtsson J, et al. (2003) Reserves, resilience and dynamic landscapes. *Ambio* 32: 389–396.

74. Rey-Benayas JMR, Bullock JM, Newton AC (2008) Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Front Ecol Environ* 6:329–336.

75. Fifield G, Streatfield S, Vanzella B (2008) *Introducing... Whole of Paddock Rehabilitation* (Greening Australia Canberra, http://www.greeningaustralia.org.au/uploads/General%20pdfs/ACT_WOPR_Brochure.pdf).

76. Murtaugh PA (2009) Performance of several variable-selection methods applied to real ecological data. *Ecol Lett* 12:1061–1068.

77. Fischer J, Stott J, Forrester R, Law B, Adams M (2009) Designing effective habitat studies: Quantifying multiple sources of variability in bat activity. *Acta Chiropt* 11: 127–137.

78. Law BS, Chidel M (2006) Eucalypt plantings on farms: Use by insectivorous bats in south-eastern Australia. *Biol Conserv* 133:236–249.

79. Adams M, Law BS, Gibson MS (2010) Reliable automation of bat call identification for eastern New South Wales, Australia, using classification trees and AnaScheme software. *Acta Chiropt* 12:231–245.