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DO TREE PLANTATIONS SUPPORT HIGHER SPECIES RICHNESS AND ABUNDANCE THAN PASTURE LANDS

Systematic Review

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Summary

1. Background

Increased worldwide demand for wood products, coupled with public concern over the loss or degradation of natural forests, has lead to a steady increase in plantation establishment throughout most regions of the world. Most of the world's new plantations are generally established on former agricultural lands that are often of declining economic value for grazing or cropping. There is an expectation that when established within intensively used landscapes, plantations can contribute positively to biodiversity conservation.

2. Objectives

We conducted a systematic global review of differences between timber plantations and pasture lands in terms of animal and plant species richness and abundance, and assessed the results using meta-analysis techniques. Our principle aim was to test the hypothesis that plantations contain higher species richness or abundance than pasture.

3. Methods

We searched multiple electronic databases and the internet using different combinations of Boolean search-terms. Search terms were run in separate or limited combinations depending on the requirements or limitations of the database used. We also obtained papers from colleagues and through reference lists from published studies including major review articles and books on plantations. Furthermore, we obtained information from some government studies and reports. Data were available for meta-analyses comparing the species richness and abundance of plantations and pasture lands for five taxonomic groups: plants, invertebrates, reptiles/amphibians, mammals, and birds. Studies that provided estimates of mean species richness and/or abundance, and the corresponding estimates of standard deviations and sample sizes, were included in the meta-analysis.

4. Main results

Our systematic literature search identified 1,967 articles of potential relevance to our study. Of these articles, 66 provided biological monitoring information for plantations

and pasture lands. Of these, 30 articles were excluded from the meta-analysis due to their lack of provision of information necessary for the analysis (eg. sample size, mean, or standard deviation). No articles were excluded due to problems with experimental design, which were not already excluded on other grounds. In total, 36 primary studies met our criteria for inclusion within the meta-analysis (Table 1). Studies varied widely in the information provided about factors affecting the species richness or abundance of different taxa within pastures and plantations. We were limited to assessing those factors that were consistently reported in the literature. The majority of studies provided multiple contrasts of species richness and/or abundance between pasture lands (control) and plantations (treatment). Some studies contrasted multiple treatments to a common control, and others contrasted multiple controls to a common treatment, hence creating divisions within studies.

Within each taxon there was considerable variation in the difference between species richness and abundance between plantations and pasture lands. Birds and reptile/amphibians exhibited significantly higher species richness, and mammals exhibited significantly higher abundance, in plantations than in pasture lands which lacked remnant vegetation. Reptile/amphibian species richness was significantly higher in plantations in general. No significant differences in species richness were found for mammals, plants, or invertebrates, and no significant differences in abundance were found for birds, reptiles/amphibians, invertebrates, or plants.

5. Conclusions

We found that for most taxa, plantations and pasture lands were not sufficiently consistent in their impact on species richness or species abundance to allow for general conclusions regarding their relative biodiversity value. Some taxa did have higher species richness or abundance in plantations than in pasture lands. However, it is only within the presence of taxonomic caveats (ie. reptiles/amphibians), or specific landscape features (ie. absence of remnant vegetation within pasture), that it can be concluded that plantations support higher species richness or abundance than pasture land. We emphasize that caution is warranted when making general statements about the inherent biodiversity value of diverse and broadly-defined land-uses.

Main Text

1. Background

Increased worldwide demand for wood products, coupled with public concern over the loss or degradation of natural forests (Lamb et al. 2001; Lindenmayer and Hobbs 2004), has lead to a steady increase in plantation establishment throughout most regions of the world (FAO 2007). Plantations are being established globally at a rate of 3 million ha per year (2000-2005, FAO 2006) and currently provide almost 50% of the world's wood production (FAO 2007). In some nations, plantations comprise a substantial proportion of national forest area (FAO 2006). The principle benefit of plantations is that they enable large volumes of wood products to be produced per unit of land area (Sedjo 1999), although their capacity to sequester carbon has made this land-use a potential contributor to climate change mitigation efforts (Laclau 2003; Miehle et al. 2006; Paul et al. 2008; Redondo-Brenes 2007).

There is a large literature assessing the relative biodiversity value of plantations versus natural forests (see Barlow et al. 2007; Hartley 2002; Lindenmayer and Hobbs 2004). In almost all cases, plantations contain fewer native fauna and flora relative to that found within natural forests, with a corresponding increased abundance and species richness of exotic species (Barlow et al. 2007; Hartley 2002; Lindenmayer et al. 2002). However, most of the world's new plantations are generally established on former agricultural lands (Sedjo 1999), that are often of declining economic value for grazing or cropping (Lamb et al. 2001). Under these circumstances, plantation establishment may provide both economic and environmental benefits. For instance, plantations can be used to sequester carbon and thereby reduce net greenhouse gas emissions (Jackson and Schlesinger 2004); lower water tables to help reduce dry land salinisation (Walker et al. 2002); and under some circumstances, relieve some of the pressure of timber demands from natural forests (Hartley 2002).

There is an emerging expectation that when established within intensively used landscapes (eg. agriculture), plantations can contribute positively to biodiversity conservation (Hartley 2002; Lugo 1997; Moore and Allen 1999). For instance, the flora and fauna of industrial scale plantations can compare favorably to that found within intensive land uses such as annual crop and pasture lands (Carnus et al. 2006; Hartley 2002; Moore and Allen 1999). For this reason, there has been promotion of the view that plantations provide higher environmental benefits, associated with increased biodiversity value, than agricultural landscapes (Moore and Allen 1999). We suggest that part of this expectation arises from plantations providing increased structural complexity relative to agricultural landscapes, which increases the variety of available resources upon which

greater species diversity can rely (August 1983; Brokaw and Lent 1999; McElhinny et al. 2005). There is empirical and theoretical support for the positive relationship between increasing structural complexity and increases in biodiversity (but see Erdelen 1984; MacArthur et al. 1966; MacArthur and MacArthur 1961; McElhinny et al. 2005). However, if increased structural complexity is to enable plantations to support higher species richness than agricultural areas, then this one factor must dominate other contributing factors to species richness, such as habitat heterogeneity and the presence of native versus exotic vegetation. If generalizations are warranted, and these are to be incorporated into environmental policy and planning, it is important that the form and direction of changes in species richness, abundance and composition associated with these land-uses are identified, as plantations are increasingly replacing a significant percentage of many nations' agricultural lands (Kanowski et al. 2005).

2. Objectives

In this paper our objective was to review existing evidence of how plantations and pasture lands influence species richness and abundance by summarizing the data from the literature using meta-analysis techniques. We formally synthesized the available evidence to test the following hypotheses for different taxonomic groups of flora and fauna,

1. That plantations support higher species richness than pasture lands.
2. That plantations support a high abundance of organisms than pasture lands.

After taking into account available explanatory variables to explain some of the between study variation.

3. Methods

3.1 Question formulation

The review topic was originally proposed by Charlie Zammit of the Department of Environment, Water, Heritage & the Arts, Australia in response to plans to treble the area of plantations in Australia. As the majority of this increase in plantation area would occur on pasture lands the question was refined to specifically address this land-use conversion. An argument for the proposed benefit of this scheme was biodiversity would increase, hence the basis for the question formulation.

3.2 Search strategy

We defined plantations as stands of trees with native or exotic species, created by the regular placement of cuttings, seedlings or seed, selected for their wood-producing potential and managed for the purposes of timber or pulp harvesting (modified from AFS

2003). We defined pasture as an area with natural or improved vegetation used for the grazing of livestock. We searched multiple electronic databases and the internet using different combinations of Boolean search-terms. The databases used were Dogpile (<http://www.dogpile.com/>), Google (<http://www.google.com.au/>), Google Scholar (<http://scholar.google.com.au/>), Web of Science (<http://www.isiwebofknowledge.com/>), and Scirus (<http://www.scirus.com/>). We used the following search terms in various combinations: (plantation* OR “planted forest*” OR afforestation OR “production forest*”) AND (agricult* OR meadow* OR crop* OR farm* OR grass* OR pastur* OR paddock* OR graz* OR field* OR range*) AND (biodiversity OR diversity OR richness OR abundance OR species OR bird* OR mammal* OR reptile* OR amphibian* OR frog* OR invertebrate* OR insect* OR arthropod* OR plant* OR flora OR fauna). Search terms were run in separate or limited combinations depending on the requirements or limitations of the database used. We also obtained papers from colleagues and through reference lists from published studies including major review articles and books on plantations (eg. Hartley 2002; Lindenmayer and Hobbs 2004; Moore and Allen 1999; Salt et al. 2004). Furthermore, we obtained information from some government studies and reports.

3.3 Study inclusion criteria

We sought data for meta-analyses comparing the species richness and abundance of plantations and pasture lands for five taxonomic groups: plants, invertebrates, reptiles/amphibians, mammals, and birds. Studies that provided estimates of mean species richness and/or abundance, and the corresponding estimates of standard deviations and sample sizes, were included in the meta-analysis.

Relevant studies included those which quantitatively compared species richness or abundance within plantation and pasture lands. Single species studies were not included to reduce the potential for publication bias in favour of those studies for which study species were more likely to show significant differences between the control and treatment. Natural experiments were considered the most likely source of data, whereby researchers use available plantations and pasturelands to compare taxa using species richness or species abundance for both treatment and control. Outcomes would by necessity be quantitative and all primary studies which report estimates of mean species richness or abundance, and the corresponding estimates of standard deviations and sample sizes, were considered for inclusion.

3.4 Study quality assessment

Variation in the scale of replication and the general quality of experimental design used in the primary studies has the potential to contribute to statistical differences in between-study results. This may result in misleading outcomes from the meta-analysis (Gates 2002), so we assigned each paper a data quality category as outlined in Table 1. Papers were excluded from analyses if they fell into category IV.

Table 1. Hierarchy of quality of evidence based on the information provided in research papers. Modified from Pullin & Knight (2003).

Category	Quality of evidence presented
I	Randomized controlled trial with matched pairs of treatments and controls, Study conducted at an adequate scale for subject taxa
II	Controlled trial of adequate scale for study organism. Unpaired treatments and controls.
III	Unpaired treatments and controls. Scale of study raises potential of confounding effects for the subject taxa considered.
IV	Evidence deemed inadequate due to inherent problems with experimental design.

3.5 Data synthesis

Due to variation in the number of suitable published studies for different taxa, our choice of how to group taxonomic categories for meta-analysis was by necessity a subjective compromise. The ecological distinctiveness of species contained within different analyzed groups varies, and this variation should be taken into consideration when interpreting results.

Data were available for meta-analyses comparing the species richness and abundance of five taxonomic groups in plantations and pasture lands: plants, invertebrates, reptiles/amphibians, mammals, and birds. Studies that provided estimates of mean species richness and/or abundance, and the corresponding estimates of standard deviations and sample sizes, were included in the meta-analysis. We tabulated the estimates of mean species richness and/or abundance, estimates of the standard deviations about the means, and the sample sizes. If an estimate of a standard deviation was not provided, it was calculated from the estimate of the standard error and sample size. In some cases, the estimate of the standard error was measured from error bars in the figures provided. This information is presented in forest plots which provide the means and 95%

confidence intervals for primary studies in a format which enables ready comparison with a common axis (Whitehead 2002).

For meta-analysis of studies with continuous measures such as species richness and abundance, a standardized difference between treatment means is typically used to summarize the findings of each study (Cooper and Hedges 1994, Whitehead 2002). This is done so that the quantitative findings from the different primary studies are in a standardized form that permits meaningful numerical comparison and analysis across studies. We used the statistic known as Hedges' g (Hedges and Olkin 1985) as a measure of effect size.

$$g = \frac{\bar{x}_1 - \bar{x}_2}{s_p} \times J$$

where \bar{x}_1 is the plantation species richness or abundance mean, \bar{x}_2 is the pasture land mean, s_p is the pooled standard deviation and J is a correction factor for small sample bias.

$$s_p = \sqrt{\frac{(n_1 - 1)s_T^2 + (n_2 - 1)s_C^2}{n_1 + n_2 - 2}}$$

$$J = 1 - \frac{3}{4(n_1 + n_2 - 2) - 1}$$

Where n_1 is the plantation sample size, n_2 is the pasture land sample size, s_1 is the plantation standard deviation and s_2 is the pasture land standard deviation.

The effect sizes (i.e. the standardized differences in mean species richness and abundance between plantation and pasture lands for each of the taxonomic groups) were analyzed using linear mixed models, which provide a flexible framework for meta-analysis, incorporating both fixed and random effect terms (Gurevitch & Hedges 1993, Stram 1996). These models allow for heterogeneity between studies in the effect of the treatment of interest. The heterogeneity is partly explained by fixed effects of study-level covariates, and partly by study-level random effects.

Studies varied widely in the information provided about study characteristics that may influence effect size. We were limited to assessing those factors that were consistently reported in the literature. Table 2 shows the covariates which we were able to extract. These variables were fitted as fixed effects to allow us to investigate and account for heterogeneity of effects across studies.

Table 2. Explanatory variables provided by primary studies and included in meta-analyses of species richness and abundance for plantations and pasture lands. Potential explanatory variables such as proximity of remnant vegetation, pasture grazing frequency, plantation tree densities, etc., were not provided consistently enough to allow analysis for any single taxa.

Explanatory variable	Description	Percentage of papers containing relevant information for explanatory variable				
		Birds	Mammals	Reptiles/ amphibians	Invertebrates	Plants
Climate	Dominant climate where study conducted (tropical, temperate, sub-tropical)	100%	100%	100%	100%	100%
Region	Geographic region where study conducted (Americas, Asia-pacific, Europe, Africa)	100%	100%	100%	100%	100%
Quality	Quality of evidence (see Table 1)	100%	100%	100%	100%	100%
Area	Area in hectares, used for plantation only	83%	73%	95%	87%	81%
Plantation age	Time since last tree planting	94%	100%	95%	97%	94%
Number of trees	Number of tree species planted in the plantation	100%	100%	100%	100%	100%
Native/ exotic	Planting of predominantly native or exotic tree species in the plantation.	100%	100%	100%	100%	100%
Remnant-veg pasture	Retention or absence of remnant vegetation in the pasture	27%	73%	55%	0%	23%
Remnant-veg plantation	Retention or absence of remnant vegetation in the plantation	31%	73%	85%	41%	35%

Study-level random effects were included to account for the effect of other unreported factors that may have contributed to differences in effects. The majority of studies provided multiple contrasts of species richness and/or abundance between pasture lands and plantations. Some studies contrasted multiple treatments to a common control, and others contrasted multiple controls to a common treatment, hence creating divisions within studies. This structure in the data meant that contrasts within a study or within a division within a study could not be assumed to be independent. Study and division within study were fitted as random effects to account for potential correlation between contrasts within a study or observations that used common treatments or controls within a study.

Fixed and random effects were estimated using residual maximum likelihood (REML) estimation (McCulloch and Searle 2001, Demidenko 2004). For each response variable, we started by fitting a model containing no fixed effects (i.e. only the mean) and study and division within study (division.study) as random effects. We then added the covariates that were available for all comparisons, and simplified these models using backwards stepwise selection. Finally, we added the incomplete covariates by fitting models to subsets of the data for which the covariate was available, and again simplified these models using backwards stepwise selection. The significance of fixed effects was assessed by computing scaled Wald statistics which were treated as having an approximate F distribution (Kenward and Roger 1997). The significance of variance components (random effects) was assessed using likelihood ratio test statistics. These were treated as being distributed approximately as chi-squared random variables (McCulloch and Searle 2001, Demidenko 2004). Non-significant effects were not included in the models. The fit of the final model for species richness and abundance for each taxonomic group was assessed by checking diagnostic plots of residuals for normality, constant variance and outliers.

For models that did not contain significant covariates, the average effect size was estimated, along with a 95% confidence interval, and the scaled Wald statistic was obtained to assess whether the average effect was different from zero. For models that did contain significant covariates, the average effect size was estimated for each level of the significant factor, along with a 95% confidence interval, to allow us to assess whether the effects were different from zero.

It is common in meta-analysis to assume that the within-study variation is estimated accurately for each study and can be treated as if it was known, for example, the DerSimonian and Laird model (DerSimonian & Laird 1986). In the majority of the studies we have considered here, the amount of replication was low, so the estimates of standard deviations were imprecise. In view of this, we decided not to assume that the standard error of each contrast was known. It is also common to use the amount of replication for each contrast to weight the contrasts in the analysis. Because of the differences in the types of experimental units in different studies, this could have given

inappropriately high weight to a few studies. We decided to give equal weight to each study.

It is also common in meta-analysis to test for heterogeneity of treatment effects across studies. Due to the nature of ecological studies, we did not expect there to be a consistent difference in biodiversity between plantations and pastures and hence we expected heterogeneity. We accounted for this heterogeneity by fitting available study-level covariates as fixed effects and study and division within study random effects to account for the effect of unreported factors.

Overall our results do not support the hypothesis that plantations (regardless of taxa or caveat) have higher species richness or abundance than pastures. So we do not think that it is necessary to provide the number of studies showing no effect that would need to be missing from the meta-analysis in order for the result to no longer be statistically significant (fail safe numbers). For each response variable, we first fitted a model containing only the mean and tested to see if the average effect size was significantly different from zero. We then added covariates to the model, initially fitting a model including only the covariates that were available for all observations, and then added the incomplete covariates by fitting models to subsets of the data for which the covariates were available.

We initially began our analysis using the software package MetaWin (Rosenburgh et al, 2000), a specialized package designed to conduct meta-analyses. However, MetaWin did not allow us to account for the correlation of contrasts within a study, or within a division within study, nor did it allow us to fit more than one covariate in the model. Meta-analysis using linear mixed models does not require specialist software and can be done using standard statistical software (Sheu & Suzuki 2001). We used functions available in GenStat (Payne et al, 2007) to fit our models.

4. Results

4.1 Review Statistics Our systematic literature search identified 1,967 articles of potential relevance to our study. Of these articles, 66 provided biological monitoring information for plantations and pasture lands. Of these, 30 articles were excluded from the meta-analysis due to their lack of provision of information necessary for the analysis (eg. sample size, mean, or standard deviation). No articles were excluded due to problems with experimental design (ie category IV), which were not already excluded on other grounds.

As our inclusion criteria were unambiguous, and any paper that provided the statistics necessary for the conduction of a meta-analysis was included, we did not see the need to use multiple assessors. As such no kappa statistics could be used to test the repeatability of inclusion decisions applied by different assessors. In total, 36 primary articles met our criteria for inclusion within the meta-analysis (Table 3).

Concern may remain regarding the potential issue of publication bias, which can result in the suppression of whole studies based on the lack of statistical significance. It is of principle concern when the meta-analysis shows strong effects as this could be due to studies that did not find strong effects not being published and hence included in the synthesis. To counter these issues, meta-analyses often include a test of publication bias (ie by using funnel plots). We have not done so here for several reasons. First, we were dealing specifically with multi species responses, not single species responses. In such studies, a range of responses is expected depending on the taxa considered which thereby reduces the motivation for authors to suppress study outcomes. Second, the studies that we looked at showed a range of effect sizes, with the confidence intervals for many studies containing zero (as shown in the forest plots provided below). For the 10 different response variables, there was no evidence of a difference for 7 of the response variables. We also emphasize that for the majority of the taxa groupings considered; the number of studies assessed fell far below that necessary for tests of publication bias to be even potentially useful. Furthermore, there are numerous shortcomings with tests of publication bias. For a discussion of these issues please see Lau et al. (2006).

Table 3. Summary table of primary studies, sample sizes, and explanatory variables for comparison of bird species richness and abundance in plantation and pasture lands used in the meta-analysis.

Author	Taxa	Region	Control sample size	Treatment sample size	Climate	Remnant-veg pasture	Remnant-veg plantation	# trees planted	Native exotic	Plantation age	Plantation size
(Borsboom et al. 2002)	Birds, mammals, reptiles/ amphibians, plants	Asia-pacific	3	2, 3	subtropical	no remnant	no remnant	1	native	1,3,16,40	6, 7, 17
(Catterall et al. 2004)	Birds, invertebrates	Asia-pacific	5	5,10	Tropical, subtropical	unknown	no remnant, unknown	1 to 13	native	7, 10, 60	6
(Cremene et al. 2005)	Invertebrates, plants	Europe	5	3	Temperate	unknown	unknown	1	native	20	12
(Cunningham et al. 2005)	Invertebrates	Asia-pacific	4	4	Temperate	unknown	remnant	1	native	5	78, 325
(Downie et al. 1996)	Invertebrates	Europe	3	3	temperate	unknown	unknown	1	exotic	37.5	unknown
(Eggleton et al. 2005)	Invertebrates	Europe	16	16	temperate	unknown	unknown	1	native	unknown	100
(Freemark et al. 2002)	Plants	Americas	10	9	temperate	unknown, remnant	unknown	1	native	unknown	unknown
(Garcia et al. 1998)	Birds	Americas	15	2,5,6	temperate	unknown	unknown	1,3	Exotic native	unknown	unknown
(Hanowski et al. 1997)	Birds	Americas	8	12	temperate	unknown	unknown	1	exotic	5,6	10
(Hicks and McCaughan 1997)	Invertebrates	Asia-pacific	4	4	temperate	unknown	unknown	1	exotic	unknown	unknown
(Hobbs et al. 2003)	plants	Asia-pacific	4	4	temperate	unknown	remnant	1	native	5	325
(Igboanugo et al. 1990)	plants	Africa	3	3	tropical	remnant	unknown	2	exotic	15	13.37
(Kanowski et al. 2006)	Reptiles/ amphibians	Asia-pacific	5	5, 10	Tropical, subtropical	unknown	no remnant, unknown	1, 13	native	7, 10, 60	6
(Klomp and Grabham 2002)	Birds	Asia-pacific	3	3	temperate	unknown	unknown	1	native	4	11
Lindemann, D.B. unpublished data	Birds, mammals, reptiles/ amphibians	Asia-pacific	10	10	temperate	remnant	remnant	1	exotic	5	10000
(Loyn et al. 2007)	Birds	Asia-pacific	25	58	temperate	remnant	remnant	1	native	6	2
(Maccherini and De Dominicis 2003)	Plants	Europe	30	30	temperate	unknown	unknown	2	exotic	26	13
(Moss et al. 1979)	Birds	Europe	3	3,4,5	temperate	unknown	unknown	1	exotic	6	6,300 to 8,900

(Munro et al. 2009)	Birds, reptiles/ plants	mammals, amphibians,	Asia-pacific	3, 6	2	temperate	no remnant, remnant	no remnant	1	native	3	8
(O'Connor 2005)	plants		Africa	3	3	temperate	unknown	unknown	1	exotic	12	unknown
(Oxbrough et al. 2006)	Invertebrates	Europe	8	8	temperate	unknown	unknown	1	exotic	5	unknown	
(Paquet et al. 2006)	Birds	Europe	41	34	temperate	unknown	unknown	1	native	16	unknown	
(Petit et al. 1999)	Birds	Americas	4	4	tropical	remnant	unknown	1	native	23	unknown	
(Pik et al. 1999)	Invertebrates	Asia-pacific	5	5	temperate	unknown	unknown	1	native	4	3.5	
(Powers et al. 1997)	Plants	Americas	4	4	tropical	unknown	unknown	1	Native, exotic	7	0.25	
(Proctor et al. 2003)	Invertebrates, plants	Asia-pacific	5	5, 10	tropical subtropical	unknown	no remnant unknown	1,13	native	10, 60, 7	6	
(Rossi 2003)	Birds, Mammals	Asia-pacific	6	13, 17	temperate	unknown	unknown	1	Exotic, native	18	unknown	
(Rossi and Blanchart 2005)	Invertebrates	Asia-pacific	5	5	tropical	unknown	unknown	1	exotic	8	unknown	
(Rotenberg 2007)	Birds	Americas	16	40	tropical	remnant	remnant	1	exotic	10	unknown	
(Schnell et al. 2003)	Invertebrates	Asia-pacific	5	5	temperate	unknown	unknown	1	native	10	3.5	
(Shakir and Dindal 1997)	Invertebrates	Americas	5	5	temperate	unknown	unknown	1,3	exotic	65,75	unknown	
(Thompson and Townsend 2004)	Invertebrates	Asia-pacific	3	6	temperate	unknown	unknown	1	exotic	30	unknown	
(Townsend et al. 1997)	Invertebrates	Asia-pacific	2	2	temperate	unknown	unknown	1	exotic	30	2510	
(Vallan 2002)	Reptiles/ amphibians	Africa	2	3	tropical	unknown	unknown	1	exotic	unknown	unknown	
(Wilson and Sykes 1988)	Invertebrates	Asia-pacific	5	5	temperate	unknown	unknown	1	exotic	75	unknown	
(Yeates and Saggard 1998)	Invertebrates	Asia-pacific	3, 10, 40	3,10,40	temperate	unknown	unknown	1	exotic	2, 13, 14, 25	2	

4.2 Species richness

Figures 1-5 display forest plots of the differences in species richness between plantations and pasture for birds, reptiles/amphibians, mammals, invertebrates, and plants. For birds, mammals, invertebrates and plants (Figures 1, 3, 4 and 5) there was a range of responses from positive to negative. Note that the most extreme responses also had wide confidence intervals. For reptiles/amphibians (Figure 2) there were no extreme negative responses.

Table 4 displays the results from the linear mixed models fitted to species richness for the five taxonomic groups. For bird species richness, the model fitted to all data did not contain any significant covariates. The estimated average effect size was not significantly different from zero; average effect size=0.45 (95% CI; -0.31, 1.20) ($p=0.27$) indicating that bird species richness was not significantly greater in plantations than pasture lands. Note that there was significant correlation between effect sizes within studies ($p<0.001$) suggesting that there was unexplained heterogeneity between studies. For the subset of studies where it was reported whether or not pastures included remnant vegetation, there was a significant effect of presence or absence of remnant vegetation ($p=0.001$), as well as an effect of the quality of study ($p=0.018$). The estimated average effect size for studies in which the pasture did not include remnant vegetation was 2.02 (95% CI: 1.12, 2.93) indicating that species richness was 2 standard deviations higher in plantations than pastures that did not include remnant vegetation. The estimated average effect size for studies in which the pasture did include remnant vegetation was -0.92 (95% CI: -1.82, -0.01) indicating that species richness was 1 standard deviation lower in plantations than pastures that included remnant vegetation. For higher quality studies, the estimated average effect size was 1.52 (95% CI: 0.60, 2.44) indicating that species richness was 1.5 standard deviations higher in plantations than pastures. For lower quality studies, the estimated average effect size was -0.42 (95% CI; -1.34, 0.50). The confidence interval includes zero indicating that in these lower quality studies there was no difference in species richness between plantations and pastures.

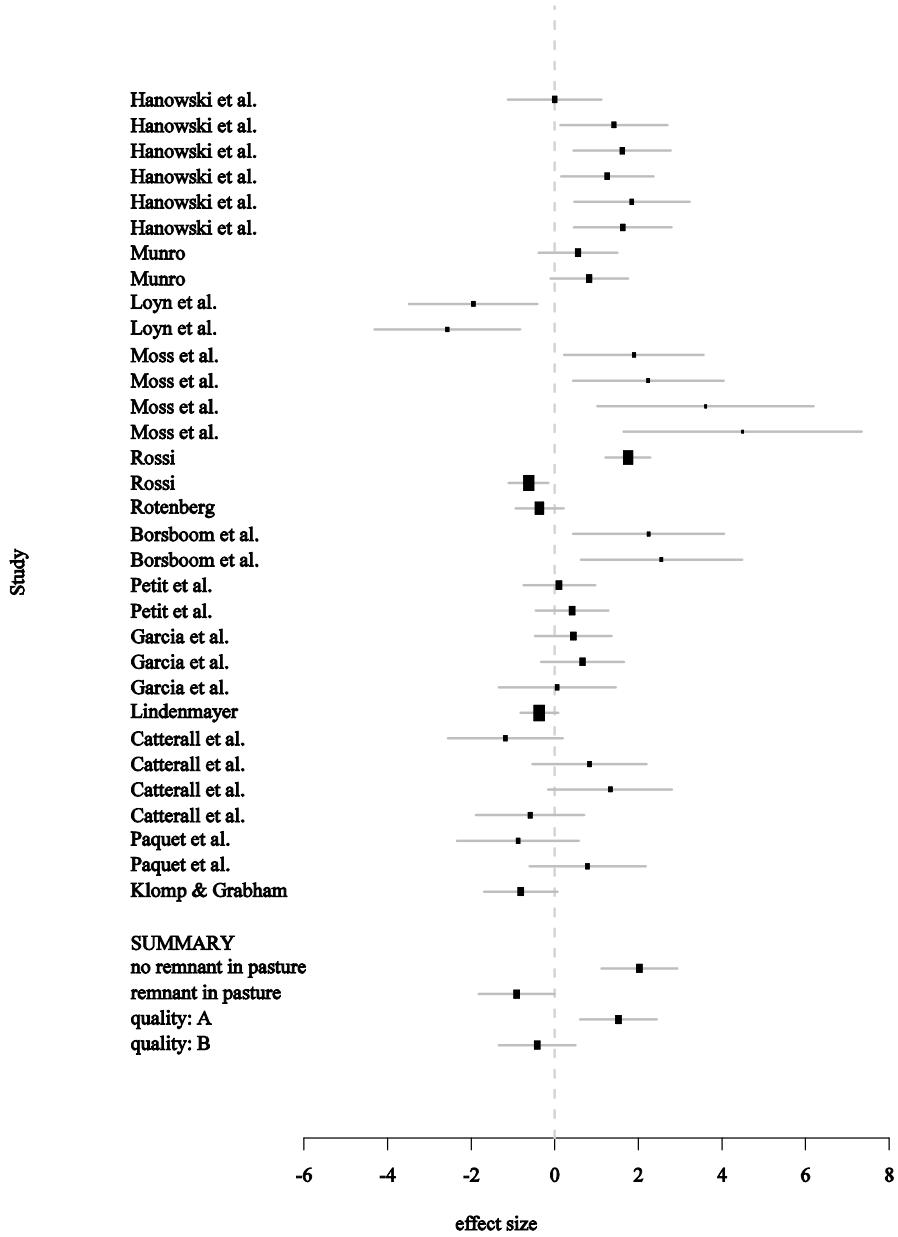


Figure 1. Forest plot of effect sizes for bird species richness (standardized differences in bird species richness between plantations and pastures) based on 13 independent studies. The dashed vertical line represents no difference. Box area is proportional to precision (1/variance) and error bars are equivalent to 95% confidence intervals. The summary outcome indicates the estimated average effect size for each level of the significant

factor, along with a 95% confidence interval, to allow us to assess whether the effects were different from zero.

For reptile/amphibian species richness, the model fitted to all data did not contain any significant covariates. The estimated average effect size was significantly different from zero ($p<0.001$); the estimated average effects size was 1.24 (95% CI; 0.72, 1.73) indicating that the species richness was 1.24 standard deviations higher in plantations than in pastures. For the subset of studies where it was reported whether or not pastures included remnant vegetation, there was a significant effect of presence or absence of remnant vegetation ($p=0.002$). Species richness was an estimated 2.06 (95% CI; 0.68, 3.43) standard deviations higher in plantations than in pastures that did not contain remnant vegetation. However there was no significant difference (95% CI; -1.94, 0.81) in species richness between plantations and pastures that did contain remnant vegetation.

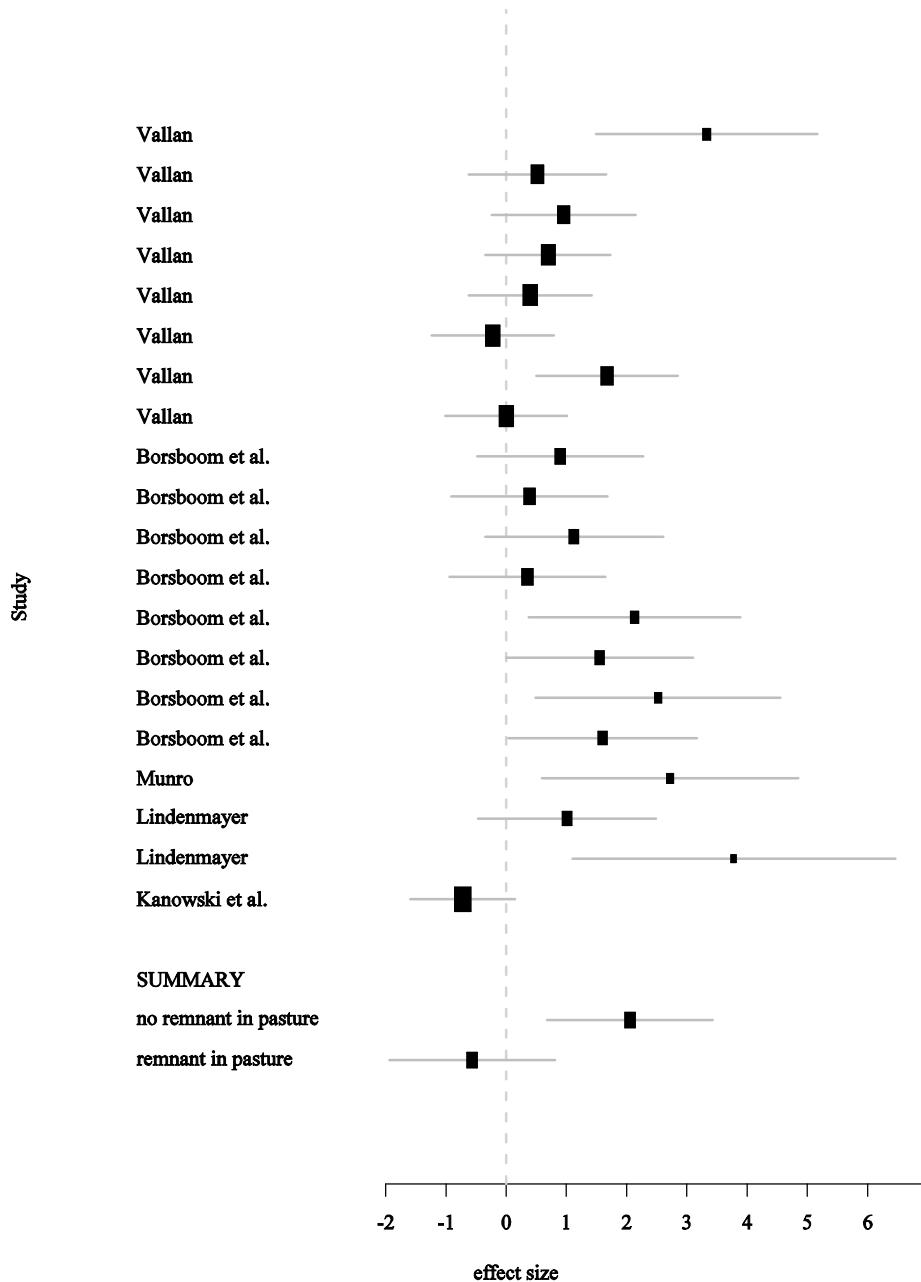


Figure 2. Forest plot of effect sizes for reptile/amphibian species richness (standardized differences in bird species richness between plantations and pastures) based on 5 independent studies. The dashed vertical line represents no difference. Box area is

proportional to precision (1/variance) and error bars are equivalent to 95% confidence intervals. The summary outcome indicates the estimated average effect size for each level of the significant factor, along with a 95% confidence interval, to allow us to assess whether the effects were different from zero.

For mammal species richness, none of the available covariates were significant. However there was significant correlation between effect sizes within division within studies ($p=0.01$) suggesting that there was unexplained heterogeneity between divisions within studies. The estimated average effect size (0.75, 95% CI; -0.49, 1.98) was not significantly different from zero ($p=0.29$) indicating that there was not a significant difference in mammal species richness between plantations and pastures.

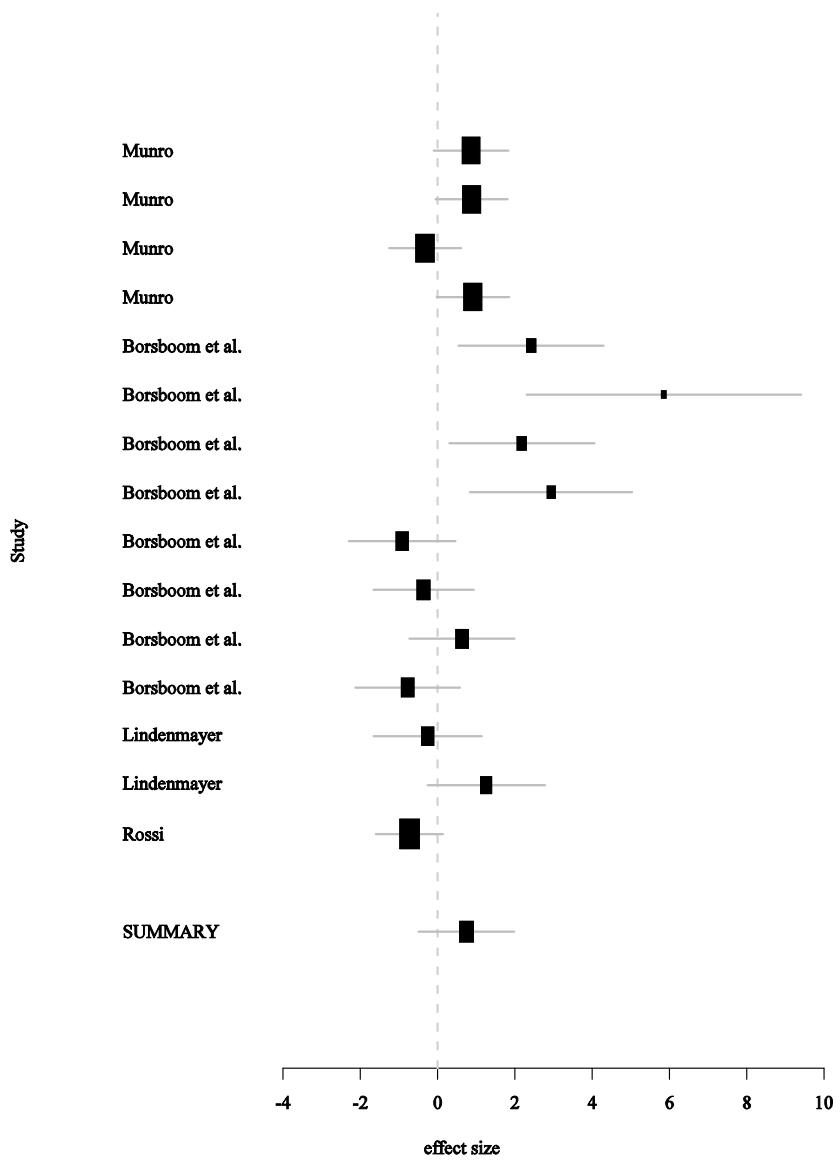


Figure 3. Forest plot of effect sizes for mammal species richness (standardized differences in bird species richness between plantations and pastures) based on 4 independent studies. The dashed vertical line represents no difference. Box area is proportional to precision (1/variance) and error bars are equivalent to 95% confidence intervals. The summary outcome indicates the estimated average effect size, along with a 95% confidence interval, to allow us to assess whether the effects were different from zero.

For invertebrate species richness, none of the available covariates were significant. However, there was significant correlation between effect sizes within studies ($p<0.001$) suggesting that there was unexplained heterogeneity between studies. The estimated average effect size (0.02, 95% CI; -1.06, 1.10) was not significantly different from zero ($p=0.97$) indicating that there was not a significant difference in invertebrate species richness between plantations and pastures.

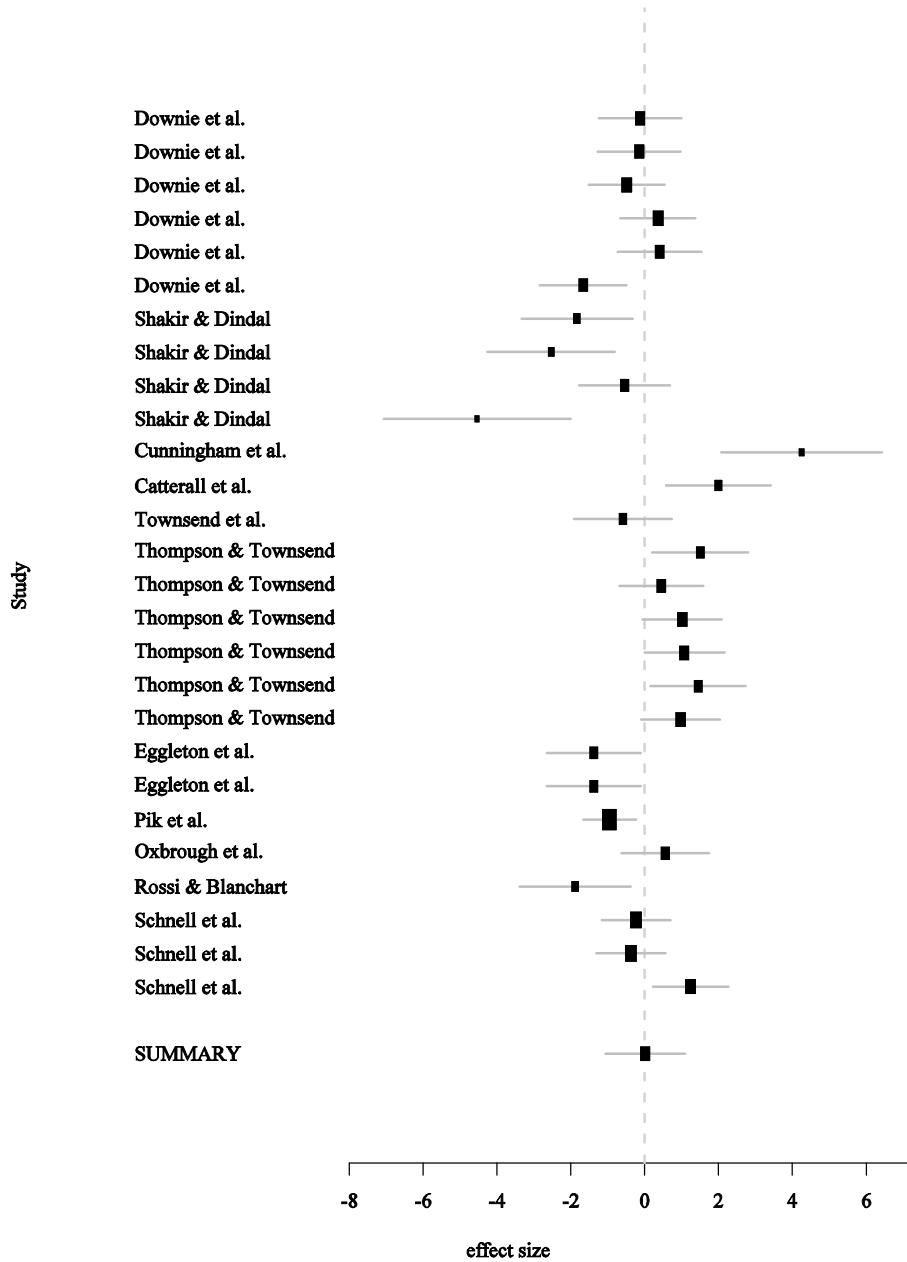


Figure 4. Forest plot of effect sizes for invertebrate species richness (standardized differences in bird species richness between plantations and pastures) based on 11 independent studies. The dashed vertical line represents no difference. Box area is proportional to precision (1/variance) and error bars are equivalent to 95% confidence intervals. The summary outcome indicates the estimated average effect size, along with a

95% confidence interval, to allow us to assess whether the effects were different from zero.

For plant species richness, none of the available covariates were significant. However there was significant correlation between effect sizes within divisions within studies ($p<0.001$) suggesting that there was unexplained heterogeneity between divisions within studies. The estimated average effect size (0.43, 95% CI; -0.59, 1.45) was not significantly different from zero ($p=0.42$) indicating that there was not a significant difference in plant species richness between plantations and pastures.

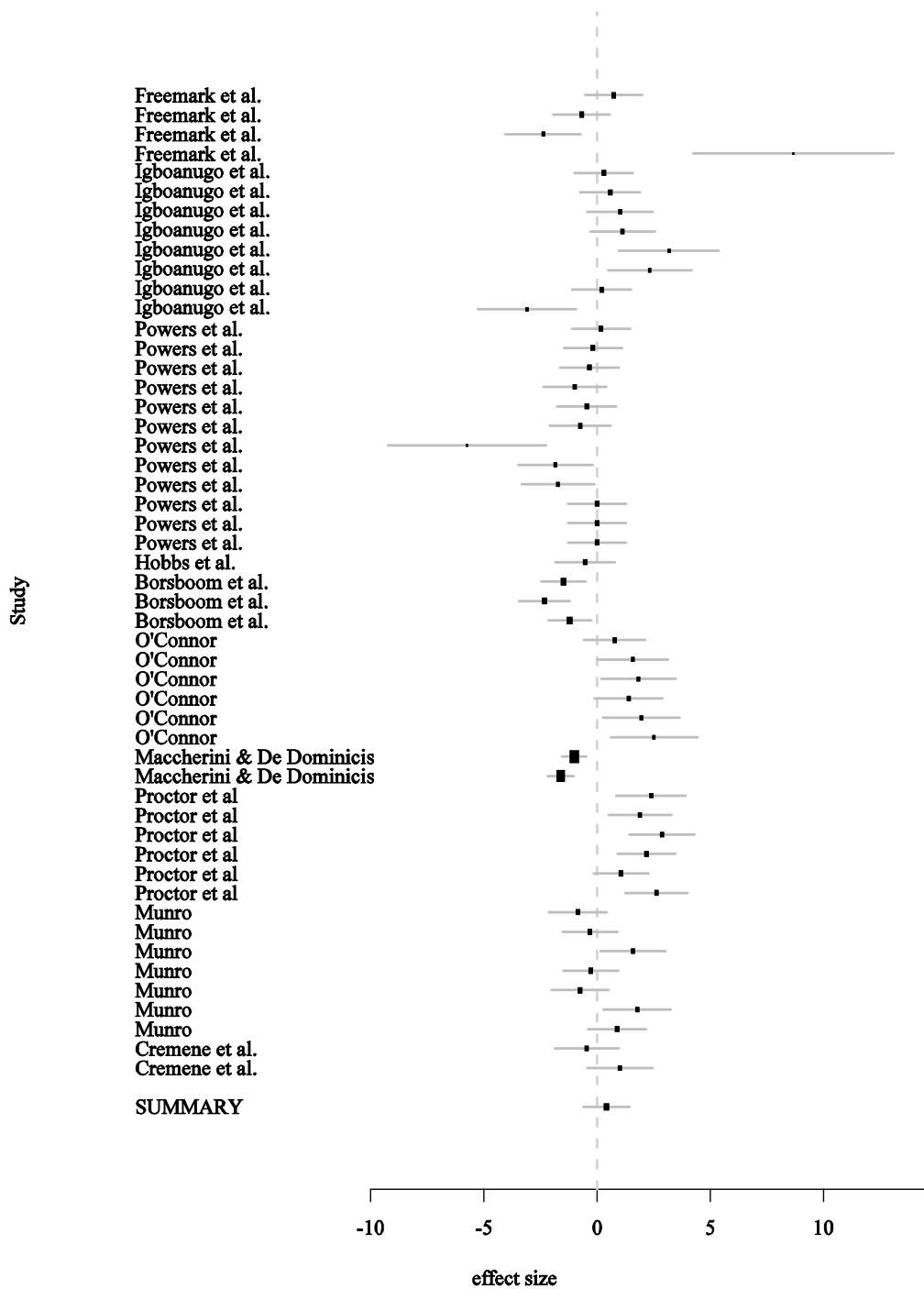


Figure 5. Forest plot of effect sizes for plant species richness (standardized differences in bird species richness between plantations and pastures) based on 10 independent studies.

The dashed vertical line represents no difference. Box area is proportional to precision (1/variance) and error bars are equivalent to 95% confidence intervals. The summary outcome indicates the estimated average effect size, along with a 95% confidence interval, to allow us to assess whether the effects were different from zero.

Table 4. Results of the models fitted for species richness for the 5 taxonomic groups.

taxa	number of studies	number of comparisons	random effects			fixed effects						average effect size	95% CI		
			random term	likelihood			scaled Wald statistic	adjusted df	P value	fixed term					
				estimate	SE	ratio statistic									
birds	13	32	study	1.53	0.79	12.98	<0.001	mean	1.33	12.1,1	0.27		0.45 (-0.31,1.20)		
			residual	0.8	0.26										
subset	6	12	residual	1.14	0.54			rem. veg pasture	20.84	9,1	0.001	no remnant	2.02 (1.12,2.93)		
								quality	8.33	9,1	0.018	remnant	-0.92 (-1.82,-0.01)		
												I	1.52 (0.60,2.44)		
												II	-0.42 (-1.34,0.50)		
Rep/amphi	5	20	residual	1.4	0.46			mean	21.76	19,1	<0.001		1.24 (0.72,1.76)		
subset	3	11	study.division	0.55	1.37	9.41	0.002	rem. veg pasture	22.28	7.6,1	0.002	no remnant	2.06 (0.68,3.43)		
			residual	0.18	0.1			quality	8.33	9,1	0.018	remnant	-0.57 (-1.94,0.81)		
mammals	4	15	study.division	1.78	1.46	6.05	0.01	mean	1.4	5.3,1	0.29		0.75 (-0.49,1.98)		
			residual	1.29	0.59										
invertebrates	11	27	study	2.77	1.53	11.51	<0.001	mean	0	9.5,1	0.97		0.02 (-1.06,1.10)		
			residual	0.87	0.31										
plants	10	51	study.division	4.39	1.8	14.65	<0.001	mean	0.67	16.4,1	0.42		0.43 (-0.59,1.45)		
			residual	1.55	0.4										

4.3 Abundance

Figures 6-10 display forest plots of the differences in abundance between plantations and pasture for birds, reptiles/amphibians, mammals, invertebrates, and plants. For all taxonomic groups, there was a range of responses from positive to negative. Note that the most extreme responses also had wide confidence intervals, except in the case of bird abundance (Figure 6).

Table 5 displays the results from the linear mixed models fitted to abundance for the five taxonomic groups. For bird abundance, the model fitted to all data did not contain any significant covariates. There was significant correlation between effect sizes within studies ($p<0.01$) suggesting that there was unexplained heterogeneity between divisions within studies. The estimated average effect size (-0.95, 95% CI; -2.70, 0.80) was not significantly different from zero ($p=0.32$) indicating that there was not a significant difference in bird abundance between plantations and pastures.

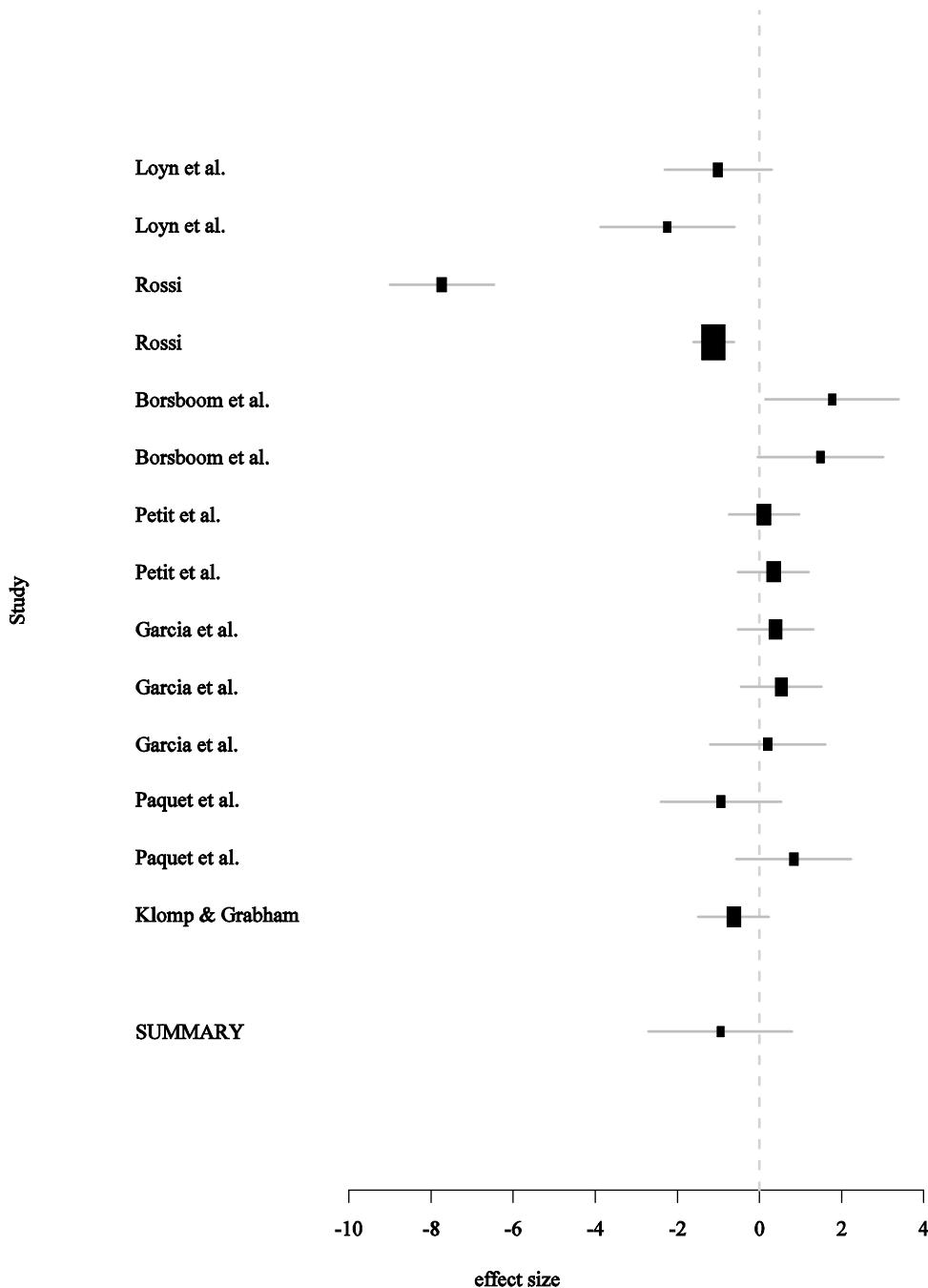


Figure 6. Forest plot of effect sizes for bird abundance (standardized differences in bird species richness between plantations and pastures) based on 7 independent studies. The dashed vertical line represents no difference. Box area is proportional to precision (1/variance) and error bars are equivalent to 95% confidence intervals. The summary

outcome indicates the estimated average effect size, along with a 95% confidence interval, to allow us to assess whether the effects were different from zero.

For reptile/amphibian abundance, the model fitted to all data did not contain any significant covariates. The estimated average effect size (1.96, 95% CI; -0.03, 3.95) was not significantly different from zero ($p=0.14$) indicating that there was no significant difference in reptile/amphibian abundance between plantations and pastures.

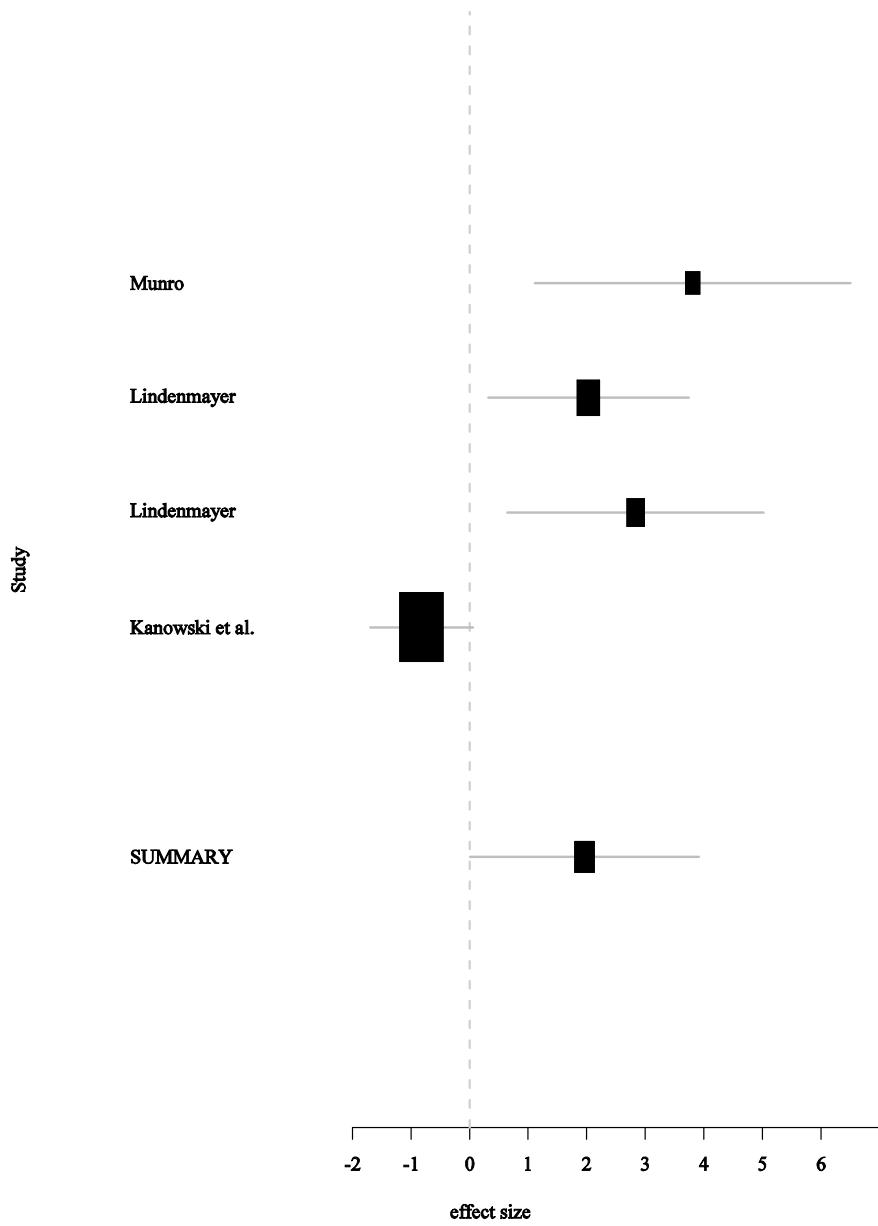


Figure 7. Forest plot of effect sizes for reptile/amphibian abundance (standardized differences in bird species richness between plantations and pastures) based on 3 independent studies. The dashed vertical line represents no difference. Box area is proportional to precision (1/variance) and error bars are equivalent to 95% confidence intervals. The summary outcome indicates the estimated average effect size, along with a 95% confidence interval, to allow us to assess whether the effects were different from zero.

For mammal abundance, the model fitted to all data did not contain any significant covariates. The estimated average effect size (0.16, 95% CI; 0.13, 2.18) was not significantly different from zero ($p=0.06$). For the subset of studies where it was reported whether or not pastures included remnant vegetation, there was a significant effect of presence or absence of remnant vegetation ($p<0.05$). The estimated average effect size for studies in which the pasture did not include remnant vegetation was 1.83 (95% CI: 0.92, 2.74) indicating that mammal abundance was almost 2 standard deviations higher in plantations than pastures that did not include remnant vegetation. Whereas the estimated average effect size for studies in which the pasture did include remnant vegetation was -0.52 (95% CI: -1.43, 0.97). The confidence interval includes zero indicating that there was no difference in mammal abundance between plantations and pastures that included remnant vegetation.

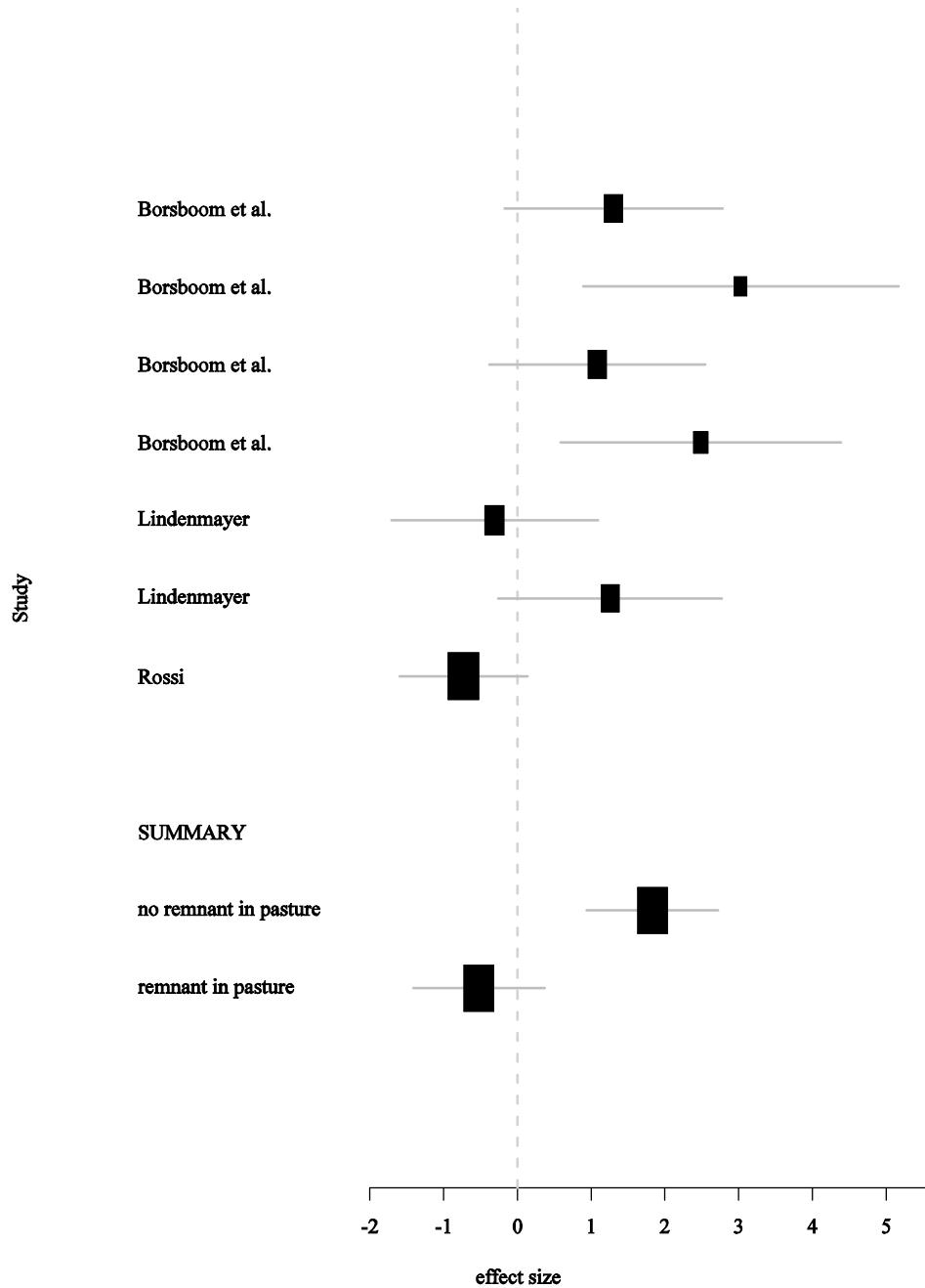


Figure 8. Forest plot of effect sizes for mammal abundance (standardized differences in bird species richness between plantations and pastures) based on 3 independent studies. The dashed vertical line represents no difference. Box area is proportional to precision (1/variance) and error bars are equivalent to 95% confidence intervals. The summary

outcome indicates the estimated average effect size for each level of the significant factor, along with a 95% confidence interval, to allow us to assess whether the effects were different from zero.

For invertebrate abundance, none of the available covariates were significant. However, there was significant correlation between effect sizes within studies ($p<0.001$) and within divisions within studies ($p<0.001$) suggesting that there was unexplained heterogeneity between studies and between divisions within studies. The estimated average effect size - 1.54 (95% CI; -3.70, 0.62) was not significantly different from zero ($p=0.2$) indicating that there was not a significant difference in invertebrate abundance between plantations and pastures.

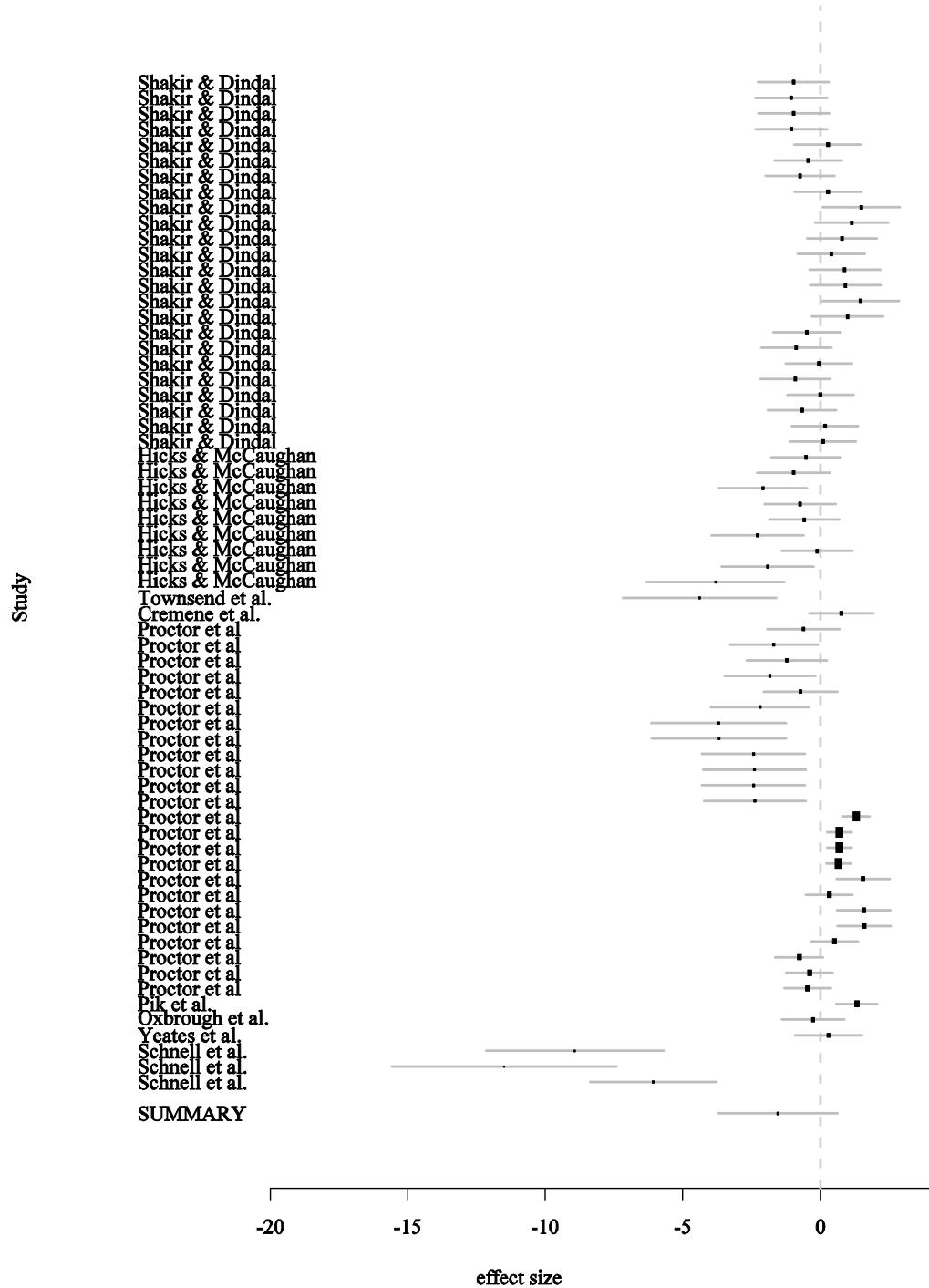


Figure 9. Forest plot of effect sizes for invertebrate abundance (standardized differences in bird species richness between plantations and pastures) based on 9 independent studies.

The dashed vertical line represents no difference. Box area is proportional to precision (1/variance) and error bars are equivalent to 95% confidence intervals. The summary outcome indicates the estimated average effect size, along with a 95% confidence interval, to allow us to assess whether the effects were different from zero.

For plant abundance, none of the available covariates were significant. However, there was significant correlation between effect sizes within divisions within studies ($p<0.05$) suggesting that there was unexplained heterogeneity between divisions within studies. The estimated average effect size 1.00 (95% CI; -1.47, 3.47) was not significantly different from zero ($p=0.46$) indicating that there was not a significant difference in plant abundance between plantations and pastures.

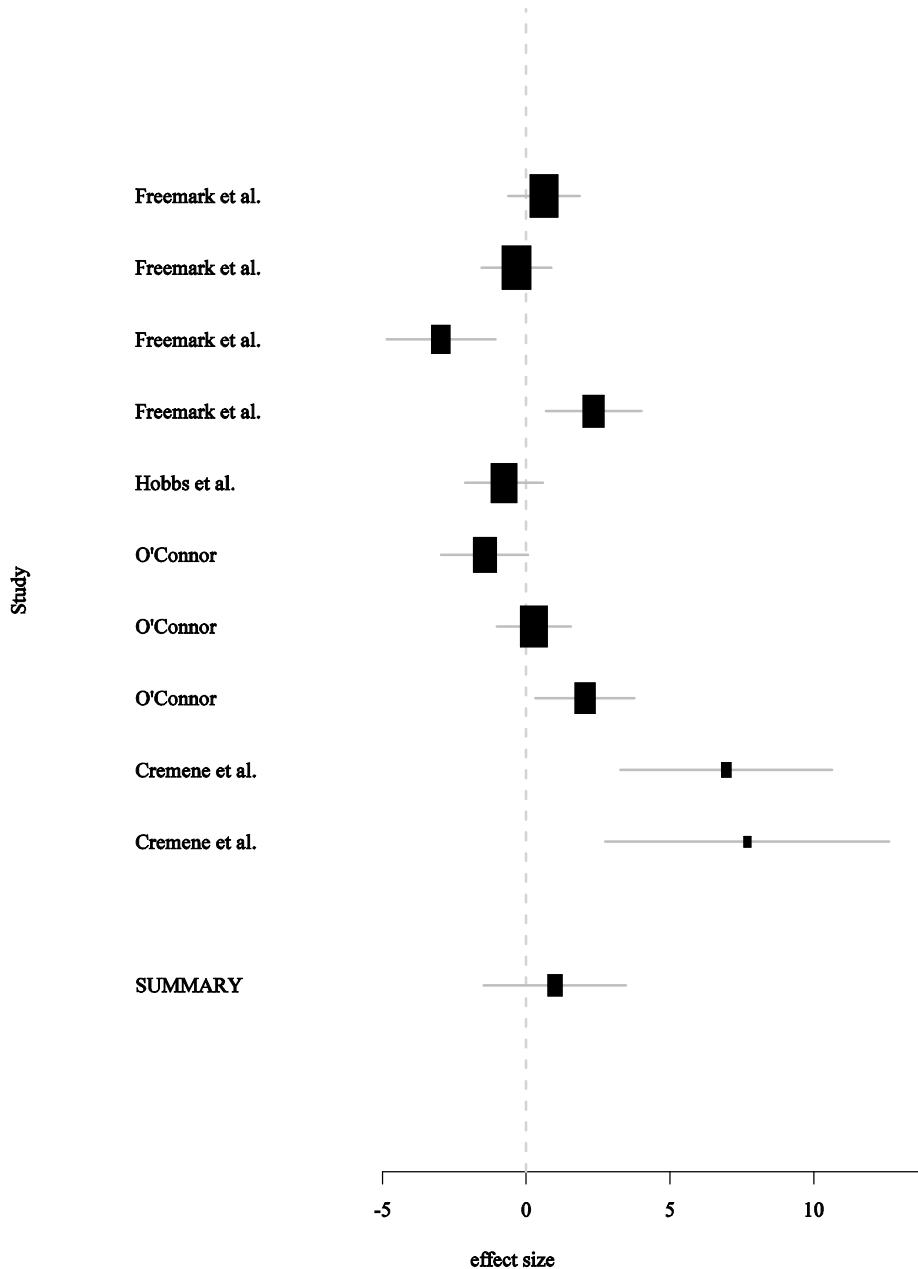


Figure 10. Forest plot of effect sizes for plant abundance (standardized differences in bird species richness between plantations and pastures) based on 4 independent studies. The dashed vertical line represents no difference. Box area is proportional to precision (1/variance) and error bars are equivalent to 95% confidence intervals. The summary outcome indicates the estimated average effect size, along with a 95% confidence interval, to allow us to assess whether the effects were different from zero.

Table 5. Results of the models fitted for species abundance for the 5 taxonomic groups.

taxa	number of studies	number of comparisons	random effects				fixed effects						average effect size	
			random term	likelihood			scaled Wald statistic	adjusted df	P value	level	95% C.I.			
				estimate	SE	ratio statistic								
birds	7	14	study.division	6.81	3.62	7.01	0.008	mean	1.13	7.9,1	0.32	-0.95	(-2.70,0.80)	
			residual	0.49	0.31									
reptiles	3	4	residual	3.97	3.24			mean	3.88	3,1	0.14	1.96	(-0.03,3.95)	
mammals	3	7	residual	1.83	1.06			mean	5.13	6,1	0.06	0.16	(0.13,2.18)	
subset	3	7	residual	0.62	0.39			rem.veg pasture	12.69	5,1	0.016	no remnant	1.83 (0.92,2.74)	
								remnant				-0.52	(-1.43,0.97)	
invertebrates	9	65	study.division	2.13	0.86	50.14	<0.001	mean	1.95	8.1,1	0.2	-1.54	(-3.70,0.62)	
			study	9.39	5.4	45.26	<0.001							
			residual	0.36	0.08									
plants	4	10	study.division	9.51	6.42	4.42	0.03	mean	0.63	6.1,1	0.46	1	(-1.47,3.47)	
			residual	2	1.59									

5 Discussion

5.1 Evidence of effectiveness

We found that for most taxa, plantations and pasture lands were not sufficiently consistent in their impact on species richness or abundance to allow for general conclusions regarding the relative biodiversity value of these two land-uses. The notable exception was reptiles/amphibians, the only taxonomic group which exhibited significantly higher species richness in plantations than in pasture lands. In addition, there was a significantly positive effect size for bird species richness when the results of only the highest quality studies were included. However, it was the variability of biodiversity responses to plantations and agricultural lands that was more informative than any single estimate of a response. In light of these results, we suggest that there is insufficient evidence to support assumptions that plantations contain higher species richness or abundance than pasture, unless caveats are taken into account regarding the taxa considered, and the specifics of how the land-use is managed.

5.2 Reasons for variation in effectiveness

Previous studies lend support to the influence that stand-level features have on plantation biodiversity. These features include: 1) the cultivation of native or exotic timber species (Hartley 2002), 2) the use of mixed species stands or monocultures (Catterall et al. 2004; Hartley 2002), 3) the retention or removal of understorey plant species (Bonham et al. 2002), and 4) the preservation or removal of biological legacies (*sensu* Franklin et al. 2000) such as remnant trees, windrows, and logging slash (Hartley 2002; Lindenmayer and Hobbs 2004, Loyn et al. 2007). For pasture lands, there are similar studies and conclusions which emphasize the importance of landscape features and management techniques as determinants of biodiversity associated with this land-use (Reid and Landsberg 2000; Carruthers et al. 2004; Manning et al. 2006). In this study, there were insufficient published papers to make definitive statements about the effect of many stand-level features of plantations on the taxonomic responses of the taxa. However, the results did highlight the importance of remnant vegetation in pastures as a determining factor influencing the relative difference between pastures and plantations in species richness as well as the abundance for some taxa.

In this study, bird and reptile/amphibian species richness, and mammal abundance, was significantly higher in plantations when remnant vegetation was absent from pastures. Notably, this response was not observed if remnant vegetation was retained in pasture lands. The retention of scattered individual trees or small tree patches (< 1 ha) within pastures can provide shelter and substrate for native flora (Reid and Landsberg 2000, Fischer et al. 2005), habitat and resources for invertebrates (Oliver et al.

2006), food for animals reliant on pollen, nectar, seeds, and invertebrates (Carruthers et al. 2004), and habitat for hollow-dependent fauna (Nilsson et al. 2005). Notably, even primarily cleared production lands may nevertheless contain higher densities of biological legacies (*sensu* Franklin et al. 2000), such as large hollow bearing trees, than forests managed for timber production (Nilsson et al. 2005). Our finding that the retention or absence of scattered trees within pastures altered the species richness or abundance for bird, reptile/amphibian, and mammal taxonomic groups within pasture lands was consistent with the evidence that scattered trees are keystone structures (Manning et al. 2006) utilized by both open country and woodland species (Fischer and Lindenmayer 2002a, b). Furthermore, this outcome is consistent with studies demonstrating the biodiversity benefits of retaining scattered trees or vegetation patches within otherwise deforested production landscapes (Carruthers et al. 2004; Fischer et al. 2005; Manning et al. 2006).

The outcome of any comparative study of the biodiversity value of different land-uses largely depends on a suite of variables operating at the scale of the stand, and at the scale of the landscape for each of the land-uses compared (Benton et al. 2003; Fischer et al. 2008a; Lindenmayer and Hobbs 2004; Tews et al. 2004). There are a suite of local stand level and landscape level issues which can alter the relative biodiversity value of both plantations (Carnus et al. 2006; Hartley 2002; Lindenmayer and Hobbs 2004) and agricultural lands (Bengtsson et al. 2005; Benton 2007; Benton et al. 2003; Fischer et al. 2008a). The use of a common scale, such as that used in this meta-analysis, with which to compare the relative biodiversity value of these two land-uses is likely to vary between a positive, neutral or negative effect size simply depending on the type of plantation and agricultural land compared. For instance, the outcome of a comparison of species richness between intensively used cropland and a complex native plantation is likely to be very different than a comparison between organic agriculture and an industrial scale homogenous exotic timber plantation. Therefore, there are likely to be legitimate ecological reasons for differences in response outcomes, as repeatedly observed in this assessment.

5.3 *Review limitations*

Careful consideration needs to be given to the interpretation of meta-analysis results when assessing questions which involve human-modified systems. In these cases, the inherent variability of biological systems is compounded by variation in the way humans can modify a system and its surrounding landscape. Inevitably the distillation of a single estimate from a meta-analysis in these cases relies on the assumption that these differences can be downplayed (see Bailar 1997), or that there is sufficient consistency between primary studies to assess the influence of these differences on the outcome

(Gurevitch and Hedges 1999). Furthermore, it is important to note that the limited number of appropriate studies for some taxa, and the way in which ecologically distinct taxa are grouped, will alter the outcomes of a meta-analysis. The quantified biodiversity value of any land-use will thereby be determined by 1) the taxa studied, 2) the measure of species diversity used, and, 3) the spatial and temporal scale of the study (Tews et al. 2004). Keeping these caveats in mind, our results indicate that plantations do provide for higher species richness or abundance than pastures for some taxa. However, even in these cases, this knowledge is insufficient to determine the relative conservation value of either land-use.

For instance, the results of this meta-analysis relied on species counts (species richness), or counts of individuals belonging to a particular taxa (abundance). However, such metrics can falsely indicate an equivalency between two different land-use types in terms of biodiversity value, regardless of the existence of substantial underlying differences in the composition of the fauna or flora considered (see Sax et al. 2005). Higher species richness may be the cumulative outcome of improving conditions for invasive exotic or otherwise unwanted species (Lindenmayer and Hobbs 2004), and therefore such metrics cannot be used in isolation to infer an increase in conservation value (Lindenmayer and Hobbs 2004).

Determining the biodiversity value of a land-use requires consideration of its impact on the landscape within which it is nested. In landscapes in which large amounts of clearing of native forest has occurred, there may be conservation benefits for remnant forest-dependent fauna and flora through the establishment of plantations in conjunction with the retention of remnant trees (Lindenmayer and Hobbs 2004). In contrast, in landscapes where native grasslands have been lost to alternative land-uses, agricultural landscapes that support a mosaic that includes native pastures and remnant grasslands may provide higher biodiversity benefits than plantations. Further consideration also may need to be given to issues involving landscape permeability and connectivity (August 1983; Pryke and Samways 2001; Suckling 1982; Taylor et al. 1993; Tews et al. 2004), invasive timber species (Richardson 1998; Williams and Wardle 2005), and hydrology (Carnus et al. 2006; Jackson et al. 2005).

6. Reviewers' Conclusions

6.1 Implications for management / policy / conservation

We conclude from our meta-analysis that whether or not plantation establishment in pasture lands will produce biodiversity benefits is a question best answered by a combination of empirical and normative considerations specific to the region and taxa in question. Just as site-specific management is needed to sustain soil quality and long-term site productivity (Fox 2000), so are site-specific approaches needed for plantations when

addressing biodiversity benefits and disbenefits. Both pasture lands and plantations can support various combinations of exotic and native taxa (Fischer et al. 2008b; Lindenmayer and Hobbs 2004), and both land-uses can be altered to make them more or less favourable for specific taxa (Bengtsson et al. 2005; Benton et al. 2003; Hartley 2002; Lindenmayer and Hobbs 2004). As such, deciding which land-use is “best” cannot be separated from (1) landscape context, 2) management practices, 3) the conservation value of the taxa being considered, and (4) the components and metrics of biodiversity that are evaluated. Our results emphasize that caution is required in making general statements about the relative biodiversity benefits of one broadly-defined land-use over another.

6.2 Implications for research

Although meta-analysis allows factors contributing to an effect to be explored (Gurevitch and Hedges 1999), relationships are often confounded by methodological differences between studies included in the analysis (Pullin and Stewart 2006; Stewart et al. 2005). For instance, in this study, differences in the quality of source material assessed (see table 1) resulted in a shift of two standard deviations in the effect size observed for bird species richness (see Table 4). Furthermore, meta-analyses are often restricted by the lack of relevant information reported in the primary studies. In this study, we were often unable to include the results of published studies for some analyses due to insufficient provision of necessary information regarding treatments and controls (see Table 3). Furthermore, we found significant study-level random effects, indicating that effect sizes were correlated within studies, thereby suggesting that these unreported factors were influencing effect sizes. One way to alleviate this problem is to develop consistency among journals regarding minimum standards for the information included in published studies.

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7. Potential Conflicts of Interest and Sources of Support

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