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# Accounting for the causal basis of collinearity when measuring the effects of habitat loss versus habitat fragmentation

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**Abstract**

Collinearity among metrics of habitat loss and habitat fragmentation is typically treated as a nuisance in landscape ecology, and it is the norm to use statistical approaches that remove collinear information prior to estimating model parameters. However, collinearity may arise from causal relationships among landscape metrics, and may therefore signal the occurrence of indirect effects (where one model predictor influences the response variable by driving changes in another influential predictor). Here we suggest that, far from being merely a statistical nuisance, collinearity may be crucial for accurately quantifying the effects of habitat loss versus habitat fragmentation. We use simulation modelling to create datasets of collinear landscape metrics in which collinearity arose from causal relationships, then test the ability of two statistical approaches to estimate the effects of these metrics on a simulated response variable: (1) multiple regression, which statistically removes collinearity, and was identified in a recent study as the best approach for estimating the effects of collinear landscape metrics (although this study did not account for any indirect effects implied by collinearity among metrics); and (2) path analysis, which accounts for the causal basis of collinearity. In agreement with this previous study, we found that multiple regression gave unbiased estimates of direct effects (effects not mediated by other model predictors). However, it gave biased estimates of total (direct + indirect) effects when indirect effects occurred. In contrast, path analysis reliably identified the causal basis of collinearity and gave unbiased estimates of direct, indirect, and total effects. We suggest that effective research on the impacts of habitat loss versus fragmentation will often require tools that can empirically test whether collinear landscape metrics are causally related, and if so, account for the indirect effects that these causal relationships imply. Path analysis, but not multiple regression, provides such a tool.

## Introduction

Effectively managing the impacts of land use change on ecological systems requires an understanding of the relative influences of habitat loss versus habitat fragmentation. These relative effects might dictate whether conservation managers should focus on managing habitat amount (i.e. preventing habitat loss or creating new habitat) or whether the negative impacts of habitat loss can be mitigated by managing the spatial arrangement of habitat remnants (Fahrig 1997, Koper et al. 2007, Smith et al. 2009, Villard and Metzger 2014). For example, conversion of natural areas to human land uses may primarily impact native species not by reducing the overall amount of habitat in the landscape, but by isolating individuals in small habitat fragments. If so, the impacts of future habitat loss might be largely mitigated by maintaining corridors among habitat remnants (Fischer and Lindenmayer 2007). Discriminating these habitat configuration effects from habitat amount per se is likely to be increasingly important in the face of a rapidly growing human population, as they potentially provide a means to minimise the trade-offs between biodiversity conservation and habitat conversion to meet human resource requirements (Sala et al. 2000, Foley et al. 2005, Day et al. 2009, Kelly and Sullivan 2010).

In recent decades, a growing body of literature has sought to measure the relative impacts of habitat loss versus habitat fragmentation on ecological systems. Despite this, our understanding of the relative effects of these processes remains poorly resolved (McGarigal and Cushman 2002, Koper, et al. 2007, Smith, et al. 2009, Didham et al. 2012). A major reason for this is that metrics of habitat loss and fragmentation are typically highly collinear, making it difficult to tease apart their true effects (Koper, et al. 2007, Didham, et al. 2012, Pasher et al. 2013, Villard and Metzger 2014, Hanski 2015). To deal with this issue, researchers have typically used regression-based approaches that statistically remove collinearity among landscape metrics before estimating their independent effects (see Smith et al. 2009 for a review). This approach is in line with the widely-held assumption that collinearity among metrics of habitat loss and habitat fragmentation is merely a nuisance that hampers effect estimation (e.g. McGarigal and Cushman 2002, Fahrig 2003, Smith, et al. 2009, Pasher, et al. 2013). However, recently Didham et al. (2012) highlighted the point that collinearity between metrics of habitat loss and habitat fragmentation may arise, at least in part, because changing habitat amount causes changes in habitat configuration. Two implications of this hypothesis are that (1) habitat amount and habitat fragmentation occur in a causal hierarchy in which habitat amount may indirectly influence ecological systems via altered habitat configuration; and (2) collinearity that results from these causal relationships represents a process that may have real effects on ecological systems. Didham et al. (2012) suggested that understanding the relative effects of habitat loss and habitat fragmentation, as well as the specific mechanistic pathways through which these variables affect ecological systems, requires a statistical approach such as path modelling which can specifically measure and account for the causal basis of collinearity when estimating effects.

Smith et al. (2009) examined the ability of a range of common statistical methods to measure the independent effects of habitat loss and fragmentation on ecological systems when these variables are collinear. To do this, they measured metrics of habitat loss and fragmentation (hereafter 'landscape metrics') from real landscapes, then used simulation modelling to generate a response variable that was a function of these metrics. They then tested how well each of six different statistical methods was able to estimate the 'true effects' of the landscape metrics, where true effects were defined as the coefficients of the equations used to generate their response variables. Smith et al. (2009) found that many statistical methods gave biased estimates of these true effects, but that the partial regression coefficients produced by multiple regression gave unbiased estimates provided that all influential predictors were included in their models. Consequently, they recommended the use of partial regression coefficients to estimate the effects of habitat loss versus habitat fragmentation, provided that these variables represent distinct ecological processes (Smith, et al. 2009). This approach has been adopted in some recent studies (e.g. Schipper et al. 2011, Smith et al. 2011, Smith et al. 2011, Thornton et al. 2011, Cushman et al. 2012, Soomers et al. 2013).

By simulating a response variable as a function of their landscape metrics, Smith et al. (2009) were able to use the coefficients that generated their response variable as a benchmark for testing the efficacy of different statistical methods. However, in defining these coefficients as 'true effects', the study did not account for the causal basis of the collinearity observed among metrics. Collinearity must have a causal basis (random co-variation notwithstanding), whether it be that metrics are jointly influenced by unmeasured variables (a 'causal independence' collinearity scenario), or that one metric influences another (a 'causal relationships' collinearity scenario, as suggested by Didham et al. 2012) (Figure 1a,b). Crucially, the 'true effects' of Smith et al. (2009) represented only the direct effects of their model predictors: that is, those effects that were not mediated by any other predictors in their model (Grace 2006; Figure 1c). However, if collinearity arose through causal relationships among metrics this would give rise to additional indirect effects that the 'true effects' did not measure (Figure 1b). Under this scenario model predictors would constitute a 'cascade' of ultimate and proximate causes, whereby the proximate (i.e. direct) effect of one predictor would also ultimately (i.e. indirectly) be caused by another predictor in the model (Figure 1b). We stress that Smith et al. (2009) acknowledged that their study was limited to the estimation of independent (i.e. direct) effects, and so their approach of measuring 'true effects' without accounting for the causal basis of collinearity among landscape metrics is appropriate under this scenario. However, the conclusions of Smith et al. (2009) may not be applicable to situations where researchers are interested in estimating indirect effects in addition to direct effects.

Accounting for indirect effects may be an important part of accurately predicting the real-world effects of land use change on an ecological system (Didham, et al. 2012). For example, in the Waikato region of New Zealand the occurrence of North Island robins (*Petroica longipes*) is mainly driven by habitat isolation (Richard and Armstrong 2010), and metrics of habitat amount and habitat isolation are correlated in this region (MfE 2004). If the underlying cause of this correlation is a 'causal relationships' scenario in which the degree of habitat isolation is influenced by the amount of habitat (as per Figure 1b), then part of the effect of isolation on robin occurrence will also ultimately be an effect of habitat amount. Given a statistical model that includes habitat amount and habitat isolation as predictors of robin occurrence, the direct effect of habitat amount (i.e. any effects that operate independently of habitat isolation) will then underestimate the real-world effects of varying habitat amount on robin occurrence, because it will not account for the fact that a portion of the effect of habitat isolation is also indirectly an effect of habitat amount. Instead, the real-world effects of varying habitat amount on robin occurrence will correspond to its total (direct + indirect) effects.

Conversely, there are situations in which indirect effects may not need to be accounted for when predicting the effects of land use change on an ecological system. First, in any scenario where model predictors are causally independent, indirect effects among model predictors will not occur and direct effects will correspond to the real-world effects of the predictor on the response variable (Figure 1a). Second, direct effects will correspond to the real-world effects of a model predictor if any indirect effects will be avoided by the particular management scenario under investigation. In the North Island robin example above, it may be possible to reduce habitat amount without reducing habitat isolation by leaving corridors of habitat between forest remnants. In this case the isolation-mediated indirect effect of habitat amount on robin occurrence will not occur, because the causal relationship between habitat amount and habitat isolation that existed during historic habitat clearance will be avoided by controlling the way in which habitat is removed from the landscape. As a result, the effect of habitat amount on robin occurrence will correspond to its direct effect alone. Third, researchers may wish to predict the levels of an ecological response variable from a set of collinear landscape metrics, but have no interest in disentangling the effects of individual metrics. Direct effects are sufficient for this purpose, provided that all modelled variables are used in the prediction. Indirect effects do not need to be accounted for in this case because they operate solely via the direct effects of other variables in the model: they contain redundant information for predicting the level of the response variable, provided that the direct effects of their mediating variables are also used in this prediction. However, as described above, failure to account for the fact that the direct effect of one variable may also represent the indirect effect of another can lead to biased estimates of the effects of individual metrics.

Here, we used simulation modelling to generate datasets that were essentially identical to those used by Smith et al. (2009), but where collinearity was known to arise from causal relationships among metrics. This knowledge of the causal basis of collinearity allowed us to calculate the 'true effects' of each landscape metric in terms of its direct, indirect, and total (direct + indirect) effects, rather than only in terms of its direct effects (Smith, et al. 2009). Our aims were to use these simulated datasets to examine (1) how collinearity which results from causal relationships among landscape metrics affects the ability of multiple regression to provide unbiased estimates of the direct and total effects of these metrics on a simulated response variable; (2) whether path analysis, a method specifically designed to test and account for the causal basis of collinearity among predictors, produces unbiased estimates of these effects; and (3) how different levels of collinearity among landscape metrics affects the extent to which these methods give biased estimates of direct and total effects.

## Methods

### *Simulating datasets of causally related landscape metrics*

We used simulation modelling to generate a multivariate normal dataset of four collinear variables, representing the four landscape metrics used by Smith et al. (2009): the amount of forest cover (Amount), the average size of forest patches (mean patch size, hereafter MPS), the total length of forest edge (Edge), and the number of natural land cover classes (landscape heterogeneity, hereafter Hetero). We generated landscape metrics under a 'causal relationships' scenario in which collinearity between the four metrics arose because Amount causally influenced the other three metrics (Figure 2). We chose this specific causal structure because we considered that it was theoretically the most likely way in which these four landscape metrics might be related, as has been suggested previously (Didham, et al. 2012). Indeed, when we applied path diagram rules to fit the pairwise correlations measured by Smith et al. (2009) to this model, the predicted correlations among variables were almost identical to those measured by Smith et al. (2009) (Figure 2), suggesting that this 'causal relationships' scenario may well have been the true basis of collinearity among predictors for their dataset.

We used the following equations to generate observations of our landscape metrics and response variable so that they closely matched those of Smith et al. (2009), while still ensuring that collinearity among metrics arose from the causal structure described above:

$$\text{Amount} = N(0,1) \quad (1)$$

$$\text{MPS} = 0.76*\text{Amount} + \varepsilon \quad (2)$$

$$\text{Edge} = 0.90*\text{Amount} + \varepsilon \quad (3)$$

$$\text{Hetero} = 0.57*\text{Amount} + \varepsilon \quad (4)$$

$$\text{Response} = 0.40*\text{Amount} + 0.40*\text{MPS} - 0.40*\text{Edge} + 0.40*\text{Hetero} + \varepsilon \quad (5)$$

where the notation N(0,1) refers to variables whose values were drawn from a normal distribution with a mean of zero and variance of one, and ε refers to normally-distributed error terms. See Appendix 1 for a description of how these equations were derived.

Equation (5) specifies that the response variable has a mean value that is linearly related to our landscape metrics, and that deviations from this mean are normally distributed. This scenario has been found to approximate empirical relationships for a range of response variables in landscape ecological studies, including the species richness of bird and lizard communities, patch visitation rates of butterflies, and demographic parameters of a simulated mustelid population (Summerville and Crist 2001, Imbeau and Desrochers 2002, Cushman and McGarigal 2003, Lindenmayer et al. 2005, Jager et al. 2006, Swift and Hannon 2010). Our simulated response variable can therefore potentially represent a wide range of real-world ecological response variables.

We note that, because our landscape metrics were created from equations rather than measured from habitat maps, our simulated landscapes may have contained combinations of metrics that could never occur in real life. In Appendix 2 we compare our combinations of metrics with those measured from real landscapes by Smith et al. (2009), and show that our simulations produced combinations of metrics that were realistic and realisable in real landscapes.

We used the above equations to produce 100 datasets, each containing data for 350 'landscapes' (i.e. simulated values of Amount, MPS, Edge, Hetero, and the response variable). Specifically, each value of Amount was a random variant drawn from a normal distribution with a mean of zero and variance of one (i.e. equation (1) above). Each value of MPS, Edge, and Hetero for the same landscape was then calculated from this value of Amount according to equations (2)-(4), while each value of the response variable was calculated from the resulting values of Amount, MPS, Edge, and Hetero according to equation (5). These datasets were essentially indistinguishable from those used by Smith et al. (Table 1), except that (1) the response variable was re-scaled to have the same mean and variance as the landscape metrics (which was necessary to calculate the size of indirect effects; Grace 2006); (2) landscape metrics had homogeneity of variance, whereas those measured by Smith et al. (2009) were heteroscedastic; and (3) collinearity among landscape metrics arose from a known process, which gave rise to indirect effects on the response variable. All simulations were conducted in the base package of R version 3.1.0 (R Core Team 2012).

***Testing bias in estimates of direct and total effects***

We calculated the true values of the direct, indirect, and total effects of our four landscape metrics on the response variable from the coefficients used to simulate the data. Following Smith et al. (2009), the true value of the direct effect of each metric was calculated as the coefficient used to simulate the response variable as a function of these metrics (i.e. a direct effect of 0.40 for all metrics). The true values for indirect effects were non-zero only for Amount. We first calculated the three individual indirect effects of Amount (i.e. it's MPS-mediated effect, its Edge-mediated effect, and its Hetero-mediated effect) by multiplying the coefficient used to simulate each metric as a function of Amount by the direct effect of that metric (e.g. $0.40 \times 0.76 = 0.30$ for the indirect effect of Amount mediated by MPS; Grace 2006). We then calculated the overall indirect effect of Amount by summing these individual indirect effects (Grace 2006). The true value of the total effect of each metric was calculated as the sum of its direct and indirect effects (Grace 2006).

We followed the methods of Smith et al. (2009) to measure the ability of multiple regression to estimate the true effects of our four landscape metrics on our simulated response variable. We used the 'lm' function in the base package of R to fit a multiple regression model to each of our 100 datasets, where the response variable was modelled as a function of the four metrics. We used the partial regression coefficients produced by these models as estimates of the true effects of these metrics. However, each model only provided a single partial regression coefficient per landscape metric, which was the estimate of its direct effect (Grace 2008). As a result, we took the estimate of the indirect effects of each metric to be zero, and the partial regression coefficients to be an estimate of both the direct and total (direct + indirect) effects of each metric. We calculated the means and 95% confidence intervals of these effect estimates over our 100 datasets, then compared these means to the true effects calculated from the coefficients used in our simulations.

We used the same approach to measure the ability of path analysis to estimate the true effects of our four landscape metrics. We used the 'lavaan' package in R (Rosseel 2014) to fit a path model to each of our 100 datasets, where the path model corresponded to the causal model which we used to simulate our data: we specified that the response variable was a function of all four metrics, and that MPS, Edge, and Hetero were a function of Amount (Figure 2). We used the path coefficients produced by these models to estimate the direct, indirect, and total effects of our landscape metrics on the response variable, using the same procedure that we used to calculate true effects from our simulation coefficients (i.e. calculating indirect effects by multiplying their constituent path coefficients, and calculating total effects by summing direct and indirect effects; Grace 2006). We calculated the means and 95% confidence intervals of these effect estimates over our 100 datasets, and compared these means to the true effects calculated from our simulation coefficients.

***Testing the ability of path analysis to identify correctly-specified path models***

The effect estimates produced by our path analyses were derived from path models that were always correctly specified. However, in real-world path analyses the causal relationships among predictors may not be known *a priori*, and the plausibility of a hypothesised set of causal relationships would need to be measured from the data (Grace 2006, Grace 2008). To examine whether we could specify the correct path model for our datasets without knowledge of the true causal relationships among predictors, we applied alternative, incorrect specifications of our path models to each of our 100 datasets, and used lavaan’s chi-squared test to measure the fit of each path model. In addition to our correctly specified 'causal relationships' model (i.e. where Amount causally influenced the other three metrics, and all four metrics causally influenced the response variable) we specified three incorrect 'causal relationships' path models, in which either MPS, Edge, or Hetero causally influenced the other three metrics, and all four metrics causally influenced the response variable. We also specified an incorrect 'causal independence' path model, in which all four metrics were only correlated because they were jointly influenced by an extrinsic variable, and all four metrics causally influenced the response variable. This required the simulation of an additional variable, which we achieved by sampling random deviates from a standard normal distribution. This approach ensured that the extrinsic variable was not causally related to our landscape metrics, consistent with our true 'causal relationships' data structure, and that it was measured on the same scale as our other variables (i.e. it had a mean of zero and a variance of one). We quantified our ability to specify the correct path model by calculating the percentage of chi-squared tests that accepted the correct model (those tests where $p > 0.05$) and the percentage of tests that rejected the incorrect model (those tests where $p < 0.05$) for each of our five path model specifications.

***Testing bias in effect estimates under different levels of collinearity***

To examine how the degree of bias in effect estimates varied with the level of collinearity among landscape metrics, we re-simulated our data while varying the level of collinearity between Amount (the only variable that produced indirect effects on the response variable) and the other metrics. We used simplified versions of our datasets for this analysis, utilising only Amount, MPS, and a response variable. This was because we would otherwise need to simultaneously vary the levels of collinearity between Amount and the three other landscape metrics, which would add unnecessary complexity to the analysis. We simulated these simplified datasets with the same causal structure as our 'full' datasets, but under five different levels of collinearity between Amount and MPS: correlations of 0, 0.25, 0.5, 0.76 and 0.90. The value of 0.76 reflected the correlation between Amount and MPS measured by Smith et al. (2009), the value of 0.90 reflected the maximum correlation these authors measured among any of their four metrics, and the other values were selected to represent the full range of possible correlations among metrics below this maximum value. For each level of collinearity we simulated 100 datasets, each of which contained 350 observations of Amount, MPS, and the response variable, re-adjusting the error terms in our equations to ensure variances of ~1 were maintained (Appendix 1). We then recalculated the size of direct, indirect, and total effects for each of these collinearity levels, and measured the degree of bias of the estimates of these effects produced by multiple regression and path analysis, as described above.

## Results

### ***Testing bias in the estimates of multiple regression and path analysis***

Consistent with the results of Smith et al. (2009), we found that partial regression coefficients from multiple regression models gave unbiased estimates of model coefficients when considering just the direct effects of our four landscape metrics on the simulated response variable (Fig 3a). However, multiple regression was unable to measure the indirect effects of Amount that arose because of its causal influence on the other metrics. This meant that partial regression coefficients from the multiple regression model were strongly biased estimates of the total effects of Amount. In our modelled example, the average multiple regression estimate for the total effect of Amount was just over half of the true total effect (Figure 3a). In contrast, our path analysis models gave unbiased estimates of the direct, indirect, and total effects of all four landscape metrics (Figure 3b). In this particular simulation, the confidence intervals for the average multiple regression estimate of the total effect of Amount did overlap the true value (Figure 3a), but we show below that the true value of this effect moves well beyond the confidence intervals of the multiple regression estimate as collinearity among predictors increases.

***The ability of path analysis to select a correctly specified path model***

Our tests of model fit suggested that path analysis had a very good ability to identify the correctly specified path model. These tests rejected all 400 of our incorrectly specified models, and accepted 91% of our correctly specified models (chi-squared tests, $\alpha$=0.05, df=3). The frequency with which these tests accepted the correct model was similar to the 95% rate expected for our alpha value.

***Bias in effect estimates under different levels of collinearity***

We found that the degree of bias in multiple regression estimates of the total effects of Amount increased with the degree of collinearity. In contrast, path analysis estimates were unbiased regardless of the level of collinearity. Only under the empirically unrealistic scenario of zero collinearity among predictors did the multiple regression estimates of total effects converge with the path analysis estimates (Figure 4).

Not only did the degree of bias in effect estimates depend on levels of collinearity among metrics, but variance in effect estimates also increased with the level of collinearity for both statistical approaches. This effect appeared to become stronger when the correlation among landscape metrics rose above 0.5 (Figure 4).

## Discussion

Understanding the relative effects of habitat loss versus habitat fragmentation may be crucial for effectively managing the impacts of land use change on ecological systems, but this understanding has been limited by uncertainty over which statistical tools can correctly estimate the effects of collinear landscape metrics (Smith, et al. 2009, Didham, et al. 2012, Villard and Metzger 2014). In this study, we found that the causal basis of collinearity among model predictors can strongly influence the ability of multiple regression to estimate 'true effects' when these correspond to total (direct + indirect) effects. In agreement with Smith et al. (2009), we found that multiple regression provided unbiased estimates of direct effects. Multiple regression will therefore produce unbiased estimates of total effects when collinearity results from a process that does not give rise to indirect effects on the response variable (i.e. 'causal independence', Figure 1a), since direct and total effects will be equivalent. However, when collinearity results from a process that gives rise to indirect effects on the response variable (i.e. 'causal relationships'; Figure 1b), partial regression coefficients from multiple regression will be biased estimates of total effects, with the degree of bias reflecting the strength of the collinearity and therefore the size of the indirect effect. Consequently, the estimated total effects given by multiple regression will be unreliable unless it is known *a priori* that the causal basis of collinearity among predictors does not result in indirect effects.

Importantly, we believe that collinearity may often result from causal relationships among landscape metrics, giving rise to indirect effects. Although habitat loss and habitat fragmentation are often treated as independent processes (e.g. McGarigal and Cushman 2002, Fahrig 2003, Smith, et al. 2009, Pasher, et al. 2013), it seems plausible that they are causally related, because habitat removal should alter the spatial arrangement of remaining habitat.

Indeed, a number of recent studies have suggested or assumed that metrics of habitat loss and fragmentation are causally related (Didham, et al. 2012, Le Tortorec et al. 2013, Rueda et al. 2013, Mairota et al. 2015). Moreover, because landscape metrics are often highly correlated (Fahrig 2003, Smith, et al. 2009, Didham, et al. 2012, Villard and Metzger 2014), there is the potential for any indirect effects that do occur to strongly contribute to total effects. Our results show that multiple regression may give strongly biased estimates of the total effects of landscape metrics under these circumstances.

We simulated our data under a 'causal relationships' scenario in which habitat amount causally influenced our other landscape metrics, and this resulted in indirect effects of habitat amount on the response variable. However, we note that this is not the only possible way in which landscape metrics could be causally related in real landscapes. Specifically, causality could potentially be reversed (for example, mean patch size could influence habitat amount, resulting in indirect effects of mean patch size), or reciprocal (mean patch size could influence habitat amount and vice versa, resulting in indirect effects of both metrics). We caution that researchers interested in accounting for indirect effects should not assume that habitat amount causally influences other landscape metrics, but should use path analysis to empirically test any form of causal relationship that they consider plausible.

We stress that the values of direct and indirect effects depend on the predictors that are included in a statistical model. Direct effects measure the effect of a predictor after controlling for other predictors in the model (Shipley 2002), so will change when different [collinear] predictors are included. Similarly, because indirect effects are the effects of a predictor that are mediated by other predictors, direct effects will also estimate the total effects of each predictor if all of its mediating predictors are removed from the model. Because of this, it is possible to use multiple regression to measure the direct, indirect, and total effects in a system by running a series of models that include different combinations of predictor and response variables (Grace 2008, Shipley 2009). However, without knowledge of the causal basis of collinearity among predictors it is not possible to know when collinear predictors should be excluded to allow measurement of total effects and when they should be included to statistically control for confounding among variables (Zuur et al. 2007). In contrast, path analysis provides a means to both examine the causal basis of collinearity and to estimate direct, indirect, and total effects within a single model.

Although we found that path analysis gave unbiased estimates of the effects of our landscape metrics, and that multiple regression gave unbiased estimates of direct effects, the variance of estimates obtained by both approaches increased with increasing collinearity. In other words, while models may have correctly estimated parameters when estimates were averaged over our 100 datasets, their ability to accurately estimate parameters within a given dataset decreased as collinearity among metrics increased. Simulations have been used to demonstrate this point previously (Freckleton 2002). Because of this, we suggest that researchers should think carefully before following Smith et al.'s (2009) suggestion that predictors should not be removed from models simply because they are collinear. This was suggested based on the finding that the omission of influential collinear predictors resulted in biased effect estimates. However, our results suggest that the decrease in bias gained from the inclusion of multiple collinear predictors comes at the expense of an increase in the variance of estimated coefficients. This increase in variance decreases statistical power (Zuur et al. 2010), which may cause real problems for landscape-scale studies in which it is not logistically feasible to obtain large sample sizes. Moreover, this increase in variance could conceivably give misleading results. For example, in a model containing two influential but strongly collinear predictors as well as a third influential but less collinear predictor, inflated standard errors around the first two predictors will decrease the statistical significance of their effects relative to the third predictor. We suggest that researchers should be cautious about interpreting effect estimates or statistical significance from models containing multiple collinear predictors, keeping in mind that the precision and statistical significance of estimates would change if some of these predictors were removed from the model.

Our simulations did not specify the range over which our metrics of habitat loss and fragmentation were measured (although the correlations used to simulate our data were drawn from landscapes where habitat cover was <30%; Smith, et al. 2009), but this may have a strong influence on the occurrence and measurement of fragmentation effects. First, the extent to which metrics of habitat fragmentation are able to vary independently of habitat loss may not be constant, with variability often being greatest at intermediate levels of habitat cover (Villard and Metzger 2014). This means that it may be more difficult to statistically disentangle the effects of habitat loss from fragmentation at high and low levels of habitat cover, because a lack of independent variation implies high collinearity, high variance inflation, and low statistical power (Figure 4; Zuur, et al. 2010). Second, fragmentation effects may only occur along particular portions of the habitat cover gradient. These effects were previously believed to occur at low levels of habitat cover (e.g. Andrén 1994), but recent work has suggested that they may predominantly occur at intermediate cover levels (Pardini et al. 2010, Villard and Metzger 2014). While accounting for the causal basis of collinearity is likely to be an important part of measuring the relative effects of habitat loss versus fragmentation, we suggest that researchers should also be aware that both the occurrence and measurement of fragmentation effects may depend on the range over which habitat cover is measured.

We also note that the estimated effects of habitat loss and fragmentation will be sensitive to the accuracy of the habitat maps used to quantify these processes. Typically, metrics of loss and fragmentation would be derived from a map of 'habitat' and 'matrix' land cover classes. However, this binary classification is unlikely to ever fully capture the complexity of real landscapes: land cover classes will not perfectly reflect 'habitat', while matrix cover classes may be used to some extent (Lindenmayer and Fischer 2007). Consequently, the estimated effects of habitat loss versus fragmentation will depend not only on the 'true' effects of these processes, but also on how well the measured landscape metrics actually represent the amount and spatial configuration of habitat from the perspective of the species under study. We stress, however, that the causal basis of collinearity among landscape metrics – and consequently, the presence of indirect effects – will be the same regardless of how well habitat maps reflect the biology of the species in question. This is because the interplay between 'habitat' (however this has been defined) and the ecological response variable occurs exclusively via the direct effect of the landscape metric on the ecological response. Substituting one response variable ('abundance of forest birds', for example) for another ('abundance of beetles') is likely to change the strength of the relationship between each landscape metric and the response variable, but will have no effect on any causal relationships among metrics.

***Conclusions***

Collinearity among metrics of habitat loss and fragmentation may be more than merely a statistical nuisance. Our results highlight the possibility that collinearity arises from causal relationships among landscape metrics, and therefore signals the occurrence of indirect effects on the response variable. If so, statistical methods such as multiple regression that remove collinear information prior to estimating effects will be inadequate for answering research questions that require an understanding of total (direct + indirect) effects, rather than direct effects alone. In contrast, path analysis can empirically test the causal basis of collinearity, explicitly model any indirect effects that this collinearity implies, and give unbiased estimates of direct, indirect, and total effects.

Nonetheless, we stress that to date there have been no empirical tests of whether causal relationships among landscape metrics, or the indirect effects that they imply, exist in real landscapes. Although this hypothesis seems likely (Didham, et al. 2012), testing it with data may reveal the alternative: that landscape metrics are only ever collinear because they are jointly influenced by external processes. If so, indirect effects on the response variable will never occur, and multiple regression will be sufficient for measuring relative effects. However, given the significant implications of causal relationships among landscape metrics for landscape ecology (in terms of both measuring the relative effects of collinear landscape metrics and understanding the mechanistic pathways through which land use change influences ecological systems; Didham, et al. 2012) we suggest that a priority for progressing understanding of the relative effects of habitat loss versus fragmentation is to (1) empirically test the causal basis of collinearity by specifying hypotheses why collinear landscape metrics are related (the causal models in Figure 1a or 1b, for example) and then measuring support for these hypotheses with empirical data, then (2) measure relative effects while accounting for any indirect effects that this causal basis implies. Path analysis, but not multiple regression, provides a tool to do so.

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**Supplementary material**

The following can be found in the online supplement:

Appendix 1. Deriving equations used to simulate datasets.

Appendix 2. Testing whether our equations produced realistic combinations of landscape metrics.

## Table and figure captions

**Table 1:** Comparison of the datasets used in this study with those used by Smith et al. (2009). We simulated our landscape metrics, habitat amount (Amount), mean patch size (MPS), amount of edge habitat (Edge), and landscape heterogeneity (Hetero), so that they matched those of Smith et al. in terms of their means, variances, and degree of collinearity, and we simulated our response variable so that it matched Smith et al.'s in terms of the proportion of its variance explained by the four landscape metrics. However, whereas the cause of collinearity among metrics in Smith et al.'s datasets was unknown, collinearity in our data was known to arise from causal relationships among metrics (see main text for description). We simulated 100 datasets of landscape metrics and response variables, and table values show means and standard deviations averaged across these datasets. Smith et al. simulated 100 datasets of response variables from a single empirical dataset of landscape metrics, so correlations among their metrics are given as a single number.

**Figure 1:** The importance of accounting for the causal basis of collinearity when quantifying the effects of correlated landscape predictors. Panels (A) and (B) show alternative causes of collinearity between two landscape metrics, habitat amount (Amount) and mean patch size (MPS), together with the direct and indirect effects of these metrics on an ecological response variable. In panel (A), metrics are causally independent, but correlated because they are jointly influenced by unmeasured variables. Because variables do not causally influence each other there are no indirect effects on the response variable. In panel (B), metrics are causally related, with collinearity occurring because changes to Amount cause changes in MPS. In this case,

Amount and MPS both influence the response variable directly (solid lines). However, because the value of MPS is partly influenced by the value of Amount, part of the direct effect of MPS is also ultimately an indirect effect of Amount (dashed line). Panel (C) shows the equation used by Smith et al. (2009) to test the ability of different statistical approaches to measure the independent (i.e. direct) effects of Amount and MPS on a simulated response variable, together with the conceptual model implied by this equation. Numbers beside single- and double-headed arrows in this panel show the coefficients used for simulated effects and the correlation observed between Amount and MPS, respectively. These coefficients were defined as the 'true [direct] effects' in this study, against which statistical estimates were benchmarked. However, without examining the causal basis of collinearity among their landscape metrics, it is not possible to know whether these direct effects also represented total effects, as would be the case if metrics were causally independent, or were biased estimates of total effects because they ignored indirect effects, as would be the case if metrics were causally related. Following path modelling conventions, double-headed arrows represent collinearity among variables whose cause is ignored, while single-headed arrows represent modelled causal effects.

**Figure 2**. Hypothetical model of causal relationships among the four landscape metrics measured by Smith et al. (2009), used in this study to examine the effects of causal relationships among landscape predictors on the efficacy of multiple regression and path analysis. In the model, habitat amount (Amount) causally influences total amount of edge habitat (Edge), mean patch size (MPS), and landscape heterogeneity (Hetero) (single headed arrows), while Edge, MPS, and Hetero are causally independent from one another but correlated because they are jointly influenced by Amount (double headed arrows). Numbers give the correlations among these metrics observed by Smith et al. (2009), and numbers in parentheses give the correlations

among Edge, MPS, and Hetero that would be predicted under this hypothetical causal model. The predicted correlations were calculated as the product of the correlations between each metric and Amount, following standard path modelling rules (Grace 2006).

**Figure 3:** Multiple regression and path analysis estimates of direct, indirect, and total (direct + indirect) effects of four collinear landscape metrics on a simulated response variable, where metrics either did (circles) or did not (triangles) indirectly influence the response variable. Metrics were: habitat amount ('A'), total amount of edge habitat ('E'), landscape heterogeneity ('H'), and mean patch size ('M'). Effect sizes were estimated separately from 100 datasets; symbols and their error bars show means and 95% confidence intervals for these estimates, respectively. Confidence intervals were measured as the effect estimates corresponding to the 2.5 and 97.5 percentiles, following Smith et al. (2009). Grey bars show the true values of effects based on the coefficients that were used to simulate the data, and braces highlight those effect estimates that deviated from these true values. We note that multiple regression is unable to measure indirect effects, so these effects were manually assigned a value of zero rather than being estimated from model output.

**Figure 4:** Estimates of the total (direct + indirect) effects of habitat amount on a simulated response variable measured by multiple regression (circles) and path analysis (triangles) under different levels of collinearity between habitat amount and a second variable, mean patch size (MPS), which also affected the response variable. Collinearity occurred because habitat amount causally influenced MPS, giving rise to indirect effects of habitat amount on the response variable. Effect sizes were estimated separately for 100 datasets; symbols and their error bars show means and 95% confidence intervals for these estimates, respectively. Confidence

intervals were measured as the effect estimates corresponding to the 2.5 and 97.5 percentiles, following Smith et al. (2009). Grey bars show the true values of the total effects of habitat amount on the response variable, based on the coefficients that were used to simulate the data. The declining multiple regression estimates reflect the fact that simulation coefficients corresponding to direct effects had to be decreased in order to keep $R^2$ values, means and variances constant while increasing collinearity among predictors.

Table 1

| | **Present study** | **Smith et al. (2009)** |
|---|---|---|
| **Variable means and variances** | | |
| Response | 0.05 ± 1.00 | Not given |
| Amount | -0.01 ± 1.02 | 0 ± 1* |
| MPS | 0.02 ± 1.02 | 0 ± 1* |
| Edge | 0.00 ± 1.01 | 0 ± 1* |
| Hetero | 0.02 ± 1.00 | 0 ± 1* |
| **Correlations among landscape metrics** | | |
| Amount:MPS | 0.76 ± 0.06 SD | 0.76 |
| Amount:Edge | 0.90 ± 0.05 SD | 0.90 |
| Amount:Hetero | 0.57 ± 0.06 SD | 0.57 |
| MPS:Edge | 0.69 ± 0.06 SD | 0.68 |
| MPS:Hetero | 0.43 ± 0.06 SD | 0.41 |
| Edge:Hetero | 0.51 ± 0.06 SD | 0.51 |
| **Strength of direct effects of landscape metrics on response variable** | | |
| Variance in response explained by Amount + MPS + Edge + Hetero | 50.70 ± 4.14 SD % | ~50 %* |

*As described in text by Smith et al. (2009)