Land-use drivers of forest fragmentation vary with spatial scale

Author

Cattarino, Lorenzo, A. McAlpine, Clive, R. Rhodes, Jonathan

Published

2014

Journal Title

Global Ecology and Biogeography

DOI

https://doi.org/10.1111/GEB.12187

Land-use drivers of forest fragmentation vary with spatial scale

Lorenzo Cattarino[1,2]*, Clive A. McAlpine[1,3] and Jonathan R. Rhodes[1,3,4]

[1] *The University of Queensland, Landscape Ecology and Conservation Group, School of Geography, Planning and Environmental Management, Brisbane, Queensland 4072, Australia;* [2] *Griffith University, Australian Rivers Institute, Nathan, Queensland 4111, Australia;* [3] *National Environmental Research Program Environmental Decisions Hub, The University of Queensland, Brisbane, Queensland 4072, Australia;* [4] *Australian Research Council Centre of Excellence for Environmental Decisions, The University of Queensland, Brisbane, Queensland 4072, Australia*

*Correspondence: Griffith University, Australian Rivers Institute, Nathan, Queensland 4111, Australia. Email: l.cattarino@griffith.edu.au

Keywords: Agriculture, scale-dependent patterns, vegetation clearing, land-use change, land sparing, land sharing, fractal geometry, thresholds.

Short running title: Scale-dependent drivers of fragmentation

Corresponding author: Lorenzo Cattarino

Number of words in the abstract: 300

Number of words in the main body (from Introduction to Biosketch): 5,889

Number of references: 47

Abstract

Aim Improving the understanding of the drivers of forest fragmentation is fundamental to mitigating the consequences of anthropogenic fragmentation for biodiversity. Moreover, the impacts of fragmentation on biodiversity depend on the spatial scale at which fragmentation occurs. Therefore, understanding how the effect of land use on fragmentation patterns varies across scales is critical to ensure that fragmentation is managed at scales relevant to the ecology of target species or land management. Here, we quantified the influence of land use on patterns of forest fragmentation at different scales using Queensland, Australia, as a case study.

Location North-eastern Australia.

Methods We combined fractal analysis with piecewise linear regression to measure patterns of forest fragmentation across a range of scales, in 5309 landscapes of ~ 50 km^2, with different proportions of cropping and grazing land uses. A significant change in fragmentation patterns occurred at approximately 1 km^2. We used beta regression to quantify the impact of land use on the degree of fragmentation at scales finer and coarser than 1 km^2.

Results Grazing land use tended to create more fragmented forest patterns than cropping land use. This difference was more pronounced at coarser than finer scales.

Main conclusions Our finding suggests that the land use where prioritizing conservation actions, such as revegetation and retention of forest patches, depends on the scale at which we measure fragmentation. This information contributes to reducing the risk of mismatches between the scale of fragmentation management and the scale at which we measure fragmentation, often dictated by the scale of species' movements or the scale of land management. Our finding also improves our capacity to discern between fragmentation

patterns typical of land-sharing and land-sparing conservation strategies, as spatial scale varies, thus aiding in implementing land sparing and land sharing at scales relevant to biodiversity conservation and land management.

Introduction

Forest fragmentation, that is the breaking apart of forest as opposed to the reduction in amount (forest loss), is a key component of global change. Fragmentation is a primary consequence of processes of land-use change, such as agricultural intensification, logging and urban development, and, at the same time, is a main cause of modification of natural landscapes (Foley *et al.*, 2005; Fischer & Lindenmayer, 2007). Quantifying the impact of land use on the degree of disaggregation of forest cover over large geographical extents ("macroecological" fragmentation patterns; Brown, 1995) is necessary to understand the drivers of forest fragmentation (Mertens & Lambin, 1997; Geist & Lambin, 2001; Lambin *et al.*, 2003), which is a fundamental issue for conservation (Sala *et al.*, 2000). Moreover, the impact of land use on fragmentation may vary with spatial scale (Ewers & Laurance, 2006), with important consequences for biodiversity (Cattarino *et al.*, 2013). Therefore, identifying the land use drivers of forest fragmentation at different scales is crucial for biodiversity conservation. However, currently there is little understanding of how land use drives macroecological patterns of forest fragmentation, and how this effect varies with spatial scale, despite a recognition that land use is a major driver of fragmentation (Riitters *et al.*, 2002; Ewers & Laurance, 2006).

The impact of land use on patterns of forest fragmentation depends on the spatial scale, or resolution, of the fragmentation pattern, because different land uses create different fragmentation patterns at different scales. For example, urban development and smallholder-based agriculture create forest patterns that are more fragmented at fine than coarse scales (Ewers & Laurance, 2006; Girvetz *et al.*, 2008), while clearing of large blocks of vegetation for large-scale farming tends to create forest patterns that are more fragmented at coarse than fine scales (Fearnside, 2005). Quantifying the impact of different land uses on patterns of forest fragmentation at different scales is important to identify the drivers of fragmentation at each scale, and therefore the conservation management actions that need to be implemented to reduce fragmentation at each scale. For instance, better farm-level management practices and land tenure reforms can be employed to reduce fine-scale fragmentation, while broader mechanisms, such as elimination of subsidies for large-scale clearing, would be more suited to target coarse-scale fragmentation (Fearnside, 2005; Ewers & Laurance, 2006). Identifying the scale at which to implement different land use policies is important to ensure that the scale at which fragmentation is managed matches the scale of relevant ecological processes, such as the scale of species dispersal, or the scale of land management (e.g., local or regional administrative boundaries) (Pelosi *et al.*, 2010; Dudaniec *et al.*, 2013). This is a critical issue for conservation because fragmentation at different scales has different effects for biodiversity (Cattarino *et al.*, 2013). Although previous studies have measured forest fragmentation at different scales (Ewers & Laurance, 2006), the relative effect of different land uses in driving fragmentation patterns simultaneously at different scales remains largely unexplored.

Understanding the link between land use and scale-dependent fragmentation is important for implementing conservation strategies at scales relevant to the ecology of species and land management. Two contrasting conservation strategies, i.e. land sharing and land sparing, have been proposed to reconcile biodiversity conservation with agricultural land use (Green *et al.*, 2005). While land sparing consists of intensively farming agricultural land and setting aside land for conservation, land sharing integrates agricultural production and conservation on the same land by farming a larger area of land at a lower intensity (Green *et al.*, 2005). Driven by different land uses, the two strategies create different fragmentation patterns, which represent the extremes in a continuum of fragmentation degrees. While land sparing tends to create less fragmented patterns, by physically separating agricultural land (e.g. crops) from land for conservation, land sharing creates more fragmented patterns, by subdividing the landscape into a heterogeneous mix of different land uses (e.g. crops, pasture and forest) (Fischer *et al.*, 2008). Land sharing and land sparing can also be implemented at different scales. Matching the scale at which land sharing and land sparing are implemented with the scale at which species move, or at which land-use management is conducted, is important for achieving effective outcomes for biodiversity conservation and land management (Phalan *et al.*, 2011). However, avoiding scale mismatches requires first understanding whether land sparing becomes land sharing, or vice versa, as scale varies (Phalan *et al.*, 2011). Following the Fischer's framework, this involves quantifying whether land use drives changes in the degree of fragmentation across scales. While scale is becoming an important aspect of the land sparing/land sharing debate (Phalan *et al.*, 2011; Chandler *et al.*, 2013), how different land uses drive land-sharing and land-sparing patterns at different scales has received relatively little attention.

In this study, we address the question: to what extent does land use drive patterns of forest fragmentation and how does this effect vary across spatial scales? To answer this question, we conducted a multi-scale analysis of forest fragmentation for Queensland, Australia. The region, which covers an area of 1.1 million km^2, has undergone extensive deforestation since European settlement of Australia (Seabrook *et al.*, 2006; McAlpine *et al.*, 2009). We adopted a regression-based approach derived from fractal geometry (Mandelbrot, 1983) to quantify how patterns of forest fragmentation at different scales vary with the proportion of different land uses. We show that the impact of land use on patterns of forest fragmentation depends on the scale at which we measure fragmentation. This suggests that the land use where to prioritize conservation actions depends on the scale at which we are interested in measuring fragmentation, such as the scale at which species of conservation move or the scale at which of land management is conducted. This information helps to improve our capacity to match the scale at which to manage fragmentation with the scale relevant to biodiversity conservation or land management.

Materials and Methods

Study region

We focused on seven Queensland bioregions of the Interim Biogeographic Regionalisation for Australia (IBRA) (Thackway & Cresswell, 1995): Brigalow Belt North, Brigalow Belt South, Central Mackay Coast, Desert Uplands, Mulga Lands, South Eastern Queensland and Wet Tropics (Fig. 1). The bioregions cover an area of *c.* 72 million ha. The climate ranges from tropical to subtropical and semiarid, with rainfall concentrated in the north and central part (Sattler & Williams, 1999). The main vegetation communities include rainforest species in the north and woodland of *Eucalyptus* and *Acacia* spp. in the southern part (Sattler & Williams, 1999). Extensive clearing of native vegetation has occurred in these regions, especially in the central and southern part (e.g., Brigalow Belt), due to cropping and cattle and sheep grazing (Department of Environment and Resource Management, 2010).

Conceptual Framework

We developed a conceptual framework for how land use drives patterns of forest fragmentation at different scales (Fig. 2). When the effect of land use is the same across scales (null hypothesis), similar patterns of fragmentation occur at different scales in different land uses, e.g., fragmentation may be higher in grazing than in cropping land use, with similar degrees of fragmentation at different scales in each land use (Fig. 2(a)). However, when the effect of land use varies across scales, patterns of fragmentation may vary across scales in different land uses, e.g., fragmentation may be higher in grazing than in cropping land use to a greater extent at the fine than at the coarse scale (Fig. 2(b)). We test this hypothesis against the null hypothesis using fractal theory and piecewise regression (see below).

Land cover mapping

We subdivided the study bioregions into 7 × 7 km square landscapes (n = 14,678) and calculated the amount of forest cover in each landscape. We selected a landscape size of around 5,000 ha to make sure we would capture the effect of processes operating within individual agricultural properties (average size 7,000 ha; Seabrook *et al.*, 2008) on fragmentation patterns, as vegetation clearing in Australia occurs mainly within properties (Seabrook *et al.*, 2007, 2008). Forest cover data for the year 2009 was derived from the Statewide Landcover and Trees Study (SLATS), derived from Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) satellite imagery (pixel size 30 meters) (Department of Environment and Resource Management, 2010). SLATS has mapped woody Foliage Projected Cover (FPC) data over the entire State of Queensland between years 1999 and 2009. For our analysis, we only considered values of FPC greater than 11% as forest, which according to the Kyoto Protocol corresponds to the definition of forest cover (i.e. trees and shrubs above 2 m and approximately 20% canopy cover) (Kitchen *et al.*, 2010).

For each landscape, we calculated the proportion of each pixel occupied by cropping and grazing, which are the major drivers of forest fragmentation in Queensland (Department of Environment and Resource Management, 2010). Land use data, in the form of a raster layer (pixel size 1000 meters), were obtained from the *Land Use of Australia, Version 4,* *2005-06* (Australian Bureau of Agricultural and Resource Economics and Sciences, 2010). As clearing of vegetation might not be representative in nature reserves, we excluded them from the analysis. At the end of the mapping process, a total of 12,134 landscapes (7 × 7 km) were identified (Table 1).

Measure of forest fragmentation

We used fractal geometry (Mandelbrot, 1983) to measure patterns of forest fragmentation at different scales. Fractal geometry has been widely used to model the spatial heterogeneity of resource distributions in real landscapes (Milne, 1992; Palmer, 1992; With, 1997). We define $p(m,L)$ as the probability of finding m forest pixels in a squared window of size L. According to fractal theory, when the degree of forest fragmentation is the same across scales, the slope of the log-log regression line of the expectation of $p(m,L)$, measured over a range of scales (i.e. resolutions), versus scale, is constant (Milne, 1992). The steeper the slope, the more fragmented is the forest pattern. However, when the degree of fragmentation changes across scales, the slope of the log-log regression line varies along the line. The change in slope is often assumed to occur as a threshold, or *breakpoint*. The number of breakpoints reflects the number of times the degree of fragmentation varies across scales. We can interpret the location of the breakpoint(s) (*Bp*) as the scale at which there is a transition between the degree of fragmentation at fine scales (slope before the breakpoint) and the degree of fragmentation at coarser scales (slope after the breakpoint).

We constructed a probability distribution of the mean amount of forest in a landscape $p(m,L)$, by counting the total number of forest pixels, m, in a moving squared window of length L centred on each forest pixel of our sample landscapes. The probabilities satisfy the condition,

$$\sum_{m=1}^{N(L)} p(m, L) = 1 \tag{1}$$

which ensures that the sum of the probabilities of finding *m* forest pixels in a window of length *L* was 1, where *N(L)* is the number of different *m* values obtained for windows of size *L*. Measurement of *p(m,L)* provides a statistic that describes the aggregation of forest cover in a patch mosaic (Milne, 1992). In order to minimize landscape boundary effects, we treated a landscape as a *torus*, where the bottom row adjoins the top row and the right most column adjoins the left most column (With *et al.*, 1997).

The expectation, *M(L)*, of *p(m,L)* was then calculated as follows:

$$M(L) = \sum_{m=1}^{N(L)} m\, p(m, L) \tag{2}$$

Based on a general property of fractal objects (Mandelbrot, 1983), the expected average amount of forest, *M(L)*, varies with the length of the squared window, *L*, through the power-law relationship $M(L) = kL^D$, where *k* is a constant and *D* is the fractal dimension of the land-cover pattern, which represents the degree of forest fragmentation. The value of *D*, which ranges from 1 to 2, increases as the degree of fragmentation increases (Milne, 1992). We selected 100 values of *L*, ranging from 1 to 280 pixels, where *L* = 280 corresponded to the size of a landscape.

For each landscape, we calculated the expectation, *M(L)*, for each value of *L*. To reduce computational time, we calculated *M(L)* for a random sample of 10% of the total number of forest pixels in each landscape. The analysis was run for all landscapes in each bioregion. However, for those bioregions with a large number of landscapes (> 1000), a random sample of 1000 landscapes was selected, limiting the analysis to a total of 5,309 landscapes.

Statistical analysis

For each landscape, we modelled the mean $M(L)$ as a function of window length L. To investigate whether forest fragmentation varied across scales, we tested for the existence of breakpoints in the log-log regression line using linear and piecewise regression. We fitted two alternative regression models: (1) a ‘null’ model - linear regression (McCullagh & Nelder, 1989), which refers to the case where there is no difference in patterns of fragmentation across scales; and (2) a ‘threshold’ model - piecewise regression (Muggeo, 2003) - which refers to the case where different patterns of fragmentation occurs at different scales. To assess the significance of a breakpoint, we fitted threshold models for a number of breakpoints ranging from 1 to 10. For each model, we then calculated the Akaike’s information criterion (AIC) and selected the model with the lowest AIC as the most parsimonious one, based on an information-theoretic approach (Burnham & Anderson, 2002). A preliminary inspection revealed that the threshold model with one breakpoint received very strong support, relative to the null model and the threshold models with more than one breakpoint (Table 2). We assumed that different degrees of fragmentation occurred at coarse and fine spatial scales (i.e., coarse-scale and fine-scale fragmentation) in landscapes for which the threshold model was the most parsimonious one. For those models, we estimated the location of the breakpoint and the fractal dimension of the forest patterns at either side of the breakpoint.

We then applied beta regression models to quantify the effect of land use in driving patterns of forest fragmentation at coarse and fine scales. Beta regression is a common approach to model variables bounded in the 0-1 range, such as proportions or rates (Ferrari & Cribari-Neto, 2004). We built two separate models and fitted them to the degree of coarse-scale and fine-scale fragmentation, which were treated as dependent variables. A value of 1 was subtracted from the raw values of the dependent variables (bounded between 1 and 2) to fit the 0-1 range of the beta regression models. In order to include land use as an independent variable, we first tested whether the proportion of cropping and grazing land use were correlated using a Spearman's correlation. The proportion of cropping land use was found to be negatively correlated to the proportion of grazing land use (r = - 0.57). We therefore interpreted the effect of cropping on patterns of fragmentation at different scales to be the inverse of the effect of grazing (g), and discarded the proportion of cropping land use from the models to reduce colinearity. We also controlled for the effect of the amount of forest cover (Gardner *et al.*, 1987), by including the amount of forest cover (p) as an independent variable in the models. We fitted the following model:

$$\mathrm{logit}(\mu_i) = \beta' \mathrm{X}_i \tag{3}$$

where μ_i is the degree of coarse-scale or fine-scale fragmentation in landscape i, β is a vector of regression coefficients and X_i is a vector of independent variables. For each dependent variable, we constructed a set of five competing models using combinations of all explanatory variables.

For each dependent variable, model comparison was conducted using an information-theoretic approach (Burnham & Anderson, 2002). We calculated good-ness of fit of each model using the R^2. To reduce model selection bias, we calculated model average parameter estimates, and the unconditional standard error of each estimate, from all the fitted models. We also estimated the relative importance of each explanatory variable by ranking them according to the sum of the Akaike weights (Σw_i) of the models where the variable occurred.

The larger the sum of the Akaike weights, the higher the importance of each variable is relative to the other variables. All statistical analyses were conducted using R version 2.14.0 (R Development Core Team, 2013).

Results

In most of the landscapes, forest fragmentation was higher at fine than coarser scales (Fig. 3). This was more evident for lower than higher amounts of forest cover ($p < 0.5$) and for grazing than cropping land use. The average value of the degree of coarse-scale fragmentation ($D1 = 1.798 \pm 0.009$) was significantly different from the average value of the degree of fine-scale fragmentation ($D2 = 1.892 \pm 0.005$) (Mann-Whitney-Wilcoxon Test, $W = 130$, $P = 0.015$) (Table 2). The average value of the breakpoint location was 3.608 ± 0.045 (Table 2), which corresponded to *c.* 100 ha (1 km^2).

The amount of forest cover and the proportion of grazing land use were both included in the most parsimonious model for coarse-scale fragmentation (AIC = -350.8; $R^2 = 0.71$; Table 3). However, the second best model also included the interaction between the amount of forest cover and the proportion of grazing (ΔAIC = 1.9). The sum of the Akaike weights showed that the amount of forest cover and the proportion of grazing were considerably more influential than their interaction in affecting coarse-scale fragmentation (Fig. 4). The most parsimonious model for fine-scale fragmentation included the amount of forest cover, the proportion of grazing and their interaction (AIC = -224.2; $R^2 = 0.84$; Table 4). The sum of the Akaike weights showed that the amount of forest cover and the proportion of grazing were more influential than their interaction in affecting both coarse-scale and fine-scale fragmentation (Fig. 4).

The model-averaged coefficients showed that as the proportion of grazing land use increased, forest fragmentation increased (Fig. 5). The coefficients also indicated that, as the proportion of cropping land use increased, forest fragmentation declined, due to the negative correlation between cropping and grazing land use. However, as the proportion of grazing land use increased, forest fragmentation increased more at coarser than at finer scales. Moreover, as the amount of forest cover increased, increasing the proportion of grazing land use reduced forest fragmentation. However, this effect was greater at coarser than at finer scales.

Discussion

Our study contributes to improving the understanding of the drivers of scale-dependent land-use change in human-modified landscapes (Lambin *et al.*, 2003; Ewers & Laurance, 2006). We found that land use is a more important driver of fragmentation at coarse spatial scales than at fine scales. Our findings suggest that the choice of land use where prioritizing conservation actions, such as revegetation and retention of forest patches, to reduce forest fragmentation, depends on the scale at which we measure fragmentation patterns. This information may improve our ability to match the scale at which fragmentation is managed with the scale relevant to ecology of species of conservation concern or existing land management (Pelosi *et al.*, 2010). This is crucial for conservation because fragmentation at different scales has different effects on biodiversity (Cattarino *et al.*, 2013). Our study also improves the capacity to discern between fragmentation patterns typical of different conservation strategies, i.e., land sharing or land sparing, across different scales. This may aid in implementing land sharing and land sparing at scales relevant to biodiversity conservation and land management.

Drivers of fragmentation at different scales

In our study, grazing and cropping land use drive different fragmentation patterns at fine and coarse scales. Since a transition between fragmentation patterns at fine and coarse scales occurred at approximately 100 ha (1 km^2), which is much smaller than the average property size in Queensland, i.e., 7,000 ha (Seabrook *et al.*, 2008), our finding suggests that different drivers of native vegetation clearing determine different fragmentation patterns between and within agricultural fields, in landscapes modified by different land uses. For example, Seabrook et al. (2007) found that cleared areas within agricultural properties were clustered around particular landscape features (e.g. riparian vegetation) and vegetation classes (e.g. dry eucalypt forests), which are indicators of high soil productivity. This may explain why, at coarse scales, cropping creates less fragmented patterns than grazing, as clustering of vegetation clearing in areas of high soil fertility determines more the physical separation of agricultural land (e.g., crop fields) from remnant vegetation in cropping than in grazing land use.

At finer scales, such as within individual agricultural fields, the processes driving clearing of vegetation in cropping and grazing land uses are different than at coarser scales. The intense removal of standing native vegetation within agricultural fields, through the use of agricultural machinery for crop cultivation and irrigation (e.g., ploughing, sowing, harvesting, irrigation systems) creates less fragmented patterns than grazing, as remnant vegetation tends to be clumped in linear strips and patches between cropped areas (Maron & Fitzsimons, 2007; Smith *et al.*, 2013). On the other hand, clearing of isolated vegetation patches is less intense within grazing properties, where all vegetation within a production area is not necessarily removed and regrowth vegetation is common (Fensham, 1997; Smith *et al.*, 2013), thus creating more fragmented forest patterns than in cropping properties.

Interestingly, the breakpoint location we found here is smaller than reported by Ewers and Laurance (2006) for the Brazilian Amazon (~ 1,200 ha). Therefore, the scale at which there is a transition between the impacts of different drivers of fragmentation is coarser in Brazil than in Australia. This may be due to different socio-economic factors. In Brazil, large-scale clearing mainly for cattle ranching is a major source of deforestation, and is a legacy of poor environmental policies and government subsidies (Fearnside, 2005). The low fertility of forest soils has also forced farmers to clear large areas of land to maintain productivity. Moreover, agricultural properties are larger, on average, than 10,000 ha, which makes coarse-scale fragmentation patterns sensitive to macroeconomic factors, such as interest rates and land prices (Walker *et al.*, 2000; Fearnside, 2001). In Queensland, on the other hand, clearing tends to be more localized, as a result of stronger vegetation management policies and occurring more on fertile than infertile soil, and is driven also by finer scale mechanisms, such as smaller property size and individual land holder's response to vegetation management policies (McAlpine *et al.*, 2002; Seabrook *et al.*, 2007, 2008). These differences suggest that the scales at which different processes of land use change drives different fragmentation patterns are also different in different regions.

Approach and limitations

We recognize three main caveats in our modelling approach. First, we assume that the land uses did not change over the period of time when the clearing occurred, as the patterns of fragmentation measured here reflect the cumulative effects of past clearing processes and not necessarily the effect of current clearing processes. Land uses may have changed over the time when clearing determined the observed fragmentation patterns, thus causing a potential scale mismatch between the time when the clearing occurred and the time when the land use data were acquired (2005-2006). Nevertheless, since most of the clearing occurred recently and in a relatively short period of time (1990-2004) (Department of Environment and Resource Management, 2010), we believe our results are still robust, because land uses may have not changed considerably over the time when most of the clearing occurred.

Second, we assumed the transition between the degree of fragmentation at different scales to be abrupt, i.e., it exhibited a threshold. A range of statistical models, including polynomial regressions and generalized additive models (Hastie & Tibshirani, 1990), could be used to capture the non-linear behaviour of the relationship between the expected average amount of forest $M(L)$ and the value of scale L. However, our aim was not to understand the nature of the transition, but rather to assess whether there was any significant change in patterns of fragmentation at different scales.

Finally, although forest fragmentation is a scale-dependent process, it is possible that we failed to detect patterns at very fine scales due to the coarse resolution of our thematic maps (30 meters). For example, processes of land-use change, such as infrastructure development and agricultural intensification, cause the removal of individual trees and small vegetation patches within agricultural fields (Maron & Fitzsimons, 2007), that we may have not captured in our analysis. Therefore, the coarse resolution of vegetation data may have contributed to the weaker effect of land use on fragmentation patterns at finer than coarser scales. Future research may benefit from the use of land cover maps derived from higher-resolution satellite imagery (e.g., SPOT, Worldview, Lidar), which may aid identifying finer patterns of fragmentation and their drivers of change.

Implications for conservation and land management

The different scale-dependent effect of land use on patterns of forest fragmentation suggests that the choice of land use where to implement conservation actions to reduce fragmentation depends on the scale at which fragmentation is measured. For example, if fragmentation is measured at coarse scales, conservation should promote revegetation and habitat restoration across multiple agricultural fields, or small properties (Smith *et al.*, 2013), on grazing land use more than on cropping land use. If fragmentation is measured at fine scales, management may still need to target grazing more than cropping by incentivizing best farm management practices within properties, such as retention of patches of vegetation and scattered paddock trees (Harper *et al.*, 2012). However, the need for conservation actions targeting grazing may be higher at coarser than finer scales, as the difference between the impacts of different land uses on fragmentation patterns is smaller at finer than at coarser scales. Thus, our findings are likely to be relevant for conservation of species moving large distances, as they are particularly affected by coarse-scale fragmentation (Cattarino *et al.*, 2013), and in the case of management across multiple planning units, such as local government areas (Dudaniec *et al.*, 2013).

Our study advances our capacity to discern between the forest patterns typical of land-sharing and land-sparing conservation strategies, as spatial scale varies. This may aid in identifying the land use where to implement agricultural policies to achieve land sparing and land sharing at different spatial scales (Phalan *et al.*, 2011). For example, at coarse scales, forest patterns are more like land sharing (high fragmentation) in grazing than in cropping land use, and more like land sparing (low fragmentation) in cropping than in grazing land use. This suggest that, at coarse scales, agricultural policies to implement land sharing should be applied to grazing rather than cropping land use, as we found higher fragmentation in grazing than in cropping. This would involve adoption of sustainable farming practices, e.g., fencing, rotational grazing and favouring native perennial ground cover (Dorrough *et al.*, 2007). However, in order to implement land sparing, cropping land use would be a more suitable target of policies and legislative mechanisms than grazing land use, due to the lower fragmentation we found in cropping than in grazing land use. This could be achieved through protection of large patches of intact vegetation and planned yield intensification (Fischer *et al.*, 2008). The need to prioritize implementation of different policies in different land uses is likely to be smaller at finer than at coarser scales, as a consequence of the smaller effect of land use on fragmentation patterns. By identifying the land use where agricultural policies should be implemented to move from the pattern typical of a strategy to the actual strategy, at different scales, our study provides guidelines for implementing land sparing vs. land sharing at scales relevant to species ecology or land management.

Acknowledgements

We thank Martine Maron and three anonymous reviewers for their helpful comments on an earlier version of the manuscript. This research was conducted with the support of funding from an Endeavour International Postgraduate Research Scholarship (LC), the Australian Government’s National Environmental Research Program (JR and CM) and the Australian Research Council's Centre of Excellence for Environmental Decisions (JR) and the Australian Research Council (Grant No. FT100100338 to CM).

References

Australian Bureau of Agricultural and Resource Economics and Sciences (2010) *Land Use of Australia, Version 4, 2005-06*. Available at: http://adl.brs.gov.au/landuse/ (accessed February 2012).

Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*, 2 edn. Springer-Verlag, New York, USA.

Cattarino, L., McAlpine, C.A. & Rhodes, J.R. (2013) The consequences of interactions between dispersal distance and resolution of habitat clustering for dispersal success. *Landscape Ecology*, **28**, 1321–1334.

Chandler, R.B., King, D.I., Raudales, R., Trubey, R., Chandler, C. & Chavez, V.J.A. (2013) A Small-Scale Land-Sparing Approach to Conserving Biological Diversity in Tropical Agricultural Landscapes. *Conservation Biology*, **27**, 785-795.

Department of Environment and Resource Management (2010) *Land cover change in Queensland 2008–09: a Statewide Landcover and Trees Study (SLATS) report*. Department of Environment and Resource Management, Brisbane.

Dorrough, J., Moll, J. & Crosthwaite, J. (2007) Can intensification of temperate Australian livestock production systems save land for native biodiversity? *Agriculture Ecosystems & Environment*, **121**, 222-232.

Dudaniec, R.Y., Rhodes, J.R., Wilmer, J.W., Lyons, M., Lee, K.E., McAlpine, C.A. & Carrick, F.N. (2013) Using multilevel models to identify drivers of landscape-genetic structure among management areas. *Molecular Ecology*, **22**, 3752-3765.

Ewers, R.M. & Laurance, W.F. (2006) Scale-dependent patterns of deforestation in the Brazilian Amazon. *Environmental Conservation*, **33**, 203-211.

Fearnside, P.M. (2001) Land-tenure issues as factors in environmental destruction in Brazilian Amazonia: The case of Southern Para. *World Development*, **29**, 1361-1372.

Fearnside, P.M. (2005) Deforestation in Brazilian Amazonia: History, rates, and consequences. *Conservation Biology*, **19**, 680-688.

Fensham, R.J. (1997) Options for conserving large vegetation remnants in the Darling Downs, South East Queensland. *Conservation outside nature reserves* (ed. by P. Hale and D. Lamb), pp. 419-423. Centre for conservation biology, The University of Brisbane, Brisbane.

Ferrari, S.L.P. & Cribari-Neto, F. (2004) Beta regression for modelling rates and proportions. *Journal of Applied Statistics*, **31**, 799-815.

Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265-280.

Fischer, J., Brosi, B., Daily, G.C., Ehrlich, P.R., Goldman, R., Goldstein, J., Lindenmayer, D.B., Manning, A.D., Mooney, H.A., Pejchar, L., Ranganathan, J. & Tallis, H. (2008) Should agricultural policies encourage land sparing or wildlife-friendly farming? *Frontiers in Ecology and the Environment*, **6**, 382-387.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570-574.

Gardner, R.H., Milne, B.T., Turner, M.G. & O'Neill, R.V. (1987) Neutral models for the analysis of broad-scale landscape patterns. *Landscape Ecology*, **1**, 19-28.

Geist, H.J. & Lambin, E.F. (2001) *What Drives Tropical Deforestation? LUCC Report Series No. 4*. Land-Use and Land-Cover Change Project, CIACO, Louvain-la-Neuve, Belgium.

Girvetz, E.H., Thorne, J.H., Berry, A.M. & Jaeger, J.A.G. (2008) Integration of landscape fragmentation analysis into regional planning: A statewide multi-scale case study from California, USA. *Landscape and Urban Planning*, **86**, 205-218.

Green, R.E., Cornell, S.J., Scharlemann, J.P.W. & Balmford, A. (2005) Farming and the fate of wild nature. *Science*, **307**, 550-555.

Harper, R.J., Okom, A.E.A., Stilwell, A.T., Tibbett, M., Dean, C., George, S.J., Sochacki, S.J., Mitchell, C.D., Mann, S.S. & Dods, K. (2012) Reforesting degraded agricultural landscapes with Eucalypts: Effects on carbon storage and soil fertility after 26 years. *Agriculture Ecosystems & Environment*, **163**, 3-13.

Hastie, T.J. & Tibshirani, R.J. (1990) *Generalized Additive Models*. Chapman and Hall, London, UK.

Kitchen, J., Armston, J., Clark, A., Danaher, T. & Scarth, P. (2010) Operational use of annual Landsat-5 TM and Landsat-7 ETM+ image time series for mapping wooded extent and foliage projective cover in north-eastern Australia. *Proceedings of the 15th Australasian Remote Sensing and Photogrammetry Conference* (ed by. Alice Spring, Australia, September.

Lambin, E.F., Geist, H.J. & Lepers, E. (2003) Dynamics of land-use and land-cover change in tropical regions. *Annual Review of Environment and Resources*, **28**, 205-241.

Mandelbrot, B.B. (1983) *The Fractal Geometry of Nature*. W.H. Freeman, New York.

Maron, M. & Fitzsimons, J.A. (2007) Agricultural intensification and loss of matrix habitat over 23 years in the West Wimmera, south-eastern Australia. *Biological Conservation*, **135**, 587-593.

McAlpine, C.A., Fensham, R.J. & Temple-Smith, D.E. (2002) Biodiversity conservation and vegetation clearing in Queensland: Principles and thresholds. *Rangeland Journal*, **24**, 36-55.

McAlpine, C.A., Etter, A., Fearnside, P.M., Seabrook, L. & Laurance, W.F. (2009) Increasing world consumption of beef as a driver of regional and global change: A call for policy action based on evidence from Queensland (Australia), Colombia and Brazil. *Global Environmental Change-Human and Policy Dimensions*, **19**, 21-33.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Chapman and Hall, London, UK.

Mertens, B. & Lambin, E.F. (1997) Spatial modelling of deforestation in southern Cameroon - Spatial disaggregation of diverse deforestation processes. *Applied Geography*, **17**, 143-162.

Milne, B.T. (1992) Spatial aggregation and neutral models in fractal landscapes. *American Naturalist*, **139**, 32-57.

Muggeo, V.M.R. (2003) Estimating regression models with unknown break-points. *Statistics in Medicine*, **22**, 3055-3071.

Palmer, M.W. (1992) The coexistence of species in fractal landscapes. *American Naturalist*, **139**, 375-397.

Pelosi, C., Goulard, M. & Balent, G. (2010) The spatial scale mismatch between ecological processes and agricultural management: Do difficulties come from underlying theoretical frameworks? *Agriculture Ecosystems & Environment*, **139**, 455-462.

Phalan, B., Balmford, A., Green, R.E. & Scharlemann, J.P.W. (2011) Minimising the harm to biodiversity of producing more food globally. *Food Policy*, **36**, S62-S71.

R Development Core Team (2013) *R: A language and environment for statistical computing*. Available at: http://www.r-project.org/ (accessed April 2011).

Riitters, K.H., Wickham, J.D., O'Neill, R.V., Jones, K.B., Smith, E.R., Coulston, J.W., Wade, T.G. & Smith, J.H. (2002) Fragmentation of continental United States forests. *Ecosystems*, **5**, 815-822.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Biodiversity - Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770-1774.

Sattler, P. & Williams, R. (1999) *The Conservation Status of Queensland's Bioregional Ecosystems*. Environmental Protection Agency and Queensland National Parks Association, Brisbane.

Seabrook, L., McAlpine, C. & Fensham, R. (2006) Cattle, crops and clearing: Regional drivers of landscape change in the Brigalow Belt, Queensland, Australia, 1840-2004. *Landscape and Urban Planning*, **78**, 373-385.

Seabrook, L., McAlpine, C. & Fensham, R. (2007) Spatial and temporal analysis of vegetation change in agricultural landscapes: A case study of two brigalow (Acacia harpophylla) landscapes in Queensland, Australia. *Agriculture Ecosystems & Environment*, **120**, 211-228.

Seabrook, L., McAlpine, C. & Fensham, R. (2008) What influences farmers to keep trees? A case study from the Brigalow Belt, Queensland, Australia. *Landscape and Urban Planning*, **84**, 266-281.

Smith, F.P., Prober, S.M., House, A.P.N. & McIntyre, S. (2013) Maximizing retention of native biodiversity in Australian agricultural landscapes-The 10:20:40:30 guidelines. *Agriculture Ecosystems & Environment*, **166**, 35-45.

Thackway, R. & Cresswell, I.D. (1995) An interim biogeographic regionalisation for Australia: a framework for setting priorities in the national reserves system cooperative program. In. Australian Nature Conservation Agency, Canberra.

Walker, R., Moran, E. & Anselin, L. (2000) Deforestation and cattle ranching in the Brazilian Amazon: External capital and household processes. *World Development*, **28**, 683-699.

With, K.A. (1997) The application of neutral landscape models in conservation biology. *Conservation Biology*, **11**, 1069-1080.

With, K.A., Gardner, R.H. & Turner, M.G. (1997) Landscape connectivity and population distributions in heterogeneous environments. *Oikos*, **78**, 151-169.

Biosketch

Lorenzo Cattarino is a research fellow at the Australian Rivers Institute, Griffith University, Australia. His research interests include movement ecology, the mechanisms determining species persistence in human modified landscapes and systematic conservation planning.

Table 1 Number of landscapes in each bioregion.

Bioregion	No. of Landscapes
Brigalow Belt South	3,903
Brigalow Belt North	2,008
SEQ	1,055
Mackay Central Coast	174
Wet Tropics	135
Mulga Land	3,638
Desert Uplands	1,221
Total	12,134

Table 2 Total number of fitted models, proportion of threshold models with one breakpoint that had better fit (based on AIC values) than the other models (null model and threshold models with more than one breakpoint), average values of coarse-scale (*D1*) and fine-scale (*D2*) fragmentation, and breakpoint location (*Bp*), with Standard Error (SE), for each bioregion.

Bioregion	Total models	Best threshold models	*D1* (SE)		*D2* (SE)		*Bp* (SE)	
Brigalow Belt South	1000	0.989	1.700	(0.007)	1.863	(0.006)	3.684	(0.033)
Brigalow Belt North	1000	0.996	1.780	(0.006)	1.858	(0.004)	3.763	(0.029)
South East Queensland	1000	0.994	1.908	(0.004)	1.900	(0.003)	3.715	(0.033)
Mackay Central Coast	174	0.994	1.815	(0.013)	1.937	(0.005)	3.480	(0.075)
Wet Tropics	135	0.993	1.726	(0.018)	1.935	(0.005)	3.391	(0.076)
Mulga Land	1000	0.982	1.815	(0.005)	1.873	(0.005)	3.844	(0.031)
Desert Uplands	1000	0.988	1.843	(0.007)	1.879	(0.004)	3.379	(0.037)

Table 3 Summary of beta-regression models (model rank and variables, Akaike's information criterion (AIC) values, delta AIC, AIC weights and R2 goodness of fit) of coarse-scale fragmentation, as a function of the amount of forest cover (*p*), the proportion of grazing land use (*g*), and their interaction (*pg*).

Model rank	Variables	AIC	ΔAIC	AIC weight (w_i)	R^2
1	p + g	-350.8	0.0	0.673	0.71
2	p + g + pg	-348.9	1.9	0.259	0.71
3	p	-346.2	4.6	0.067	0.71
4	g	-59.6	291.2	0.000	0.00
5	only intercept	-58.7	292.2	0.000	0.00

Table 4 Summary of beta-regression models (model rank and variables, Akaike's information criterion (AIC) values, delta AIC, AIC weights and R2 goodness of fit) of fine-scale fragmentation, as a function of the amount of forest cover (p), the proportion of grazing land use (g), and their interaction (pg).

Model rank	Variables	AIC	ΔAIC	AIC weight (w_i)	R^2
1	p + g + pg	-224.2	0.0	0.539	0.84
2	p + g	-223.9	0.3	0.459	0.81
3	p	-212.3	11.9	0.001	0.85
4	g	-14.5	209.7	0.000	0.03
5	only intercept	-16.3	207.9	0.000	0.00

Figure 1 Study region in Queensland, north-eastern Australia.

Figure 2 Conceptual framework of how land uses drive patterns of forest fragmentation at different scales. The diagram shows different spatial configurations of forest cover at coarse (large grey quadrats) and fine (small grey quadrats) scales, in cropping and grazing land use. When the effect of land use is the same across scales (null hypothesis), similar patterns of fragmentation occurs at different scales in different land uses (Fig. 2a). However, when the effect of land use varies across scales, patterns of fragmentation may vary across scales in different land uses (Fig. 2b).

Figure 3 Bar chart showing the average degree of coarse-scale and fine-scale fragmentation (± 1 Standard Error), in landscapes with different dominant land uses, for different amounts of forest cover (p). The term “cropping” indicates landscapes with a higher proportion of cropping land use than grazing land use, and vice versa for “grazing”.

Figure 4 Relative importance of the explanatory variables, for the models for fine-scale and coarse-scale fragmentation, based on the sum of the Akaike weights (Σw_i) of the models where the variable occurred.

Figure 5 Coefficient averages from beta regression models explaining variations in the degree of fragmentation at the coarse scale and the degree of fragmentation at the fine scale, as a function of the amount of forest cover, the proportion of grazing land use and their interaction.