Contributed Paper

The Future of Scattered Trees in Agricultural Landscapes

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Abstract: *Mature trees scattered throughout agricultural landscapes are critical habitat for some biota and provide a range of ecosystem services. These trees are declining in intensively managed agricultural landscapes globally. We developed a simulation model to predict the rates at which these trees are declining, identified the key variables that can be manipulated to mitigate this decline, and compared alternative management proposals. We used the initial numbers of trees in the stand, the predicted ages of these trees, their rate of growth, the number of recruits established, the frequency of recruitment, and the rate of tree mortality to simulate the dynamics of scattered trees in agricultural landscapes. We applied this simulation model to case studies from Spain, United States, Australia, and Costa Rica. We predicted that mature trees would be lost from these landscapes in 90–180 years under current management. Existing management recommendations for these landscapes—which focus on increasing recruitment—would not reverse this trend. The loss of scattered mature trees was most sensitive to tree mortality, stand age, number of recruits, and frequency of recruitment. We predicted that perpetuating mature trees in agricultural landscapes at or above existing densities requires a strategy that keeps mortality among established trees below around 0.5% per year, recruits new trees at a rate that is higher than the number of existing trees, and recruits new trees at a frequency in years equivalent to around 15% of the maximum life expectancy of trees. Numbers of mature trees in landscapes represented by the case studies will decline before they increase, even if strategies of this type are implemented immediately. This decline will be greater if a management response is delayed.*

Keywords: agricultural-landscape trees, management of scattered trees, paddock trees, recruitment, scattered-tree ecosystems, set-aside forest, tree decline, tree patches

El Futuro de Árboles Dispersos en Paisajes Agrícolas

Resumen: *Los árboles dispersos en paisajes agrícolas son hábitat critico para la biota y proporcionan una variedad de servicios ecológicos. Estos árboles están declinando globalmente en paisajes agrícolas manejados intensivamente. Desarrollamos un modelo de simulación para predecir las tasas a las que están declinando estos árboles, identificamos las principales variables que pueden ser manipuladas para mitigar esta declinación y comparamos propuestas de manejo alternativas. Utilizamos el número inicial de árboles en el sitio, las edades de estos árboles, su tasa de crecimiento, el número de individuos reclutados, la frecuencia de reclutamiento y la tasa de mortalidad de árboles para simular la dinámica de árboles dispersos en paisajes agrícolas. Aplicamos este modelo a estudios de caso de España, Estados Unidos, Australia y Costa Rica. Pronosticamos que los árboles maduros se perderán de estos paisajes entre 90 y 180 años bajos las condiciones de manejo actuales; las recomendaciones de manejo existentes - enfocadas en el incremento del reclutamiento - no cambiarían esta tendencia. Mediante la simulación de escenarios representando observaciones que abarcan todos los estudios de caso y una gama de opciones de manejo pudimos hacer recomendaciones*

genéricas sobre el manejo de árboles dispersos en paisajes agrícolas. La pérdida de árboles maduros dispersos fue más sensible a la mortalidad de árboles, edad del sitio, número de reclutas y frecuencia de reclutamiento. Predecimos que la perpetuación de árboles maduros en paisajes agrícolas en o por encima de las densidades existentes requiere de una estrategia que mantenga la mortalidad de árboles establecidos por debajo de 0.5% por año, que reclute árboles a una tasa mayor que el número de árboles existentes y reclute árboles nuevos en una frecuencia en años equivalente a alrededor de 15% de la esperanza de vida máxima de los árboles. Sin embargo, el número de árboles maduros en los paisajes representados por los estudios de caso declinará antes de incrementar, aun si estrategias de este tipo son implementadas inmediatamente. Esta declinación será mayor si se posterga una respuesta de manejo.

Palabras Clave: árboles en paisajes agrícolas, árboles en praderas, bosque reservado, declinación de árboles, ecosistemas con árboles dispersos, manejo de árboles dispersos, reclutamiento, parches de árboles

Introduction

Scattered trees are a prominent feature of agricultural landscapes globally (Gibbons & Boak 2002; Manning et al. 2006). They have been nominated as keystone structures because of their ecological importance relative to their low abundance (Munzbergova & Ward 2002; Plieninger et al. 2004; Manning et al. 2006). Scattered trees can be critical habitat for biota (Dean et al. 1999; Western & Maitumo 2004; Manning et al. 2006) and contribute to the viability of wildlife populations in fragmented landscapes (Fischer & Lindenmayer 2002). Scattered trees provide a range of ecosystem services—shade for stock (Harvey & Haber 1999) or shade-tolerant crops (Bentley et al. 2004), a buffer against soil acidity (Wilson 2002), control against erosion and desertification (Plieninger et al. 2004), and insect control (Lumsden & Bennett 2005)—and are a cost-effective source of seed for revegetation (Dorrough & Moxham 2005).

Only mature trees can provide many of the ecological functions and ecosystem services provided by scattered trees. Several animal species in South Africa prefer to use large *Acacia* spp. rather than saplings (Dean et al. 1999). Only *Eucalyptus* spp. from 120 to 250 years old typically produce hollows suitable for vertebrates (Gibbons & Lindenmayer 2002). Agricultural soils under large trees contain more soil moisture, carbon, and nitrogen than soils under small trees or away from tree cover (Jonsson et al. 1999).

Intensive agriculture is associated with the decline of scattered trees. Scattered trees are declining in remnant oak (*Quercus*) woodlands in Europe (Mountford et al. 1999; Pulido et al. 2001), North America (Griffin 1971; Lathrop et al. 1991), and Asia (Saxena et al. 1984); remnant *Eucalyptus* and *Allocasuarina* woodlands in Australia (Ozolins et al. 2001; Maron 2005); rainforest remnants in Central America (Harvey & Haber 1999); and grazed landscapes, such as *Aspidosperma* stands in arid South America (Barchuk & Diaz 1999). These declines are due to clearing (Harvey & Haber 1999; Ozolins et al. 2001; Pulido et al. 2001); lack of sufficient recruitment due to intensive grazing by stock (Pigott 1983);

cultivation (Pulido et al. 2001); browsing by dense populations of invertebrate (Landsberg & Wylie 1983) and vertebrate (Griffin 1971; Barnes 1983) herbivores; competition with other plant species (Humphrey & Swaine 1997); and physiological stress precipitated by drought, salinity, soil compaction, and elevated nutrients from congregating stock (Landsberg & Wylie 1983).

Perpetuating a cover of scattered mature trees should therefore be an objective for the sustainable management of agricultural landscapes (Manning et al. 2006; Vesk & Mac Nally 2006). We addressed 3 questions: (1) At what rate are scattered mature trees declining? (2) What are the key variables that can be manipulated to mitigate this decline? (3) What are appropriate management recommendations for perpetuating scattered mature trees in agricultural landscapes?

Methods

Case Studies

To address these research questions we compiled data from case studies of scattered trees in 4 agricultural landscapes (Table 1): (1) holm oak (*Quercus ilex*) in southern Spain, where land was partially cleared between 80 and 500 years ago and subsequently grazed by stock or cropped (Plieninger et al. 2004), (2) Engelmann oak (*Q. engelmannii*) in California (U.S.A.), where trees were partially cleared and land was grazed by cattle from the early to mid 1800s (Lathrop et al. 1991), (3) yellow box (*Eucalyptus melliodora*) in southeastern Australia, where land was cleared beginning in the late 1800s and subsequently grazed by cattle and sheep (Ozolins et al. 2001; A. Weinberg, unpublished data), and (4) primary forest trees on farms in Costa Rica, where land was cleared for dairy farming and sugar and coffee production in the 1950s and 1960s (Harvey & Haber 1999).

Rates of Decline among Scattered Mature Trees

We developed a simulation model parameterized with the initial number of trees in the stand, predicted ages of

Table 1. Data for the different case studies and scenarios used to simulate the number of mature scattered trees that occur over time in agricultural landscapes.

Tree species	Scenario	Initial trees per ba (SE)	Diameter (cm) (SE)	Time step (years)	New trees recruited each time step	Probability of mortality each time step (annual in parentheses)	Max. age (years)	Slope (β) of age vs. diameter (SE)	Primary source of data
Holm oak (Spain)	status quo	27.7 (1.2)	31.0 (0.2)	30	0–2/ha	0.1–0.3[a] (0.004–0.012)	200–250[b]	2.19 (0.085)	Plieninger et al. 2003
	existing proposal			30	2/initial tree in first 30 years only	0.1–0.3 (0.004–0.012)			
	our proposal			60	2/initial tree	0.10–0.28 (0.002–0.005)			
Engelmann oak (U.S.A.)	status quo	30–52	46–55	30	0	0–0.44[c] (0–0.019)	200–300	1.9–2.9[d]	Lathrop et al. 1991
	existing proposal			30	0.23/initial tree[e]	0–0.44 (0–0.019)			
	our proposal			60	2/initial tree	0–0.45 (0–0.009)			
Yellow box (Australia)	status quo	10–25	101–132	30	0	0.15–0.51[f] (0.006–0.024)	400–600	1.97–2.71[g]	A. Weinberg, unpublished data
	existing proposal			30	2/initial tree	0.15–0.51 (0.006–0.024)			
	our proposal			60	2/initial tree	0.07–0.24 (0.003–0.010)			
Primary forest species (Costa Rica)	status quo	7.4 (1.8)	38.9 (0.5)	30	0–5[b] per tree	0.42–0.49[i] (0.018–0.022)	200–400	2.50–3.75[j]	Harvey & Haber 1999
	existing proposal			30	2/initial tree in first 30 years only	0.42–0.49 (0.018–0.022)			
	our proposal			60	2/initial tree	0.42–0.49 (0.009–0.011)			

[a] *Estimated from Fig. 1 in Perez-Fernandez and Gomez-Gutierrez (1995).*
[b] *The most conservative estimates in Panaiotis et al. (1997) were used.*
[c] *From data for canopy oak over 46 years (Maball et al. 2005).*
[d] *From slope for relationship between diameter and age reported by Latbrop et al. (1991) for the species, ± 20% to account for variation.*
[e] *Rate of recruitment observed by Latbrop et al. (1991) on a site with long-term grazing exclusion.*
[f] *From data from Ozolins et al. (2001) and Leaby (2003 cited in Carruthers and Paton [2005]).*
[g] *Slopes for this linear relationship were derived from fitting a line with linear regression to age versus diameter data in Banks (1997) with and without an outlier in these data.*
[b] *Conservatively estimated from Fig. 5 in Harvey and Haber (1999).*
[i] *The range of data reported for intact rainforest by Lieberman and Lieberman (1987).*
[j] *Derived from the range of values plotted for Ocotea hartshorniana by Lieberman and Lieberman (1987).*

trees, tree rate of growth, frequency of tree recruitment, number of recruits established each recruitment event, and rate of tree mortality (Table 1) to track scattered mature trees. Predictions were calculated from 1000 runs of the simulation model. Different values for each parameter were selected randomly for each run of the simulation model to reflect the uncertainty of parameter estimates and variability within and between stands.

There were 7 steps in the simulation model: (1) the number of trees and their diameters in the initial stand, (2) the time step, (3) the number of trees recruited, (4) tree growth, (5) survival and mortality of trees, (6) maximum age, and (7) outputs.

We characterized the initial stand as an even-aged cohort with a defined number of trees and a mean diameter value rather than the number of trees in each diameter class because only summary statistics for stands (rather than individual diameter classes within stands) were reported in the case studies and stands represented by the case studies had bell-shaped diameter distributions and were dominated by trees in a narrow range of diameter classes. Across the 1000 runs of the simulation model, the number of trees in the stand and the diameter value used to characterize the stand were drawn randomly from the reported range of values (Table 1) so as to reflect variation between stands in each case study.

The time step was the period between predictions in each run of the simulation model and the period between recruitment events. The maximum number of time steps in the simulation model was 10. The time step was kept constant (30 years) in scenarios representing status quo and existing management recommendations for each case study. The period between recruitment events was largely irrelevant for scenarios representing the status quo because virtually no recruitment was observed (Table 1). We chose to fix, at 30 years, the period between recruitment events because Plieninger et al. (2004) recommended recruitment every 20–30 years in the holm oak case study, and Lathrop et al. (1991) provided recruitment data under a scenario of no grazing for approximately 20 years in the Englemann oak case study. The implications of this model specification were tested in the sensitivity analysis.

The number of new trees recruited each time step remained constant for each run of the simulation model, but were varied randomly across the 1000 runs of the simulation model on the basis of data reported for each of the case studies (Table 1). Trees established in any one time step were tracked as a separate age cohort throughout each run of the simulation model. Thus, a maximum of 11 age cohorts could occur at the end of a run of the simulation model (i.e., a new cohort established in each of the 10 time steps plus the cohort representing initial trees in the stand).

All trees were grown for a period commensurate with each time step, and then the diameter for each tree in the

cohort was calculated at the end of each time step. We assumed a significant linear relationship between diameter and age in the form diameter = β(age), where β is the slope of the line describing the relationship between diameter and age. Significant linear relationships between tree diameter and tree age were reported for tree species in 3 of the 4 case studies (Lieberman & Lieberman 1987; Lathrop et al. 1991; Plieninger et al. 2004), and we fit a significant linear relationship to raw diameter-age data for the other (yellow box) case study with data reported by Banks (1997) (Table 1). The constant for each linear relationship was set to zero because, by definition, at zero age diameter is also zero. The implication of this model specification was tested by varying β randomly in each run of the simulation model (Table 1). The diameter for trees in each cohort at the end of each time step was estimated with the inverse of the same relationship we used to estimate age from diameter for these trees.

The proportion of trees that survived a given number of time steps was considered to be a series of independent events between time steps and was given as $(1 - m)^r$, where m is the probability of mortality for each time step and r is the number of time steps. For comparative purposes, annual mortality was calculated as $1 - s^{(1/y)}$, where y is the years between time steps and s the proportion of trees that survived each time step. We considered mortality to be independent of stand age (or tree diameter) and stand density because data suggesting otherwise were not reported in any of the case studies. If a tree exceeded the estimated maximum age for the tree species, then it was removed. The maximum age that a tree could attain before it was removed was selected randomly for each run of the model from the range of values reported in Table 1.

The predicted mean proportion ($\pm$95% pointwise prediction interval) of mature trees that persisted in the stand (relative to the number at time zero) was calculated for each time step from data pooled over 1000 runs of the simulation model. We considered trees mature if they had a diameter greater than or equal to the mean diameter of the stand at time zero. Trees are variously considered mature on the basis of characteristics such as the abundance of hollows or cavities, height, crown size, and degree of senescence, so there is no single diameter threshold that can be used for this definition. In the absence of a simple ecological definition, we defined *mature* as trees with a diameter greater than or equal to the diameter of the initial stand at time zero.

We also simulated scenarios representing our interpretation of existing management proposals for each case study. These scenarios all focused on increasing recruitment. Plieninger et al. (2004) suggest parcels of holm oak should be set aside for 20–30 years to encourage regeneration. To simulate this scenario, we increased the number of recruits established in the first 30 years to 2.0 for each initial tree and then returned recruitment to baseline

levels for the remainder of the simulation. We simulated the removal of cattle grazing from the landscape containing Engelmann oak by recruiting new trees at the rate of 0.23 for each tree that occurred initially every 30 years on the basis of observations by Lathrop et al. (1991). We simulated regeneration in yellow box stands by increasing the number of recruits from 0 to 2.0 for each tree occurring initially in the stand every 30 years. In Costa Rica Harvey and Haber (1999) recommended farmers plant trees to replace those they may use in the future. We simulated the immediate establishment of 2.0 trees for each tree occurring initially with no follow-up recruitment in the simulation period.

Variables That Can Be Manipulated to Mitigate the Decline of Scattered Mature Trees

To examine which variables can be manipulated to mitigate the decline of scattered mature trees, we performed a sensitivity analysis on simulations with data spanning all case studies and scenarios. We assumed these data represent the range of conditions likely to occur in intensively managed agricultural landscapes more broadly. The aim was to test the relative sensitivity of the predicted outcomes (number of mature trees) to each of the variables in the simulation model. To test the sensitivity of the predicted outcomes separately at three different levels for each of seven variables in the simulation model would yield 3^7 or 2187 possible combinations, which would be difficult to interpret. McCarthy et al. (1995) approached this problem by repeatedly populating their simulation model with random data (within an observed or feasible range) for each variable and then fitting a regression model to the results in which the outcome (in this case number of mature trees) was the response variable and the variables in the simulation model the explanatory variables. The significance of each explanatory variable when added or dropped from the chosen regression model was used to indicate the relative sensitivity of the outcome to each variable.

To perform a sensitivity analysis with this method, we ran the simulation model 1000 times, with each run of the model parameterized with random data drawn from uniform distributions within ranges observed across the case studies (Table 1): number of initial trees per ha (7–52); mean diameter of these trees (31–132 cm); time step (10–150 years); number of trees recruited each time step for every initial tree in the stand (0–10); annual mortality (0–0.024); maximum tree age (200–600 years); and the slope of the linear relationship between age and diameter (1.0–3.75). Random values were drawn from a wider range than observed across the case studies for variables that can be manipulated by management (i.e., number of trees recruited each time step and the period between recruitment events). The response variable for regression modeling was the predicted number of

mature trees expressed as a multiple of the number of trees initially present in the stand averaged across predictions from each of the 10 time steps of the simulation. Potential explanatory variables were each parameter in the model, although some parameters were standardized so the results were comparable between scenarios: the number of trees recruited each time step was divided by the number of initial trees in the stand (recruits); the diameter of trees in the initial stand was divided by the maximum expected diameter that the trees could attain (diameter); the period between recruitment events was divided by the maximum expected age the trees could attain (period); and the period between recruitment events was multiplied by the number of time steps (duration).

For the sensitivity analysis, we used generalized additive modeling because exploratory data analysis indicated responses were not always linear. Analyses were undertaken with the Generalized Regression and Spatial Prediction package (Lehmann et al. 2003) in the *R* statistical software. We built a quasi-Poisson generalized additive model (sensu Lehmann et al. 2003) with a log-link function (the response variable approximated a Poisson distribution) to identify the variables to which changes in mature trees in agricultural landscapes were most sensitive. The variable duration (i.e., the period between recruitment events × the number of time steps) was excluded from model building because it was highly correlated ($r = 0.84$) with the variable period (i.e., the period between recruitment events the maximum expected age that the trees could attain) and was least instructive of the 2 variables for managing these stands. We selected a regression model of best fit with a forward and backward stepwise procedure. The significance of adding or removing terms was tested with analysis of variance (ANOVA; F test; $p < 0.05$). We used 4 degrees of freedom to smooth the lines of best fit for each significant explanatory variable. We used 2 analyses to interpret sensitivity of the response (number of mature trees) to each variable: plots of individual effects of each significant explanatory variable on the response made with the other significant explanatory variables held at their mean values and a table indicating the relative contributions of each variable (i.e., change in deviance) when dropped, in turn, from the final model. We used results from the sensitivity analysis to devise and simulate an alternative management scenario for each case study.

Results

Rates of Decline among Scattered Mature Trees

Using the simulation model, we predicted declines in the number of mature scattered trees for scenarios representing the status quo (existing management) in each of the 4 landscapes represented by the case studies (Figs. 1a–d).

For holm oak the 95% prediction interval for the number of mature trees included zero mature trees within 150 years (Fig. 1a). The 95% prediction interval for Engelmann oak included zero within 90 years under a scenario of continued grazing and no recruitment (Fig. 1b). For yellow box the 95% prediction interval included zero within 120 years (Fig. 1c). We predicted rapid declines in the mean number of mature trees in the case study from Costa Rica, although the 95% prediction interval included zero only after 180 years (Fig. 1d). Declines were also predicted for each case study if observations were based on the upper 95% pointwise prediction intervals for these scenarios (Figs. 1a–d).

In scenarios representing our interpretation of existing management proposals for each of the case studies, we predicted increases in numbers of mature trees relative to the status quo, but we still predicted declines relative to the initial numbers of trees in these stands (Figs. 1e–h). For those scenarios in which we simulated only 1 recruitment event (holm oak in Spain and primary forest species in Costa Rica), there was an initial decline in mean numbers of mature trees similar to the status quo

scenarios that was followed by increases in numbers of mature trees and then a return to the downward trends observed in the status quo scenarios (Figs. 1e & 1h). In the other scenarios in which recruitment was repeated at intervals throughout the simulation period, we predicted increases in mean numbers of mature trees, but only after an initial period of decline that was similar to the scenario representing status quo (Figs. 1f & 1g).

Variables That Can Be Manipulated to Mitigate the Decline of Scattered Mature Trees

The significant explanatory variables in the regression model we built for sensitivity analysis—and therefore the variables to which the number of scattered mature trees in agricultural landscapes are most sensitive—were (1) number of recruits expressed as a proportion of the initial number of trees in the stand (recruits), (2) period between recruitment events expressed as a proportion of the maximum age trees can attain (period), (3) annual rate of mortality among trees (mortality), and (4) diameter of the initial stand expressed as a proportion of the maximum diameter trees can attain (diameter) (Fig. 2). The
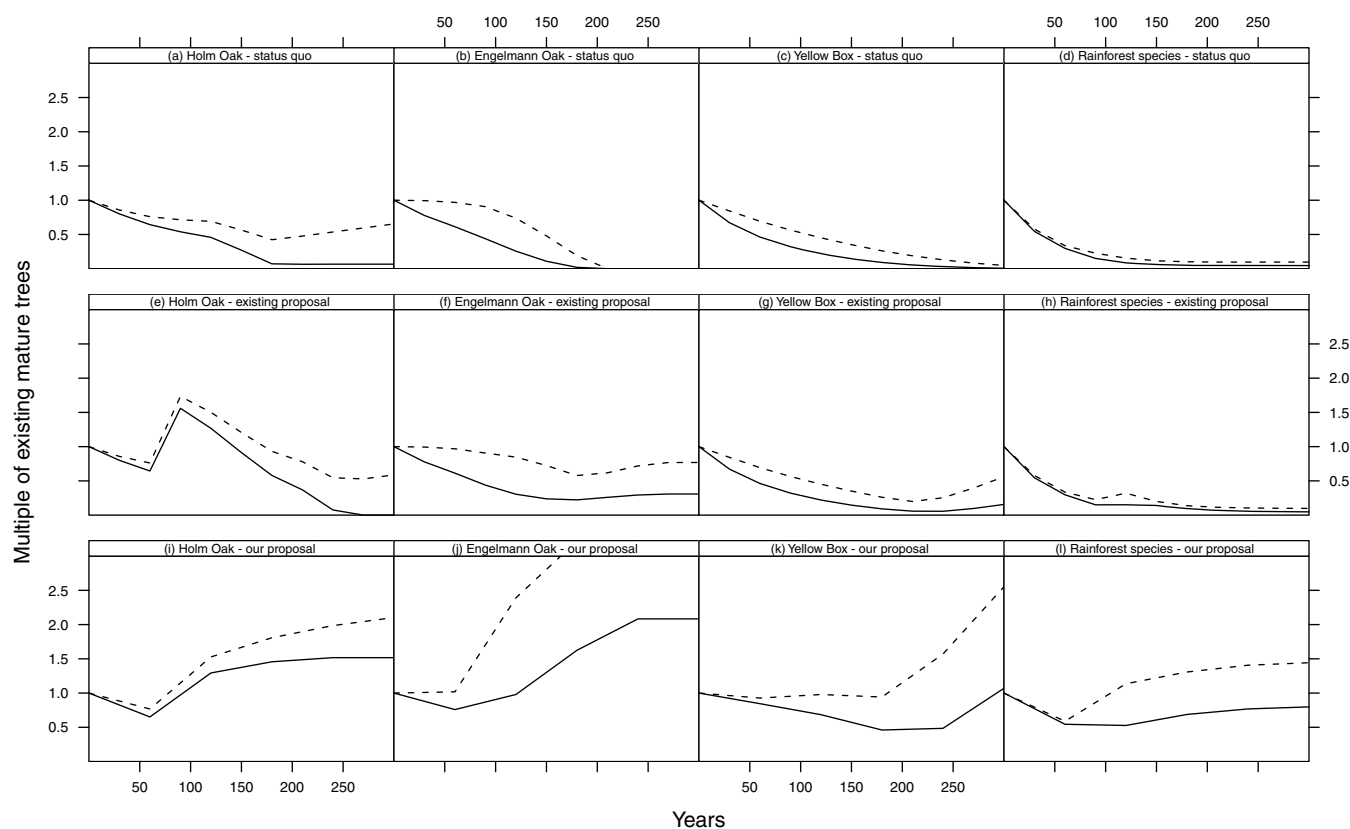

Figure 1. The number of mature trees (mean and 95% prediction interval) expressed as a multiple of the existing number of mature trees predicted to occur over 300 years in 4 different agricultural landscapes (holm oak in Spain, Engelmann oak in California, yellow box in Australia, and primary forest species in Costa Rica) under 3 different scenarios: (a–d) status quo, (e–h) increasing recruitment only, and (i–l) increasing recruitment plus reducing mortality.

rate of mortality made the greatest relative contribution to the number of mature trees perpetuated, followed by the diameter (or age) of the stand and the number of recruits (Table 2). The period between recruitment events made a relatively small contribution (Table 2). The slope of the linear relationship between diameter and tree age (β) was not selected in the regression model. That is, the number of mature trees was not sensitive to the growth rate of different tree species. Fitted values from the regression model were highly correlated with observed values ($r = 0.96$), which indicated the regression model was a good predictor of the number of mature trees predicted by the simulation model.

We plotted predictions from the regression model to illustrate under what combinations of mortality, recruitment, and stand age mature trees can be perpetuated above existing numbers (Fig. 3). Each prediction was made by holding the period between recruitment events at 0.15 times the maximum age of the stand (which is the approximate optimum period under average conditions according to the regression model; Fig. 2), and we made predictions for stands with mean diameters (or ages) that were 50% (Fig. 3a) and 75% (Fig. 3b) of the expected maximum that trees in these stand can reach. The mean predictions indicated that mature trees can be perpetuated at existing densities in the younger stands (50% of expected maximum age) at levels of mortality around 0.5% per annum provided at least 2 new trees are recruited for each existing tree (Fig. 3a), whereas mature trees can be perpetuated only at existing densities in the older stands (75% of maximum age) at levels of mortality

Table 2. Significant explanatory variables and change in deviance in the regression model used for sensitivity analysis of simulations of the number of mature scattered trees that occur over time in agricultural landscapes.

Variable	Change in deviance*	p
Recruits	−354.97	<0.001
Diameter	−788.53	<0.001
Period	−23.03	0.001
Mortality	−1559.20	<0.001

Change in deviance when each variable was dropped, in turn, from this model.

around 0.4% per annum provided at least 4 new trees are recruited for each existing tree (Fig. 3b).

Management Recommendations

Drawing on results from the sensitivity analysis, we simulated increased recruitment and reduced mortality in each case study as follows: (1) we fixed, at 2, the numbers of recruits established for each initial tree in the stand and kept this level of recruitment constant for the duration of the simulation period, (2) we increased the period between recruitment events by changing the time step from 30 to 60 years, and (3) we cut annual mortality by 50% (Table 1). For each of these alternative management scenarios, we predicted higher numbers of mature trees relative to the scenarios representing increased recruitment alone (Figs. 1e–h), although in 2 of the 4 case studies, the number of mature trees averaged over 300 years
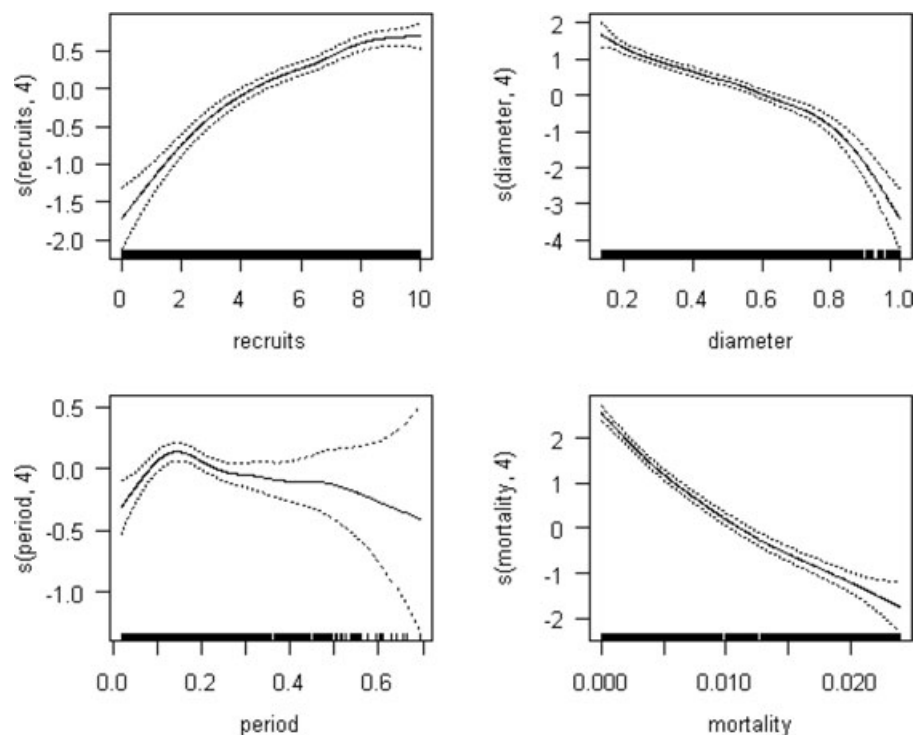

Figure 2. Partial response curves (mean and 2 × SE) for the significant explanatory variables (recruits, diameter, mortality, and period) in a regression model used to predict the number of mature trees perpetuated over time relative to the existing number of mature trees. In each graph the response is plotted on the scale of the additive predictor with a smoothing function (s) with 4 df.
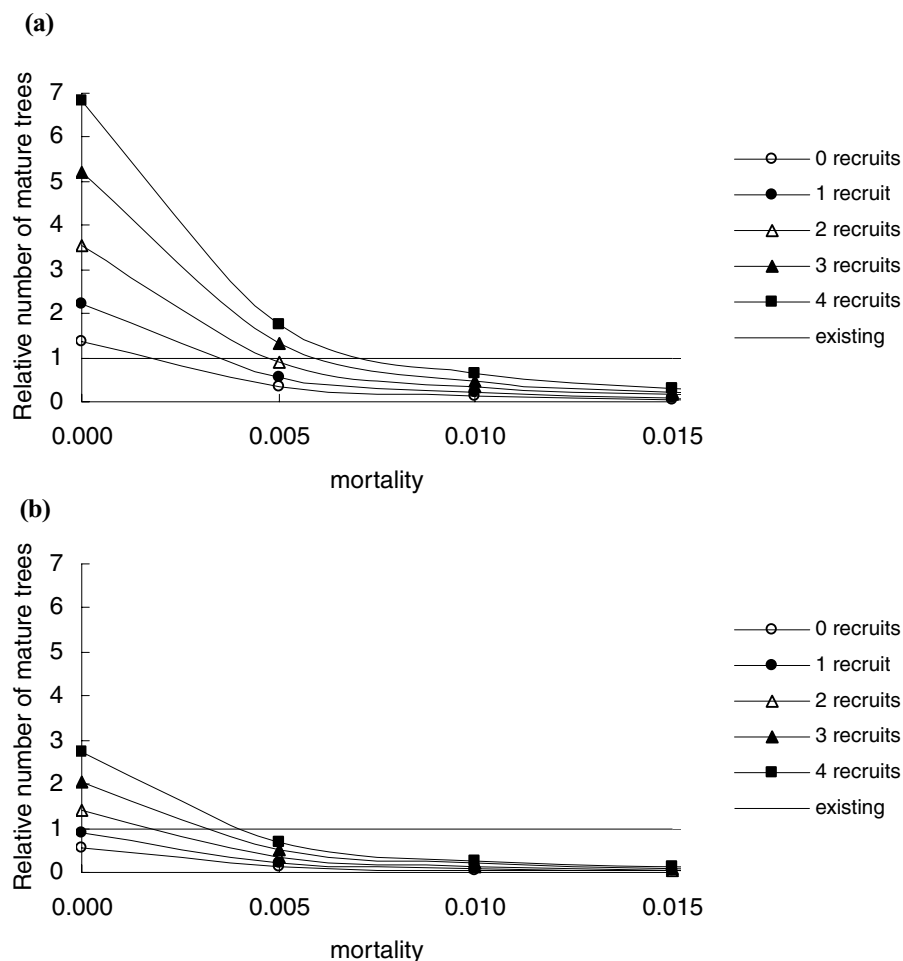
(a)

(b)

Figure 3. Predictions from the regression model indicating scenarios in which the mean number of mature trees is perpetuated above the initial number of mature trees in the stand (above solid line). Predictions were made under scenarios representing different rates of annual mortality (among all trees in the stand), recruitment (number of trees established for each tree in the initial stand), and stand age (mean diameter of trees is [a] 50% of maximum likely diameter and [b] 75% of maximum likely diameter).

remained below initial levels (i.e., <1), and in each of the 4 case studies, the predicted mean numbers of mature trees fell below current numbers before increasing (Figs. 1i–l).

Discussion

We predicted that the abundance of mature trees would decline to zero within 90–180 years under existing agricultural practices in the landscapes represented by the case studies (Figs. 1a–d). By implication the ecological values (e.g., wildlife habitat) and ecosystem services (e.g., soil conservation) provided by scattered mature trees in these landscapes would also decline under existing management. On its own this information is not new. There is a sufficient body of literature that establishes the values of scattered trees in agricultural landscapes; that scattered trees are generally declining in agricultural landscapes; and that there are negative consequences of this for biological conservation and agricultural productivity (reviewed by Manning et al. 2006).

We sought to provide management recommendations that apply to agricultural landscapes more broadly by undertaking a sensitivity analysis on simulations based on data that spanned observations across the 4 case studies and a range of feasible management responses. Increasing recruitment—the principal strategy recommended for mitigating the loss of scattered mature trees in agricultural landscapes (Harvey & Haber 1999; Reid & Landsberg 1999; Gibbons & Boak 2002; Plieninger et al. 2004; Vesk & Dorrough 2006)—was not, on its own, an adequate strategy for achieving this (Figs. 1e–h). Manipulating the number of trees recruited, the period between recruitment events, and the rate of mortality among trees was a more effective way to minimize the loss of mature trees in these landscapes.

Recruitment

Recruiting new trees is not a sufficient strategy on its own with which to perpetuate scattered mature trees because the diversity of age classes in these stands has become so reduced that the period it takes for new recruits to reach maturity is typically longer than the period before
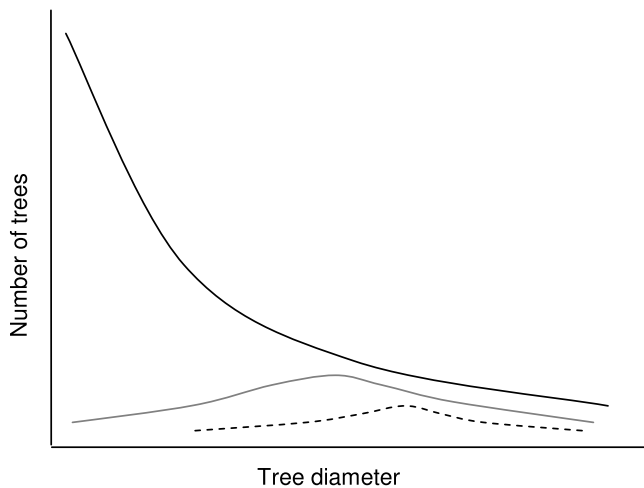
Figure 4. Typical frequency distributions of tree diameters for stands with a long history of poor recruitment (broken line), shorter history of poor recruitment (gray line), and relatively unmodified stands (black line). Diameter values increase from left to right on the x-axis.

existing trees will be lost to mortality (Parker & Peet 1984; Plieninger et al. 2004) (Fig. 4). In all scenarios representing existing proposals for mitigating the loss of scattered trees (i.e., an increase in recruitment), mature trees continued to decline at the same rate as scenarios representing the status quo until the first cohort of recruits reached maturity, which was 60–200 years (Figs. 1e–h). A further result with respect to recruitment with implications for management is that under relatively low rates of mortality and the establishment of multiple recruitment trees for every existing tree in the stand, mature trees could be perpetuated in these landscapes with relatively long periods between recruitment events (i.e., periods in years equivalent to around 15% of the life expectancy of the trees) (Fig. 3). This means mature trees can potentially be perpetuated in these landscapes with recruitment events occurring every 30–90 years. This is an important consideration because there is typically a cost associated with tree recruitment in agricultural landscapes because of the need to reduce or temporarily remove grazing by stock, prepare a receptive seed bed, or direct seed or plant new trees. The longest possible interval between these events is likely to be the most cost-effective strategy.

Mortality

Recruitment should always be considered in concert with mortality when perpetuating mature trees in these landscapes. The number of mature trees perpetuated over time was strongly and negatively associated with the rate of mortality (Fig. 2). Elsewhere it has been found that sustaining densities of mature trees is sensitive to levels of recruitment and mortality (Condit et al. 1998). Long-lived organisms, especially if they have slow growth rates (e.g., orange roughy [*Hoplostethus altlanticus*]), are vulnerable to increases in mortality even under conditions of high fecundity (Clarke 2001). There are several causes of mortality among scattered trees in agricultural landscapes for which there is scope for mitigation: land clearing (Maron 2005), herbicide spray drift (Marrs et al. 1993), nutrient enrichment (Landsberg & Wylie 1983), fire (Gibbons et al. 2000), salinity (Manning et al. 2006), and severe browsing by vertebrates (Mountford et al. 1999) or invertebrates (Lumsden & Bennett 2005).

Despite an inability to perpetuate mature trees under high levels of mortality, there are few data on mortality for scattered trees. None of the case studies we used contained estimates of tree mortality. Thus, we had to obtain estimates of mortality from studies in other landscapes. Nevertheless, only one of these studies identified which trees in the stand were most vulnerable to mortality, even though it is known that mortality among scattered trees can be density dependent or density independent (Barnes 1983) and vary with the size, or age, of trees (Mountford et al. 1999). Thus, applying mortality uniformly to all trees in a stand (as we did for each case study) is a crude way of developing management regimes and predicting outcomes for scattered trees in these landscapes. Furthermore, an understanding of the major causes of mortality is important for devising strategies to reduce it.

Time Lags

Pressures that increase rates of mortality among existing trees and inhibit recruitment of new trees progressively reduce the diversity of age classes in scattered-tree landscapes (Fig. 4). In each landscape represented by the case studies, the structural diversity of stands was so simplified that no amount of management intervention could avert declines in the numbers of mature trees before new trees could grow to replace them (Figs. 1i–l). The time lag is exacerbated for old stands because the time before trees reach their life expectancy is relatively short, so strategies to reduce mortality will not be as effective as for younger stands, and there is relatively little recruitment of new mature trees from the existing stand because the age-class distribution is relatively narrow (Fig. 4).

The period over which mature trees will become depleted in agricultural landscapes is described as a "bottleneck" by Manning et al. (2004) and Vesk and Mac Nally (2006) because this is the period when the resources provided by mature trees will be most limiting. Although our model predicted that a bottleneck would be inevitable in each landscape represented by the case studies, it is not too late to influence the point at which it will occur, its duration, and therefore its impacts on biota and ecosystem services.

Conclusions

The effects of an approaching bottleneck of mature trees in agricultural landscapes can be mitigated with a strategy that reduces mortality of existing trees with a particular emphasis on reducing mortality in stands with a high mean diameter (or age), recruits new trees at a rate that is higher than the existing number of trees and at a frequency equivalent to around 15% of the maximum age of the trees, and institutes these changes as soon as possible. Nevertheless, this strategy must also consider alternative ways of mitigating the impact of an inevitable temporary reduction in the resources provided by mature trees in these landscapes, such as artificial tree hollows and alternative sources of shade and deep-rooted perennial vegetation.

Acknowledgments

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