Assessing the impact of agricultural transformation on avian taxonomic and functional richness.

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Abstract: As human populations continue to rise and pressure continues to mount on protected areas to safeguard the world’s biodiversity, new solutions must be sought to ensure the functioning of ecological systems. Agricultural transformation of the global landscape has been extensive and the potential conservation value of agricultural areas is only just beginning to be investigated. I used an explicitly process-oriented classification to place the South African avifauna into nine functional groups. I then tested for differences in functional group structure between agriculturally transformed and protected area landscapes using a matched pair data format to control for confounding sources of variance. The results show that most avian functional groups respond in qualitatively different ways to agricultural transformation. Raptors and scavengers displayed the most consistent losses in agriculturally dominated landscapes (80% and 92% of permutations respectively), while nutrient dispersers and grazers were almost never richer in protected landscapes (6% and 8% of permutations respectively). Spatial detrending suggested that only raptors and scavengers are negatively affected by agriculture independently of contagion. Thus, protected areas are serving as important reservoirs of functionally important upper trophic species whereas agricultural lands seem to be facilitating the presence of functional groups that operate across water-terrestrial interfaces. The species richness of functional groups does not appear to influence their probability of decline in agricultural landscapes, supporting recent findings that species and functional richness are poorly correlated across space. Furthermore, in 26% of observations, species richness was higher in agricultural landscapes. These results highlight the scale dependent nature of ecological phenomena and provide a preliminary empirical foundation for using agricultural landscapes as part of extended conservation networks. The differential responses of functional groups to agricultural transformation can be combined in complementary conservation strategies, thereby ensuring the stability of ecosystem processes over broad spatial and temporal scales.
Key words: protected areas, agricultural transformation, ecosystem functioning, functional groups, conservation planning
Introduction

Biodiversity is globally threatened. Conservationists must confront the synergistic effects of human-induced climate change (Thomas et al. 2004) interacting with the loss of habitat due to human land-use activities (Matson et al. 1997, Sala et al. 2000, Tilman et al. 2001). Dramatic range shifts are being documented for an alarming number of taxa as climatic regimes alter the suitability of contemporary habitats (Parmesan & Yohe 2003). Such distributional turmoil is juxtaposed against a global landscape in which croplands and pastures have become one of the largest terrestrial biomes on the planet, occupying around 40% of the land surface (Foley et al. 2005). The conversion of natural habitat into an agricultural ‘biome’ has often been thought of by conservationists as an overwhelming threat to species and ecosystems (Lemoine et al. 2007), with many studies demonstrating the link between agricultural intensification and declines in avian species richness at localised spatial scales (Fuller et al. 1995, Flather 1996, Chamberlain & Fuller 2000, Donald et al. 2001, Gaston et al. 2003, Rodríguez-Estrella 2007). It now seems unequivocal that most avian species are significantly negatively affected by agriculture at these scales (Guénette & Villard 2005, Tscharntke et al. 2005). However, agricultural habitats have the potential to serve as complementary conservation areas at landscape scales (Robinson et al. 2001, Hughes et al. 2002, Bengtsson et al. 2003, Daily et al. 2003, Jones et al. 2005). By combining ecologically relevant practices on farmlands with broad-scale habitat restoration, agricultural landscapes may become a net benefit for biodiversity (Sutherland 2002).

The importance of agricultural landscapes becomes evident as pressure from anthropogenic activities increasingly compromises the effectiveness of reserve networks (Chown et al. 2007, Hansen & DeFries 2007). It seems likely that reserves alone will not be able to maintain biodiversity in perpetuity if they are viewed as being isolated from the
surrounding matrix (DeFries et al. 2007). What is needed is not so much a dichotomy between ‘protected equals safe’ and ‘unprotected equals doomed’ but a dynamic strategy that integrates protected and unprotected habitat types into fully functional ecosystems. This is tantamount to preserving functional landscapes at multiple scales (Poiani et al. 2000). Agricultural landscapes, although probably unable to support most habitat specialist species in themselves (Franklin 1993), can be important matrix ecosystems, which are key to the long-term persistence of large and small patch ecosystem processes (Poiani et al. 2000). Furthermore, identifying sites that are reservoirs of functional diversity is especially important when integrating functional landscapes into social-ecological systems such that the resilience and adaptive capacity of the system is maximised (Cumming et al. 2005).

Traditionally, species-area curves and associated species ‘hotspots’ have been used extensively in conservation planning (Zimmerman & Bierregaard 1986, Pearson & Carroll 1998, Myers et al. 2000, Gotelli & Colwell 2001), which has produced reserve networks based on species representation rather than on ecosystem reasoning (Gaston et al. 2001, Wiersma & Urban 2005). However, using species richness as the primary determinant of reserve selection is ecologically insufficient (Doak & Mills 1994). It has recently been recognised that species per se do not contribute to the functional diversity of a community (Diaz & Cabido 2001, Petchy & Gaston 2002, Reich et al. 2003, Naeem & Wright 2003). Functional diversity arises from the relative functional trait richness that species possess (Tilman et al. 1997, Hector et al. 1999, Naeem et al. 1999, Naeem & Wright 2003, Petchey & Gaston 2006). Using the functional traits of organisms has been seen as a way to bridge the divide between community and ecosystem ecology (McGill et al. 2006). Surprisingly, however, current global biodiversity scenarios lack process-oriented metrics of ecosystems (Cumming 2007), focusing more on easily measurable variables such as species richness. Thus, scenario planning at landscape levels is constrained by the simple lack of knowledge as
to whether ecosystems are robust to species loss or not (Naeem 2002) as well as the distribution of functional groups across space (Bengtsson et al. 2003). Although species richness is strongly positively correlated with functional richness, the former is a poor spatial predictor of the latter (Cumming & Child, in review). In lieu of this, studies detailing the cause and effect of functional diversity patterns across space are sorely needed for effective conservation management, especially if we are to incorporate these patterns into functional reserve networks (Cowling et al. 1999, Rouget et al. 2003).

The aim of this study is to provide an exploratory analysis of the patterns of avian functional group richness following agricultural conversion at landscape scales. If agricultural landscapes are to sustain the provision of ecosystem services then functional groups must be available for renewal and reorganisation following disturbances (Lundberg & Moberg 2003). Although there is no perfect way to define functional groups (Simberloff & Dayan 1991), it seems that a composite measure, rather than purely resource or life history approach (Wilson 1999), captures ecosystem-relevant properties most effectively (Schweiger et al. 2007). In this study, I use the functional group classification of Sekercioglu (2006) because of its explicit focus on birds as multifaceted actors in ecosystem dynamics. Even though this is a predefined classification, birds are extremely well-studied species and their importance as mobile links in the dynamics of both natural and human-transformed landscapes is extensively documented (reviewed by Sekercioglu 2006). Furthermore, declines in avian functional richness are predicted to have dire consequences for the maintenance and provision of a diverse array of ecosystem services (Sekercioglu et al. 2004). How the maintenance of such ecosystem services is altered after agricultural transformation is less well known. Previous studies have shown that avian species richness and abundance are positively correlated with human population density at broad scales (Chown et al. 2003, Fairbanks et al. 2002), while avian community evenness suffers under human transformation
(Fairbanks et al. 2002). These results have been interpreted to mean that agricultural practices may provide novel resources, which some species are better at exploiting than others. Thus, community structure may simplify while maintaining similar population abundance (McKinney & Lockwood 1999, Fairbanks et al. 2002, La Sorte 2006). Indeed, Okes et al. (2008) have recently documented the westward expansion of many generalist waterfowl across agricultural landscapes in South Africa. Increased incidence of such generalists has been demonstrated to negatively affect local avifaunal abundance (Curtis et al. 2007), which is likely to have pervasive effects within communities. Consequently, if agricultural transformation has the power to reorganise avian communities at local scales (Avecedo & Restrepo 2008), the question becomes whether these effects translate into emergent landscape patterns that can be used in conservation planning. In this study I provide the first step in answering this question.

Methods

I compared the differences in functional group richness between protected and agriculturally transformed (unprotected) areas. I used a paired sampling design in an attempt to isolate the effects of the ‘treatment’ (agricultural transformation) by controlling for potentially confounding variables. The primary assumption for these analyses was that both members of a pair could support identical avian communities were it not for the observed agricultural transformation. Thus, pairs were matched as closely as possible in terms of sampling effort, climatic variables, topographic variables and land-use intensities.
Table 1. Functional group categories derived from Sekercioglu (2006) and their definition. The numbers in each cell are defined by the scores listed under ‘functional trait’. Note that ‘raptors’ as used here includes animals not traditionally considered raptors, such as herons and egrets that feed on fish and frogs; and that birds can belong to more than one functional group.

<table>
<thead>
<tr>
<th>Functional Trait</th>
<th>Categories</th>
<th>Seed dispersers</th>
<th>Pollinators</th>
<th>Nutrient dispersers</th>
<th>Insectivores</th>
<th>Granivores</th>
<th>Grazers</th>
<th>Raptors</th>
<th>Scavengers</th>
<th>Ecosystem engineers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>Includes wetland, estuarine, coastal, marine</td>
<td>2,3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>3 main habitat</td>
<td>Carrion</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1,2,3</td>
</tr>
<tr>
<td>2 secondary habitat</td>
<td>Mammal</td>
<td>2,3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>1 occasional habitat</td>
<td>Bird</td>
<td>2,3</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>0 not used</td>
<td>Reptile</td>
<td>2,3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Food Source</td>
<td>Fish</td>
<td>2,3</td>
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<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>0 not eaten</td>
<td>Other aquatic vertebrates</td>
<td>2,3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Terrestrial invertebrates</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Freshwater invertebrates</td>
<td></td>
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<td></td>
<td></td>
<td>3</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Marine invertebrates</td>
<td>2,3</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td></td>
<td>Fruits</td>
<td>2,3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Seeds</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Nectar</td>
<td>1,2,3</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Other plant parts</td>
<td>2,3</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Engineering</td>
<td>Makes cavities or burrows; or has large or highly colonial nests</td>
<td>1</td>
<td></td>
<td></td>
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</table>

Species data and functional groups

The distributional data for the selected bird species were collated from the Southern African Bird Atlas Project (SABAP, Harrison et al. 1997), which provides the most comprehensive information available on the distribution of bird species in southern Africa (van Rensburg et
al. 2002). The surveys took place from 1988 to 1992 using expert-vetted checklist returns collected at the end of each month (Allan et al. 1997). All vagrant and recent ‘new’ species (whose distributional data was not captured during the time of the SABAP collection) were excluded from the analyses. For coastal cells, only species that frequent the coastline (and are thus members of the ‘nutrient dispersers’ functional group, Table 1) were included. There was no discernment between native and exotic species. Overall, 826 species were used and distributed into nine functional groups (Table 1). Functional group assignments were determined using life-history and ecological data from the compiled Robert’s VII bird species database (Hockey et al. 2005). Each species could belong to multiple functional groups.

**Protected and unprotected matched pair selection**

A protected cell was considered one in which the area under formal protection was greater than the extent of agricultural land (protected area / agricultural area > 1). Conversely, an unprotected cell was one in which there was no land under formal protection while the amount of agriculture was considerable relative to that of the protected cell (difference >30%). ‘Agriculture’ in this study is an integrated measure of both irrigated and dryland farming practices (sensu Fairbanks et al. 2000). The basic sampling unit of this analysis is the quarter degree grid cell (15 min × 15 min; ~25 km × ~25 km), which is at a broader scale than that of the experimental ‘manipulation’ (agricultural land use at a local scales). Thus, the analysis avoids the pseudoreplicative problems that arise when the treatment encompasses many sample units (reducing them to subsamples, Hurlbert 1984). Land-use patterns across South Africa and Lesotho were assessed using data from the National Land-cover Database project (NLC, Fairbanks et al. 2000). The land-cover information was mapped directly from a series of 1:250 000 scale, geo-referenced Landsat TM images captured between 1994 and 1996 (Figure 1, appendix). The location and extent of protected areas within South Africa and
Lesotho were determined through a composite geographic layer of both private and governmental protected areas (Rouget et al. 2004, Figure 2, appendix). Potential matched pairs were chosen manually by scrutinising the degree of congruence of five criteria: the amount of agricultural land in the putative unprotected cell (the ‘treatment’ level), the extent of the reserve area in the putative protected cell (the ‘null’ level), similar numbers of checklists in each cell, similarities in the climatic regime of each cell (temperature and rainfall variables), and similarities in the topography of each cell. The null hypothesis that the matched pairs had checklist, climatic and topographic differences of zero was assessed through matched t-tests on these variables. Cells with less than 10 checklists are unreliable (Harrison et al. 1997, van Rensburg et al. 2004) and so were not considered for selection. Climatic and topographic data were obtained from the topographic and climatic database for Africa (Hutchinson et al. 1995), compiled by the Centre of Resource and Environmental Studies of the Australian National University.

By using matched pair t-tests as the predominant statistical tool in this study I hoped to avoid the confounding effects of continuous ecological gradients, such as the energy-area relationship (Bonn et al. 2004), which have been shown to exist for the South African avifauna (van Rensburg et al. 2002) and that have the ability to confound analyses based on generalised linear models (Rodríguez-Estrella 2007). Matched t-tests are more robust than student’s t-test because there is no assumption on the homoscedasticity of variances, which more often bedevils analyses in the biological sciences than does the assumption of normality (Chinn 1996). Through analysing differences variables based on functional group richness, I have also avoided the parameterisation problems associated with binary format data (La Sorte & McKinney 2007, Fischer et al. 2008).
Permutations

In order to assess the differences in functional structure between protected and unprotected areas, matched pair t-tests were performed for each functional group as well as aggregate species and functional richness (the latter being the sum of all functional attributes present in a cell). These tests were run in Statistica 8 (Statsoft, Inc. 2004) and, unless otherwise stated, all difference variables were normally distributed (Zar 1999). Even though the data were in matched pair format (and thus intrinsically controlled) it was possible for subsamples of the data to leverage the results. Thus, permutations of the data were analysed in an attempt to break any confounding linkages among pairs as well as to test different hypotheses. A preliminary power analysis suggested that the matched pair test statistic remains significant down until a sample size of 50 pairs (Figure 3, appendix). Given the stringent matching criteria, coupled with the patchy distribution of agricultural land-use and protected areas (Figures 1,2), such a sample size was not possible for all permutations. However, I was interested in the relative difference in functional structure between protected and unprotected landscapes, meaning that slightly lower average sample sizes should not have altered the interpretation of the results.

The most comprehensive set of permutations were those based on ‘quality scores’. Each matched pair was scored on how well they maximised the ‘treatment’ (agriculture to protected area ratio) while minimising the potentially confounding variance of differential sampling effort as well as climatic and topographic variability between pairs. The penalties for these scores were derived not only from the magnitude of the difference for each variable but also from their relative consistency within the sample. For the latter criterion, penalties were more severe when difference values exceeded the standard deviation of the difference mean. These scores were used to divide the data into four quality groups and analysed separately. Cluster analysis is also used to minimise intra-group variance (Quinn & Keough...
A cluster analysis using Ward’s linkage algorithm and standardised Euclidean distances was run on checklist, climatic and topographic variables. Four clusters were identified from the dendrogram and analysed separately.

Additionally, permutations were run that focused on specific aspects of the data. For climatic and topographic variables, the 50 ‘best matched’ and ‘worst matched’ pairs were run as separate permutations. Both agricultural (cells over 60%) and protected area (cells >50%) extent were maximised in separate permutations to test for threshold effects of functional group richness. Differential sampling effort could produce spurious threshold effects in the data. Thus, several permutations were run that analysed only pairs with average checklists numbers over 100 and again over 200 (see Figure 4 below for justification) as well as pairs whose difference in checklist number was minimised. The effects of agricultural transformation can interact with biome type to produce qualitatively different patterns of avian distribution (Fairbanks et al. 2002). Separate permutations were run on data within each biome (sample size permitting) as well as biome boundaries (‘ecotones’, van Rensburg et al. 2004).

Spatial autocorrelation is a common phenomenon in ecological datasets (Dormann et al. 2007). Although I address this problem in more formal analyses (see below), I used spatial clustering as two permutation categories. In the first category, a cluster analysis was run on the geographic coordinates of the matched pairs. A suitable cut-off was determined heuristically through analysing the plateau of a linkage distance against amalgamation plot. The centroid pairs of the resultant clusters were then collected and analysed. Additionally, the data from each cluster were pooled and the means and standard deviations of each cluster were analysed separately. Secondly, correlograms were used to determine the sampling grain of each functional group, which was then used to select spatially independent pairs for analysis.
The last main type of permutation was a randomisation test. The data were shuffled five times to produce random groupings of mixed matching ‘quality’. These groups were then analysed separately.

**Confounding variance**

The interpretation of these analyses, although designed to minimise the effects of confounding variance, may still be influenced by broad-scale gradients or patterns not detected by univariate analyses. Firstly, differential sampling could undermine the comparison of avian communities since the species richness of a cell positively correlates with the number of checklists in that cell ($r=0.53$, $p<0.05$, $n=1956$, Figure 4). However, this relationship appears to saturate at high checklists numbers (Figure 4). The correlation is far stronger with low checklist numbers ($r_s = 0.76$, $p<0.05$, $n=1677$ for checklists per cell $<100$; $r_s = 0.19$, $p>0.05$, $n=173$ for checklists per cell between 100 and 200; and $r_s = 0.11$, $p>0.05$, $n=106$ for checklists per cell above 200, Figure 4). To incorporate this relationship into the sampling phase, pairs were more stringently matched if their checklist numbers were less than 100. Another potentially confounding property of differential sampling effort is temporal consistency. Checklists were collected at the end of each month (Harrison et al. 1997), which meant that pairs could have significantly different temporal distributions of checklist densities. The seasonal differences in species richness could, therefore, bias results (Erasmus et al. 2002). This possibility was assessed by performing a one-way ANOVA on the temporal distribution using ‘protected’ versus ‘unprotected’ as a categorical predictor.
Avian species richness has been shown to correlate positively with human population density in South Africa (Chown et al. 2003). I tested the null hypothesis that both protected and unprotected grid cells possessed, on average, similar amounts of urban land-use using a matched pair t-test. I also tested the null hypothesis that degraded land was more common in unprotected cells, stands of natural vegetation were more widespread in protected cells and that water bodies were similarly distributed between both protected and unprotected landscapes.

The distribution of avian species richness in South Africa is strongly influenced by environmental variables and habitat diversity (van Rensburg et al. 2002, 2004). To test whether the members of each pair had similar environmental characteristics, the broad-scale,
interactive effects of climate and topography were assessed using a one-way ANOVA. The means, standard deviations, minimums and maximums of rainfall, temperature and topography were first compared in a correlation matrix. As expected, there were significant correlations between all variables (-0.73< r<0.94, all p<0.05, n=234). Such collinearity inflates the chance of committing a Type I error in parametric analyses (Quinn & Keough 2002). To reduce collinearity, the variables were entered into a Principal Component Analysis (PCA) to extract composite orthogonal variables. The number of components to retain was determined by a combination of the latent-root criterion, scree plot analysis and broken stick criteria (Jackson 1993). All three tests suggested extracting the first two components, which together accounted for 73.6% of the variation in the sample. The component scores for each component were then entered into an ANOVA model as independent variables.

Both agricultural and reserve land-use are patchily distributed across South Africa (Figs 1,2), making variability in land-use extent between pairs unavoidable. Too much variability in treatment levels may confound the true effect of the treatment at broad spatial scales (sensu Pascual et al. 2001). Thus, the variance in extent of both agricultural and protected areas between sites was explicitly analysed. The variances used in the analysis were calculated as the squared distance of each observation from its variable mean (Zar 1999). Furthermore, the fluctuating distance between members of a pair might compound the variability of treatment levels. In lieu of this, the distance (km) between members of a pair was added as another predictor variable. All three variables were then entered into a multiple regression analysis using species richness as a null response variable. In all multivariate models, the fit of the model was assessed through an inspection of the plot of residuals against predicted values and abnormal leverage of individual cases was assessed through Cook’s D statistic (Quinn & Keough 2002).
Spatial autocorrelation leads to the non-independence of samples and the potential for inflated Type I error (Diniz-Filho et al. 2003). In order to assess the degree to which the data were spatially structured, I used a combination of spatial correlation and generalised least squares modelling (GLS) in Spatial Analysis for Macroecology (SAM, Rangel et al. 2006). Spatial correlation adjusts the degrees of freedom, according to Dutilleul’s (1993) method, to compensate for pseudoreplication across space. I used spatial correlation to assess the spatially independent relationship of land-use types with each functional group using pooled data (both members of a pair treated as independent samples). I used GLS-based models to assess spatial structure in the difference variables of the matched pair format, which was appropriate because the difference variables of each functional group had a normally distributed error structure. GLS-based methods are regressions in which the spatial component is explicitly modelled in the residuals (Dormann et al. 2007). These residuals are then decomposed into spatially structured error and error resulting from ‘noise’. In the case of simultaneous autoregressive models (SAR), the spatially structured error is then incorporated into the parameter estimates directly (Rangel et al. 2006). SAR was run for each functional group using geodesic coordinate data. Variogram modelling was used to assess the spatial sampling extent of each functional group (for use in the matched pair analyses). Moran’s I coefficients (from correlograms) were used over semivariograms because they are statistically robust and because they can be calculated for multiple distance classes (Tiefelsdorf 2000). The area of each grid cell, per se, was unlikely to be a confounding variables in these analyses as all grid cells are approximately equal in area. Analyses were run at two different scales (pooled versus matched pair format) to look for both overall trends as well as specific spatial structure in the paired samples.
Results

Matched pair analyses

Figure 5. A map of South Africa showing the matched pair sample of quarter degree grid cells. Agriculturally transformed cells are in black while protected area cells are in grey. Map boundaries denote biome types.

Overall, 117 matched pairs were selected (n=234 grid cells, Fig. 5). Agricultural land-use covered an average of 39.9±18.6% of unprotected cells while nature reserves covered an average of 31.4±27.8% of protected cells. Matched pairs contained similar numbers of checklists per cell (an average of 85±75 and 88±85 checklists per cell for unprotected and protected cells respectively). The average difference in checklist numbers between all pairs was 3±36. For pairs with an average checklist number of less than 100 the average difference was only 1±14.
Protected areas contained more species than agricultural lands in only 74% of the observations. The other 26% of observations showed that species richness was higher in the agricultural landscape (Difference = -27±20, t_{30}=-7.55, n=3, Figure 6). The extent of reserve area in the protected cells does not correlate significantly with the difference in species richness or the richness of any of the functional groups (average $r^2=2.1±1.2$, all $p>0.05$, all $n=31$). Similarly, the difference in the extent of agriculture between protected and unprotected cells could not explain the patterns of difference in species or functional group richness (all $r^2<0.05$, all $p>0.05$, all $n=117$). Thus, neither the variability in protected area

**Figure 6.** A map of South Africa showing the distribution of the agriculturally transformed cells that displayed higher species richness than their protected cell counterparts. Map boundaries denote biome types.
extent nor the variability of net agricultural extent in the unprotected cell was confounding the above results.

The matched t-test analyses were run in 51 separate permutations (Table 2, appendix). Table 3 displays a summary of these permutations by providing the average difference values, standard deviations, test statistics and significance of the runs. Although the aggregate variables of species and functional richness showed significantly higher values in the protected cells of the matched pairs in about two thirds of the permutations (66% and 60% respectively), different functional groups exhibit highly idiosyncratic responses to agricultural transformation (net significant decrease in agricultural cells ranges from 6% to 92%, Table 3). Scavengers and raptors most often exhibit a decrease in richness following agricultural conversion (92% and 80% of the permutations respectively). Nutrient dispersers and grazers show very little amounts of significant loss in agricultural lands (6% and 8% of the permutations respectively), often displaying significantly positive increases in richness in unprotected cells (n=9 permutations). Seed dispersers and granivores also show fewer losses in agricultural landscapes than declines in species richness would suggest (32% and 20% negative responses for seed dispersers and granivores respectively). Engineers, insectivores and pollinators displayed similar amounts of loss to that of species and functional richness (Table 3). These patterns of gains and losses for each group are not an artefact of the sample size of each permutation as sample size does not significantly correlate with the number of ‘positive’ (significantly higher functional group richness in protected areas) outcomes for each permutation ($r^2=0.07$, $p>0.05$, $n=51$, Table 2). Neither does the species richness within each functional group determine the group’s probability of decline in an agriculturally transformed landscape ($r^2<0.01$, $p>>0.05$, $n=9$).
Although both scavengers and raptors displayed high levels of significant losses in agricultural lands (Table 3), the magnitude of these losses were far less than either species or insectivore loss (Table 7). In general, functional group richness showed significantly lower amounts of loss than species richness (47±32% compared to 67%, Chi-square goodness of fit: $X^2_{0.05,8}=175.4$, $p<<0.05$, n=9). The functional groups also displayed significantly lower variance in loss between matched sites than species richness did, as indicated by the standard errors (Chi-square goodness of fit: $X^2_{0.05,8}=375.1$, $p<<0.05$, n=9, Table 3). The majority of overall functional group loss arose from one particular functional group, the insectivores (Table 3, Fig. 7). The average species and insectivore loss in agriculturally transformed landscapes was 22±11 and 16±9 species and functional units respectively (Table 3, Fig. 7). The average loss in agricultural lands for the rest of the functional groups was only 2±2 functional units. However, although the insectivores show the greatest losses in agricultural landscapes, their relative signal of loss (measured by the ratio of average matched pair test statistic to the average difference value) was the weakest (13% compared to the scavengers’ 110%).
Table 3. Summary statistics for the matched pair t-tests run between protected and agriculturally transformed grid cells (n=117 pairs). ‘Net loss’ refers to the percent of permutations where the functional group was significantly higher in richness in the protected cell of the matched pair.

<table>
<thead>
<tr>
<th>Group</th>
<th>Difference</th>
<th>Standard deviation</th>
<th>Test statistic</th>
<th>Significance</th>
<th>Standard error of sample means</th>
<th>Standard error of permutation means</th>
<th>Net loss (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species richness</td>
<td>22 ± 11</td>
<td>40.9 ± 6.1</td>
<td>2.87 ± 1.51</td>
<td>0.12 ± 0.23</td>
<td>7.12 ± 5.47</td>
<td>0.79</td>
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<td>Functional richness</td>
<td>33 ± 20</td>
<td>73.3 ± 12.0</td>
<td>2.37 ± 1.41</td>
<td>0.17 ± 0.26</td>
<td>12.77 ± 9.80</td>
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<td>Seed dispersers</td>
<td>2 ± 2</td>
<td>5.6 ± 1.4</td>
<td>1.77 ± 1.83</td>
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<td>4.66 ± 0.74</td>
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<td>4 ± 3</td>
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<td>2.58 ± 1.46</td>
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<td>1.43 ± 1.10</td>
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<td>Nutrient dispersers</td>
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<td>0.37 ± 0.29</td>
<td>3.39 ± 2.60</td>
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<td>Insectivores</td>
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<td>29.9 ± 4.6</td>
<td>2.77 ± 1.56</td>
<td>0.12 ± 0.23</td>
<td>5.20 ± 4.00</td>
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<td>Granivores</td>
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<td>1.15 ± 0.88</td>
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<td>0.82 ± 0.63</td>
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<td>Engineers</td>
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<td>0.19 ± 0.30</td>
<td>0.65 ± 0.50</td>
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Figure 7. The average differences between protected and unprotected cells of each functional group (black columns). The average test statistic of the matched pair analyses for each functional group are also shown (grey columns). Error bars denote standard deviations.

The species richness within each functional group is a good indicator of the functional group’s response diversity (Elmqvist et al. 2003). When the average difference in richness between agricultural and protected areas of each functional group is plotted against the species richness of each functional group, functional group loss seems to strongly covary with species richness ($r=0.90$, $p<0.05$, $n=9$, Fig. 8). However, when we exclude the insectivores as an outlier, the species richness of each functional group is found to not affect the magnitude of loss in agricultural lands at all ($r=-0.09$, p $>0.05$, $n=8$, Fig. 8).
Figure 8. The relationship between the average loss of functional group richness in agricultural lands and each functional group’s total species richness. Insectivores (top graph) are a clear outlier in the relationship between the two variables.
Figure 9. A map of South Africa showing the different impacts that agricultural land-use has on functional group loss in different biomes. Black pie chart area represents the average proportion of functional groups that displayed significant decreases in agricultural landscapes. The size of the pie chart is proportional to the sample size of the analysis. Map boundaries denote biome types.

The effects of agricultural land-use on avian functional group richness are not homogenous across biomes (Chi square goodness of fit: $X^2_{0.05,5} = 97.5, p<0.05, n=6$). Figure 9 shows that in biomes with more structurally complex landscapes, such as savannahs and biome boundaries (Mucina & Rutherford 2006), agricultural transformation causes a proportionately greater loss of functional group richness (56% and 78% respectively). In structurally simpler biomes, such as grassland and nama karoo ecosystems (Mucina & Rutherford 2006), the level
of functional group loss in agricultural areas is far less (22% and 11% respectively). Furthermore, the most common groups that are lost from these structurally simple biomes are raptors and scavengers (67% of functional group richness loss).

**Sources of confounding variance**

The main concern of this analysis was controlling for differential sampling effort across grid cells. Overall, the differences between the protected areas checklist number and that of the agriculturally transformed lands were non-significant (Wilcoxon matched pair test: Z=0.27, n=117, p=0.79). Furthermore, the temporal distributions of checklist densities between protected and unprotected grid cells were highly similar (0.04 < F< sub>1,232 < 1.12, all p>>0.05, n=234). The ANOVA model satisfied the assumptions of homoscedasticity (0.04 < F< sub>1,232 < 2.38, all p>>0.05, n=234) as well as linearity of dependent variables (Kolmogorov-Smirnov test for normality: 0.06 < D < 0.11, all p>>0.05, all n=234).

Although I was testing the effect of agricultural ‘treatments’ on the functional structure of avian assemblages, it was possible for other land-use variables to confound the effect of the treatment. However, neither the distribution of urban developments or of water bodies within the landscape was significantly different between the matched pairs (Wilcoxon matched pair test: Z=0.91, p=0.37 and Z=1.71, p=0.08 respectively, both n=117). As expected, degraded land was significantly more extensive in agriculturally transformed cells (Wilcoxon matched pair test: Z=3.04, p<0.05, n=117), while the land-cover of natural vegetation was significantly more extensive in protected area cells (t< sub>1,16 >10.92, p<0.05, n=117). Interestingly, although protected landscapes clearly have more remaining natural vegetation (74.3±19.6%), agricultural landscapes still contain 48.6±21.3% of natural vegetation per cell. However, much of this ‘natural’ vegetation may consist of invasive species (Fairbanks et al. 2000).
Avian species richness correlates positively with rainfall and net primary productivity (van Rensburg et al. 2002). Although both mean elevation and temperature were not significantly different between matched pairs ($t_{116}=0.65$ and $-1.66$ respectively, both $p>0.05$, both $n=117$), there was a significant difference of $1.7\pm8.3$ mm in annual rainfall between the pairs ($t_{116}=2.16$, $p<0.05$, $n=117$). Protected cells had slightly higher amounts of rainfall, on average, than unprotected cells ($51.5\pm17.2$ mm compared to $49.8\pm15.4$ mm per annum respectively). Additionally, the ANOVA model showed that, although the composite climatic component 1 was highly insignificant between protected and unprotected areas ($F_{230}=0.96$, $n=234$, $p=0.33$), component 2 was significantly different ($F_{1,230}=5.26$, $n=234$, $p<0.01$). However, component 2 only accounted for 2% of the variation between the samples ($F_{1,232}=5.64$, $r^2=0.02$, $p=0.02$). Overall, component 1 captured 55% of the total variance of the climatic and topographic variables while component 2 captured 19% of the total variance (Eigenvalues = 3.27 and 1.15 respectively).

To be able to convincingly test for the effect of agricultural transformation on the functional structure of avian communities the variability, per se, between pairs had to be assessed. All variables were lognormally distributed. Collinearity of the dependent variables were assessed through a correlation matrix. No predictor variables were significantly correlated ($-0.09 < r <0.08$, $n=117$, all $p>>0.05$). No value contributed disproportionately to the overall analysis (all $D_i<1$, max = 0.14). The plot of residuals against the predicted values of the response variable was uniformly distributed, which indicated homoscedasticity of variance among the predictor variables (Quinn & Keough 2002). Plots of residuals against the partial regression values of each dependent variable were also uniformly distributed. Thus, the model fitted the data well. Overall, the multiple regression model could not explain the distribution of the data ($F_{3,113} = 0.71$, $n=117$, multiple $r^2=0.02$, $p=0.55$). The null hypothesis that all partial regression slopes equal zero could not be rejected ($0.75< t_{113} <0.95$, $n=117$, all
p>>0.05). I also reran the analysis including the potential interaction of distance between pairs and variance in land-use extent. To avoid the obvious collinearity inherent in using lower order terms to produce a multiplicative interaction the predictor variables were first centred (by subtracting their mean from each observation, Quinn & Keough 2002). Once again the model failed to fit the response variable ($F_{3,113} = 0.70$, $n=117$, multiple $r^2=0.01$, $p=0.54$) and no partial regression coefficients were significant (-1.26$< t_{113}<$1.28, $n=117$, all $p>>0.05$). Thus, the inherent variance in the land-use predictors, as well as the distance between members of a pair, had little influence on the results.

Spatial autocorrelation can manifest to varying degrees at different scales of ecological phenomena (Legendre 1993). To test for broad scale spatial structure in the data, both protected and unprotected sites were pooled. Table 4 (appendix) shows the relationship of each functional group with agricultural and protected area extent. Moran’s $I$ coefficients (absolute value) and associated p-values were averaged across 14 distance classes. Significance values were determined using Monte Carlo simulations ($n=10000$, Rangel et al. 2006). When the covariance of spatial structure is taken into account, no functional group besides nutrient dispersers, grazers and scavengers significantly correlate with the land-use variables (Table 4).

Although spatial autocorrelation exists for most functional groups when looking at the pooled data per se, the effect of spatial structure is far less pronounced when looking at the difference variables. Table 5 (appendix) shows that space in itself is a poor predictor of the differences in functional richness between pairs. Both the coefficient of determination and Akaike’s Information Criterion (AIC) were better fits holding space constant than when space was included as an explicit predictor in all functional groups (Table 5: $R^2$ and AIC for predictors alone / space included). Indeed, no functional group displayed positive or negative autocorrelation consistently throughout the range of the sample (all average Moran’s $I$
coefficients $< 0.08$, $0.16 \pm 0.14 < p < 0.60 \pm 0.28$). Figure 10 shows that the difference variables of nutrient dispersers, grazers, raptors and scavengers are particularly robust to spatial structuring ($0.02 < \text{Moran's } I \text{ coefficient } < 0.03$, all $p > 0.41$, all $n=117$).

![Figure 10. The average Moran’s I spatial autocorrelation coefficient for each functional group across 12 distance classes. Values above the dotted line are significantly autocorrelated.](image)

Interestingly, when the matched pair t-tests are adjusted for the range of spatial autocorrelation, almost no functional groups besides the scavengers, raptors and pollinators (less often) are significantly negatively affected by agricultural transformation (Table 2). This result is not an artefact of increased variability between spatially distant samples (sensu Fairbanks 2004) because the standard deviations of the samples are not significantly different ($-1.04 < t_{116} < 1.19$, all $p > 0.05$, all $n=117$).
Discussion

The relationship between the loss of species and the loss of functional group richness in an agricultural landscape is not straightforward. Overall, most functional groups are less negatively affected by agricultural transformation at a landscape level than species themselves (Fig. 7). Furthermore, all functional groups, besides the insectivores, appear to respond independently of response diversity (indicated by the species richness of each functional group) to agricultural transformation of the landscape. The nutrient disperser and grazer functional groups were richer, on average, in agriculturally transformed cells (Table 3, Fig. 7), which echoes the results of Fairbanks et al. (2002) who found that there was a significantly positive relationship between high levels of transformation and avian species diversity. Raptors and scavengers were the only functional groups to be consistently negatively affected by agricultural transformation (Tables 2-5). Thus, protected areas act as important reservoirs of functionally important upper trophic species that might otherwise be lost from agricultural landscapes. In general, however, the finding that the average amount of loss per functional group is little to none in agricultural landscapes (besides insectivores, Figs. 7,8), combined with the lack of strong spatial structure in the difference variables (Table 5, Figs. 6, 10), means that conservationists can more confidently use agricultural landscapes as part of extended and effective functional reserve networks.

The winners and losers of agriculturally-transformed landscapes
Clearly, species themselves are the most numerically hard hit by agriculture (Fig 7). However, in a surprising number of cases, species richness was higher in agricultural landscapes (Fig. 6). Such a result immediately suggests that, at a landscape scale, agricultural transformations may not be as detrimental to avian communities as they are at local scales (Chamberlain & Fuller 2000, Hughes et al. 2002). Insectivores almost exactly tracked the patterns of loss displayed by species richness (Table 2) and accounted for most of the observed functional group richness loss (Fig. 7). This result is congruent with Sekercioglu et al. (2002) who found that insectivores are particularly sensitive to the effects of habitat fragmentation. Insectivores, furthermore, appear to be the only functional group whose probability of decline in an agricultural landscape is a function of species richness (Fig. 8). Thus, in current reserve networks, where maximising species richness is a primary goal (Myers et al. 2000), insectivores are likely to be maximised as well. Although not perfectly tracking the patterns of species loss, pollinators showed an overall proportion of loss identical to species and insectivore loss (Table 2,3). Pollinators rely on highly connected and integrated systems that allow the existence of specialist interactions (Kolasa 2005). Thus, the fragmentary and homogenising effects of agriculture are likely to interrupt these fine-scale interactions (Sekercioglu 2006). Once again, reserve networks designed for species richness are likely to sample more pollinator richness than agricultural landscapes do at present.

The most consistent losers in agricultural lands are raptors and scavengers (Table 1-5). Scavengers are one of two functional groups to exhibit a test statistic that is higher in signal strength than the actual difference value (Table 3, Fig. 7). These results suggest that higher order trophic levels are most susceptible to the effects of agricultural conversion of habitat, as trophic cascade hypothesis predicts (Dobson et al. 2006). Furthermore, the high stability of raptor and scavenger functional group loss throughout all permutations of the data (80% and 92% respectively, Table 2) means that the signal of such loss overrides broad-scale
climatic and topographic gradients, to which the South African avifauna is known to respond strongly (van Rensburg et al. 2002). These observations provide evidence for the fact that agricultural transformation is causing a significant shift towards lower order trophic groups (sensu Duffy 2003), with the subsequent community consequences associated with the loss of top predators (Finke & Denno 2004, Schmitz et al. 2004). Losses of species from upper trophic levels are likely to ramify not only ecologically but economically as well because these species usually generate disproportionately greater revenue from ecotourism (Dobson et al. 2006). Protected areas, then, have a hugely important role to play in preserving raptor and scavenger functional group richness.

While many papers have focused on the species or functional groups that are adversely affected by agricultural transformation of the landscape, few have provided empirical evidence of those groups that respond positively to the same transformations (Jones et al. 2005). Recently, Okes et al. (2008) have documented the expansion of many species of generalist waterfowl into the arid, western parts of South Africa following the instalment of artificial water sources that are associated with agricultural development. This study directly supports their results by showing that nutrient dispersers and grazers (predominantly waterfowl, Sekercioglu 2006, Hockey et al. 2005) are often richer on agricultural lands than they are in protected lands (Table 3, Figs. 5,6,8). These results are not an artefact of there being more water bodies in agricultural lands because both protected and unprotected cells had similar distributions of water bodies. It may be possible, however, that water bodies in agricultural landscapes exhibit greater spatial regularity, are less ephemeral and are relatively free from predators, which makes them ideal habitats in an otherwise stochastic environment. Interestingly, the results of Okes et al. (2008) show that, although there has been a general gain of generalist species in the western parts of the country, there has been a simultaneous loss of more specialist species from the eastern parts of the country due to the destruction of
natural wetland areas caused by agricultural transformation. This is undoubtedly true when looking at species per se but our results demonstrate that this species loss bears little impact on functional group richness at the scale of landscapes across South Africa. This finding is similar to that of Fonseca and Ganade (2001) who discovered that a loss of 75% of species richness from a plant community still did not result in the extinction of a functional group. Lemoine et al. (2007) found that wetland birds in the Lake Constance regions of Central Europe increased in prevalence, despite agricultural intensification, due to dispersal from a single large nature reserve in the region. Such a scenario is not possible in the essentially random spatial arrangement of this study (Fig. 4, appendix). Thus, I argue that it is agricultural intensification itself that has led to the increase in nutrient dispersers and grazers. Consequently, agricultural landscapes may have increasingly important roles to play in the conservation of functional groups that operate across the water-terrestrial ecotone as climate change alters the distribution and availability of natural water bodies (Arnell 1999).

It is interesting to note that the species richness of every functional group, besides the insectivores, did not seem to determine its probability of being negatively affected by agricultural transformation (Fig. 8). Schweiger et al. (2007) also found that the species richness of each hoverfly functional group in Europe does not correlate with its probability of extinction in agricultural landscapes. Similarly, Dunne et al. (2002) found that the food-web structure of terrestrial and aquatic ecosystems are largely independent of the species richness of the community. Since the species richness data used in this study were collected consistently through time and were free from seasonal bias, these results bring into question the usefulness of the insurance effect of species richness on ecosystem functioning (sensu Walker et al. 1999, Loreau et al. 2003) as well as the general causality of biodiversity on functional diversity (Elmqvist et al. 2003, Tscharntke et al. 2005, Schweiger et al. 2007, Cumming & Child, in review).
Overall, the magnitude of difference in functional group richness loss between protected and unprotected areas is not likely to be a major concern for conservation practitioners (Table 3, Fig. 7). Instead, it is encouraging to see that the potential may exist for agricultural landscapes to support functional ecosystems (Poiani et al. 2000). What is worrying, however, is the systematic impact of agriculture on key functional groups (raptors and scavengers) across broad spatial extents (Table 4,5, Fig. 10), thereby significantly reducing the resilience of these functions across scales (Peterson et al. 1998, Elmqvist et al. 2003). Furthermore, if raptors and scavengers are repeatedly adversely affected by agricultural conversion of habitat there may be dire consequences for ecosystem stability and evolutionary dynamics (Olden et al. 2004). Such selective impacts on certain functional groups are unlikely to be detected when simply using species or functional richness as composite indicators of ecosystem ‘integrity’ (sensu De Leo & Levin 1997, Pinto et al. 2008, Table 3). Thus, conservationists should begin to use process-oriented metrics of biodiversity routinely in reserve planning exercises (Cumming & Child, in review).

**Using agriculture-reserve landscapes in integrated conservation plans**

Unfortunately, protected areas often exclude portions of habitat that are necessary to maintain ecological processes (Sanderson et al. 2002, Hansen & DeFries 2007). Although much thought has gone into conservation planning based on representation of species ‘hotspots’ (Myers et al. 2000) or minimum ‘sets’ (Gaston et al. 2001), little progress has been made in producing functional agriculture-reserve mosaics across landscapes (Poiani et al. 2000, Cumming & Spiesman 2006). We as conservationists can no longer afford to fight for scraps of protected land; we must integrate and incorporate existing landscapes into conservation plans. In this study, 26% of agricultural landscapes possessed species richness greater than their protected landscape counterparts. These sites appear to be evenly distributed across
South Africa (Fig. 6), which could make their implementation into broad-scale reserve networks more beneficial to cross-landscape dynamics (Bengtsson et al. 2003). Furthermore, the spatially detrended results suggest that most functional groups (besides raptors and scavengers) are similarly distributed between protected and unprotected landscapes (Table 2). Thus, great potential exists for developing agricultural landscapes as functional landscapes that are complementary to established reserve networks. That the agricultural landscapes in this study contained an average of 48.6±21.3% natural to semi-natural land-cover (sensu Fairbanks et al. 2000), combined with the ability of avian species to use the vegetation structure of farmstead landscaping as habitat corridors (Daily et al. 2001, Hughes et al. 2002, Duelli & Obrist 2003), may facilitate the use of agricultural habitats by conservationists as functional connections in regional conservation plans. An explicitly process-oriented agri-ecosystem scheme, similar to the agri-environment scheme launched in the U.K. (Ovenden et al. 1998, Vickery et al. 2004), would go a long way toward preserving biodiversity at multiple scales by maintaining ecological and evolutionary connections over disparate landscape mosaics (Levin 2000, Poiani et al. 2000).

Foley et al. (2005) rightly contend that effective conservation requires management of landscape structure through the strategic placement of managed and natural ecosystems, so that the services of such natural ecosystems (pest control, pollination, reduced erosion, flood abatement and more) are available at key points across a landscape mosaic. For example, landscape management can take measures to ensure ‘functional insectivores’ aid agricultural systems in cost-effective manners (Jones et al. 2005). Raptors and scavengers can also be encouraged to return to agricultural landscapes through a cessation of poisoning (Boshoff & Vernon 1980, Davies 1999) and the regeneration of natural prey species in interlocking habitat types within farmlands (Settle et al. 1996). Through the return of both lower and upper trophic level functional groups into anthropogenically dominated lands, the extended
ecosystem (protected and unprotected landscapes) might provide a multi-scale, resilient mechanism of pest control (Peterson et al. 1998). Furthermore, by integrating two landscape mosaics, conservationists may be able reconnect key-resource areas that have been cut-off during the fragmentary process of agricultural conversion (Saunders et al. 1991).

However, the interaction between agricultural and protected landscapes can be mutually beneficial. Farms and agricultural matrices in general should be positioned such that they can become net source areas of functionally important species when stochastic events severely reduce functional group richness within protected areas. This study suggests that it may be possible for farmsteads to act as reservoirs for nutrient dispersers, grazers and granivores (Table 2). Indeed, Robinson et al. (2001) found that granivorous species were conserved more effectively on agricultural lands due to the year round provisioning of seeds from arable weeds and spilt cereal grains. The results from this study suggest the same might be possible for South African granivores (Table 3, Fig. 7,9). So long as ecologically relevant practices occur on agricultural patches, such as next boxes and microhabitat generation (Maestas et al. 2003, Pywell et al. 2002), farmsteads might provide climatic and stochastic refugia of functional diversity for protected areas. For example, the stability of resource provision of agricultural habitats may provide similar amelioration to the effects of climate change, by extending the temporal distribution of key food resources, as the reintroduction of grey wolves has done in Yellowstone National Park (Wilmers & Post 2006). The importance of such refugia is enhanced by the fact that protected areas tend to be late-successional habitats while agricultural habitats are necessarily early-successional (Tscharntke et al. 2005). Thus, the interaction between an agricultural and protected landscape constitutes a shifting mosaic of successional phases (Sutherland 2004). The impact of agriculture as a reorganising force for avian communities varies from biome to biome (Fig. 9). In regions that have high levels of structural complexity (savannahs and
biome boundaries, Mucina & Rutherford 2006) the loss of functional group richness is far more pronounced. In regions that have relatively simple vegetation layers and habitat types, such as the grassland and nama karoo biomes (Mucina & Rutherford 2006), the impact of agricultural conversion of ecosystems is met with a relatively low loss of overall functional group richness. Furthermore, the main functional groups lost from these latter biomes are raptors and scavengers (Table 2). These results directly support the textural discontinuity hypothesis (Holling 1992) as well as trophic cascade hypothesis (Dobson et al. 2006). It has previously been shown that the South African avifauna correlates positively with increased habitat complexity (van Rensburg et al. 2004) and that some biomes, such as the karoo biomes, support increased species diversity and evenness (Fairbanks et al. 2002). However, this is the first study, to the best of the authors’ knowledge, demonstrating that functional group richness not only responds in a similar manner but that the agriculturally affected groups can be accurately predicted.

Reserve networks that view protected areas as static and unmov ing bastions of biodiversity, insulated from the encroachments of humanity, are no longer tenable due to the synergistic effects of climate change and habitat loss (Sala et al. 2000). Conservationists must consider the ecological role of how reserve sites interact in space in relation to the long term persistence of functional ecosystems (Jiang et al. 2007). Therefore, identifying the biomes in which agricultural land-use can be co-opted into achieving more of the functional potential of the original ecosystems is essential in designing active and cost-effective conservation plans. For example, despite the grassland biome being South Africa’s most endangered habitat type (Neke and Du Plessis 2004), perhaps its conversion into agricultural land is more compliant with the persistence of ecological processes over landscapes than other biomes (such as savannahs) can be (Fig. 9).
This study has shown that agricultural and protected landscapes possess, on average, complementary functional group richness (Tables 1-5). By using both the similarities and differences in functional structure we might begin to bridge the biodiversity divide between these two landscape types. At local scales, natural areas and agricultural landscapes can be designed to be mutually beneficial to one another (Sutherland 2002). The same principle should apply to landscapes.

Conclusions

All global biodiversity scenarios focus mainly on changes in the richness and abundance of faunal taxa across landscapes (Cumming 2007). However, if we wish to truly envisage the impact of intensifying land-use practices on ecological communities we must understand its impact on spatially explicit, process-oriented metrics (Rouget et al. 2003, Cumming and Child, in review). In this study, I have controlled for differential sampling effort, climate, topography and spatial structure. The results have shown that agricultural transformation of the landscape impacts avian functional groups in qualitatively different directions. Scavengers and raptors are the most consistently adversely affected by agricultural transformation, whereas nutrient dispersers and grazers are the most consistently benefitted from agricultural practices. Moreover, once spatial structure is accounted for, raptors and scavengers (and possible pollinators) appear to be the only functional groups to be truly negatively affected by agricultural conversion at the landscape scale. Most functional groups, besides the insectivores, appear to be less negatively affected by agricultural land-use at a landscape scale than the average loss of species or species richness of the functional group would suggest (sensu Elmqvist et al. 2003). Furthermore, the original underlying vegetation structure also plays a large part in determining how detrimental agricultural transformation
will be to the functional richness of a community (Fischer et al 2008), which necessitates biome-specific conservation management practices.

Such results may have major implications for conservation planning. Whereas protected areas are clearly acting as reservoirs of functionally important upper trophic species, agriculturally transformed areas have the potential to safeguard aspects of functional diversity as well. Thus, by integrating aspects of agricultural landscapes into existing reserve networks (sensu Jiang et al. 2007) more multifunctional and resilient ecosystems will be fostered (Tscharntke et al. 2005). Although climate change is seen as increasingly major threat to biodiversity in South Africa (Erasmus et al. 2002, Williams et al. 2005), without understanding the functional dynamics of both intact and impacted landscapes, mitigating the effects of climate change will not ensure the persistence of functioning ecological communities in perpetuity.

Acknowledgments

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Literature cited


Appendix
Figure 1. A quarter degree grid cell layered map of South Africa showing the distribution of agricultural intensity. Note that cells containing over 50% agricultural land cover are patchily distributed.

Figure 2. A map of South Africa showing the distribution of composite protected areas. Map boundaries denote biome types.
Figure 3. The results of a power analysis showing that signal strength is strongest at sample sizes of >50 matched pairs. The horizontal dotted line denotes the significance cut-off (above the line all $p<0.05$).
Table 2. Combined results of the permuted matched t-tests between agriculturally transformed and protected sites. + signs indicate that the functional group was significantly higher in protected cells, - signs denote the opposite and n.d. means that there was no significant difference between the matched cells. The last row (percent ‘positive’ difference) denotes the percentage of permutations where the functional group was significantly higher in richness in the protected landscape.

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<td>-</td>
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<td>+</td>
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| Percent 'positive' difference | 67 | 61 | 31 | 67 | 6 | 67 | 18 | 8 | 80 | 92 | 59 |
Table 4. Results of the comparison between OLS and spatial regression analyses for functional groups at a broad scale. SAC = spatial autocorrelation. n* = degrees of freedom. All original n* = 232 and ‘corrected’ n* indicates the spatially appropriate n* used for analysis. Only nutrient dispersers, grazers and scavengers show significant relationships with land-use variables after spatial structure is accounted for.

<table>
<thead>
<tr>
<th>Group</th>
<th>Predictor</th>
<th>Moran’s I</th>
<th>SAC range (km)</th>
<th>SAC p-value</th>
<th>Pearson’s r</th>
<th>Spearman’s r</th>
<th>corrected n*</th>
<th>p-value</th>
<th>corrected p-value</th>
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<td>400</td>
<td>0.13±0.20</td>
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<td>0.21</td>
<td>126.1</td>
<td>0.13</td>
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<td></td>
<td></td>
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<td>Agriculture</td>
<td>0.06±0.06</td>
<td>200</td>
<td>0.17±0.25</td>
<td>-0.15</td>
<td>-0.16</td>
<td>86.1</td>
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<td>Agriculture</td>
<td>0.20±0.17</td>
<td>380</td>
<td>0.03±0.10</td>
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<tr>
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<td></td>
<td>0.19</td>
<td>86.8</td>
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<td>Agriculture</td>
<td>0.07±0.07</td>
<td>200</td>
<td>0.17±0.27</td>
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<td>0.20</td>
<td>162.9</td>
<td>0.01</td>
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<td>Agriculture</td>
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<td>400</td>
<td>0.10±0.22</td>
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<td>-0.11</td>
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Table 5. Results of the simultaneous autoregressive (SAR) models for each functional group. For both the coefficient of determination ($R^2$) and AIC the first value of the column is when space is included as an explicit predictor variable followed by the parameter estimate when the effect of space is held constant. The model was always a poorer fit when space was included as a predictor of functional group difference patterns.

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<th>SAC p-value</th>
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<td>0.93 / 0.55</td>
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