

Which landscape size best predicts the influence of forest cover on restoration success? A global meta-analysis on the scale of effect

Renato Crouzeilles^{1,2*} and Michael Curran³

¹Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro CEP 21941-590, Brazil; ²International Institute for Sustainability, Rio de Janeiro, Rio de Janeiro CEP 22460-320, Brazil; and ³Swiss Federal Institute of Technology (ETH) Zürich, Chair of Ecological Systems Design (ESD), Institute of Environmental Engineering (IfU), Zürich 8093, Switzerland

Summary

1. Landscape context is a strong predictor of species persistence, abundance and distribution, yet its influence on the success of ecological restoration remains unclear. Thus, a primary question arises: which landscape size best predicts the effects of forest cover on restoration success?

2. To answer this question, we conducted a global meta-analysis for biodiversity (mammals, birds, invertebrates, herpetofauna and plants) and measures of vegetation structure (cover, density, height, biomass and litter). Response ratios were calculated for comparisons between reference (e.g. old-growth forest) and disturbed sites (degraded or restored). Using an information-theoretic approach, mean response ratio (restoration success) and response ratio variance (restoration predictability) within each study landscape were regressed against the percentage of overall (summed forest cover) and contiguous (summed pixels of $\geq 60\%$ forest cover) forest within eight different buffer sizes of radius 5–200 km (at 1-km resolution).

3. We included 247 studies encompassing 196 study landscapes and 4360 quantitative comparisons. The best buffer (landscape) size varied for the following: (i) overall and contiguous forest cover, (ii) biodiversity and vegetation structure and (iii) mean response ratio and response ratio variance. Only plant biodiversity was influenced by overall forest cover (buffer size of 5, 10 and 200 km radii), while plants (10 and 200 km radii), mammals (5, 10 and 50–200 km radii), invertebrates (5 and 10 km radii), cover (5 km radii), height (5 km radii) and litter (100 km radii) were influenced by contiguous forest cover. Overall, mean response ratio and response ratio variance were positively and negatively nonlinearly related with both overall and contiguous forest cover, respectively.

4. We reveal for the first time a clear pattern of increasing restoration success and decreasing uncertainty as contiguous forest cover increases. We also indicate preliminary recommended buffer sizes for investigating landscape restoration effects on biodiversity and vegetation structure. However, the coarse grain and variability in the data mean the optimal landscape size may not have been detected; thus, further research is needed.

5. *Synthesis and applications.* When setting targets for ecological restoration, policymakers and restoration practitioners should account for the following: (i) the landscape context, particularly the amount of contiguous habitat up to 10 km around a disturbed site, and (ii) the uncertainty in restoration success, as it increases when contiguous forest cover falls below about 50%.

Key-words: amphibians, birds, buffer size, fragmentation, habitat loss, invertebrates, mammals, reptiles, species composition, vegetation structure

*Corresponding author. E-mail: renatocrouzeilles@gmail.com

Introduction

Landscape context is a strong predictor of species persistence, abundance and distribution (e.g. Ewers & Didham 2006; Villard & Metzger 2014), but yet to understand how it affects ecological restoration remains unclear (Leite *et al.* 2013). Most restoration assessments have been carried out at a local scale (<1 ha), potentially missing the effects of landscape context (>1000 ha) on the success of ecological restoration, that is return to a condition used as reference (hereafter restoration success) (Bowen *et al.* 2007). In 2004, the Society of Ecological Restoration produced a document entitled '*Primer on Ecological Restoration*', recognizing landscape context as an important variable to be considered in restoration assessments (Society of Ecological Restoration International Science and Policy Working Group 2004), yet it is rarely assessed in practice.

The surrounding forest cover has been documented as a key predictor of where ecosystem recovery take holds (Leite *et al.* 2013). Forest areas can act both as a source of seeds for the colonization of disturbed sites and as critical habitat for seed dispersers (Chazdon 2003; Helmer *et al.* 2008). Contrarily, many forests around the world are theorized to be sink habitats, that is areas where mortality rates are higher than reproduction rates (Pulliam 1998; Bowen *et al.* 2007); thus, one would expect local extinctions unless viable populations of dispersers remain in nearby source habitat (Brook, Sodhi & Ng 2003; Dunn 2004). A recent global meta-analysis showed a slower development of plant and animal communities in both replanted and naturally regenerating sites that are isolated from source forests, compared to connected sites (Curran, Hellweg & Beck 2014). Therefore, restoration assessments should explicitly quantify the effects of landscape context on restoration success. To do this, a primary question arises: which landscape size (i.e. scale of effect) is most relevant to predict the influence of landscape context on restoration success?

A common procedure to identify the scale of effect is by establishing hierarchical, multilevel buffers around sampling locations to detect species' responses at different or even multiple scales (Brennan *et al.* 2002; Boscolo & Metzger 2009). Species traits such as body size, dispersal ability and home range size can help to explain such variability (Jackson & Fahrig 2012; Stevens *et al.* 2014). Most studies applying multiple buffer sizes to identify the scale of effect showed highest predictive power at either the largest or the smallest scales observed, indicating the strongest predictive scale was potentially outside the range included in the study (Jackson & Fahrig 2015). For example, the number of species in a restored site can be poorly estimated if forest cover is not measured at the strongest predictive scale. To identify the strongest scale of effect, forest cover should be measured encompassing different orders of magnitude and based on biological reasons (Jackson & Fahrig 2015).

Here, we assess whether, and at which landscape size, the percentage of both overall (all forest remnants ≥ 9 ha) and contiguous (1-km pixels with $\geq 60\%$ forest cover only) forest cover is relevant to predict restoration success of biodiversity and vegetation structure. We hypothesize that the scale of effect of forest cover on restoration success is as follows: (i) stronger for contiguous than overall forest cover as contiguous forests are more likely to be less disturbed by humans and consequently harbour populations of dispersers and (ii) more variable and stronger at larger scales for biodiversity than vegetation structure as dispersal ability may permit species to explore larger portions of a landscape. To do so, we conducted a global meta-analysis of restoration success for biodiversity and vegetation structure in forest ecosystems. We calculated an effect size for each comparison between reference (*less disturbed forests* in an old-growth state) and disturbed sites (*restored or degraded*) within the same assessment. The *restored sites* represent selectively logged forests, or actively or passively restored forests in an initial or secondary stage of succession, and the *degraded sites* represent different types of human land use like plantation or agriculture – the starting point of the restoration process (e.g. Rey Benayas *et al.* 2009). We also estimated both overall and contiguous forest cover within different buffer sizes at each study landscape. Our results revealed for the first time a clear pattern of increasing restoration success and decreasing uncertainty as the amount of contiguous forest cover increases.

Materials and methods

META-ANALYSIS OF RESTORATION SUCCESS

We conducted an extensive analysis of all recorded studies in seven key reviews on either biodiversity recovery or ecological succession of vegetation structure in degraded and/or restored forest ecosystems (Dunn 2004; Ruiz-Jaen & Aide 2005; Bowen *et al.* 2007; Rey Benayas *et al.* 2009; Gibson *et al.* 2011; Wortley, Hero & Howes 2013; Curran, Hellweg & Beck 2014). Despite a common focus on degraded and/or restored forest ecosystems, many of the studies included in each review were exclusive (i.e. selected by one review only), indicating variable search and inclusion criteria (Table S1, Supporting Information). We included studies that were: (i) conducted in forest ecosystems, (ii) used multiple sampling locations (replicates for both reference and disturbed sites) to measure biodiversity and/or vegetation structure and (iii) included less disturbed forest in an old-growth state as a comparable reference for the disturbed sites under study. In each study, we characterized results for biodiversity into five taxonomic groups (mammals, birds, invertebrates, herpetofauna and plants) and results for vegetation structure indicators into five measures related to ecological succession (cover, density, height, biomass and litter) (Ruiz-Jaen & Aide 2005).

To quantify restoration success, we used response ratios, measured as the standardized mean effect size of each comparison within the same assessment (Hedges, Gurevitch & Curtis 1999). The response ratio is measured as $\ln(\bar{x}_{\text{disturbed}}/\bar{x}_{\text{reference}})$,

where \bar{x} is the mean value for a quantified variable within all sampling locations. It ranges from negative to positive values, with negative values implying that either biodiversity/vegetation structure decrease in disturbed compared with reference sites, while the opposite holds for positive values. Response ratio values around zero are the desired outcome of restoration projects, that is success in bringing a quantified variable in a disturbed site back to the reference state. For our statistical analysis, we inverted response ratios of biodiversity and vegetation structure that are *a priori* expected to exhibit positive values (i.e. higher in disturbed than in reference sites). These are, for example, measures of openness, introduced species, grasses (e.g. Gibson *et al.* 2011). As our main interest was to represent restoration outcomes for multiple species, community-level biodiversity data were gathered for ecological metrics that assess multiple species (richness, diversity and similarity) or population patterns in a community (abundance). To facilitate a deeper understanding of biodiversity responses to restoration, we analysed the response ratios of each taxonomic group separately, pooling data from different ecological metrics.

LANDSCAPE DATA

We mapped forested areas within each study landscape to estimate the percentage of forest cover. When geographic coordinates were not available, we contacted the corresponding authors. As restoration success was calculated for an average number of sampling locations (replicates) per treatment, we tried to position geographic coordinates in the centre of location clusters from each study. Thus, we refer to the 'study landscape' as the unit of analysis rather than the sampling location. Forest cover data were based on a recent 1-km resolution consensus land cover data set (Tuanmu & Jetz 2014), derived from combining three existing land cover products (GLC 2000, MODIS 2005 and ESA GlobCover 2008). We chose to use the 'reduced' data set (Tuanmu & Jetz 2014), excluding the DISCover product from 1995 to avoid the influence of pre-2000 deforestation. The land cover data express subpixel coverage of 12 land cover types (evergreen/deciduous needleleaf trees, evergreen broadleaf trees, deciduous broadleaf trees, mixed/other trees, shrubs, herbaceous vegetation, cultivated and managed vegetation, regularly flooded vegetation, urban/built-up, snow/ice, barren and open water). To represent as robustly as possible the extent of forest vegetation within the landscape, we included only the first three land cover classes, excluding the 'mixed/other trees' that contains both forest and non-forest land cover types.

The finest resolution of the land cover products included in the consensus data set (ESA GlobCover 2008) has a spatial resolution of 300 m, implying subpixel information can detect forest remnants ≥ 9 ha. Higher resolution forest cover data sets are available (e.g. 30-m resolution), but we considered the consensus data set more robust to temporal variation due to the need for agreement between products of different time periods. In addition, this consensus data set was tested for accuracy in an ecological modelling context (Tuanmu & Jetz 2014). The relatively coarse resolution of our biodiversity/vegetation structure data (i.e. a collection of locations representing a landscape sampling unit) meant high resolution forest cover data was not necessary, and the subpixel information of the consensus data set was sufficient for our purposes.

We estimated percentage of forest cover within each study landscape in two ways, considering: (i) all forest remnants ≥ 9 ha (*over-*

all forest cover) and (ii) forest cover defined as those pixels with a minimum forest cover proportion of 0.6 (*contiguous forest cover*) (Fig. 1). The overall forest cover map was constructed based on total subpixel proportional forest cover (0–1) within each 1-km pixel, summed up across all pixels in the landscape. Contiguous forest cover was estimated based on Percolation theory (Stauffer 1985), which predicts that above 60% habitat within simulated artificial landscapes forest cover becomes highly or completely connected (i.e. contiguous), independent of the landscape size. We classed contiguous forest as a binary forest/non-forest map, in which only forest pixels ($\geq 60\%$ cover) were summed up.

The percentage of forest cover for both maps (overall and contiguous) was estimated within each study landscape using eight different buffer sizes: 5, 10, 25, 50, 75, 100, 150 and 200 km (as a radius of a circle), that is ranging from 7854 to 12 566 400 ha. A recent review of comparative diversity studies in restored habitats (Curran, Hellweg & Beck 2014) found the median distance between sites to be 5.3 km (M. Curran unpublished data). Thus, we judged a 5 km radius to be a suitable lower bound for this type of analysis. Hence, we increased the range of buffer sizes up to two orders of magnitude following the recommendations of Jackson & Fahrig (2015). All area calculations were conducted within the equal-area World Mollweide projection (EPSG: 54009). All geographic analyses were carried out using the Geographic Resource Analysis Support System GIS, vers. 6.4.3 (GRASS Development Team 2013), and Quantum GIS, vers. 2.6.1 (QGIS Development Team 2014).

MODEL SELECTION

To avoid spatial pseudo-replication (multiple samples for the same study landscape), we modelled the mean response ratio (i.e. restoration success) for each study landscape and biodiversity/vegetation structure as a function of the percentage of overall and contiguous forest cover within the eight different buffer sizes. In addition, we modelled the response ratio variance to investigate the predictability (i.e. uncertainty) of restoration success across the gradient of overall and contiguous forest cover. Thus, only study landscapes with more than one response ratio for the same quantified variable were used. Study landscapes could have multiple response ratios if they were the focus of multiple studies, or the same study analysed the following: (i) multiple ecological metrics (abundance, richness, diversity and/or similarity), (ii) more than one guild (e.g. frugivores and insectivores birds), (iii) lower taxonomic group divisions than applied in our analysis (e.g. hemiptera and hymenoptera) or (iv) different years or seasons separately.

We used an information-theoretic approach (Burnham & Anderson 2002) to identify whether and at which buffer size (scale of effect) the percentage of both overall or contiguous forest cover best predicts mean response ratio and response ratio variance. We fitted generalized linear models to compare a set of candidate buffer sizes for each taxonomic group and measures of vegetation structure. The mean response ratio was modelled assuming a normal distribution where the values were continuous and varying between negative and positive infinite (Bolker 2008). The response ratio variance was modelled assuming a gamma distribution where the values were continuous but varying between 0 and positive infinite (Bolker 2008). We used the identity link function for all models. Models with normal residuals were fitted separately for each data set, totalling 40 separate analyses: five taxonomic groups and

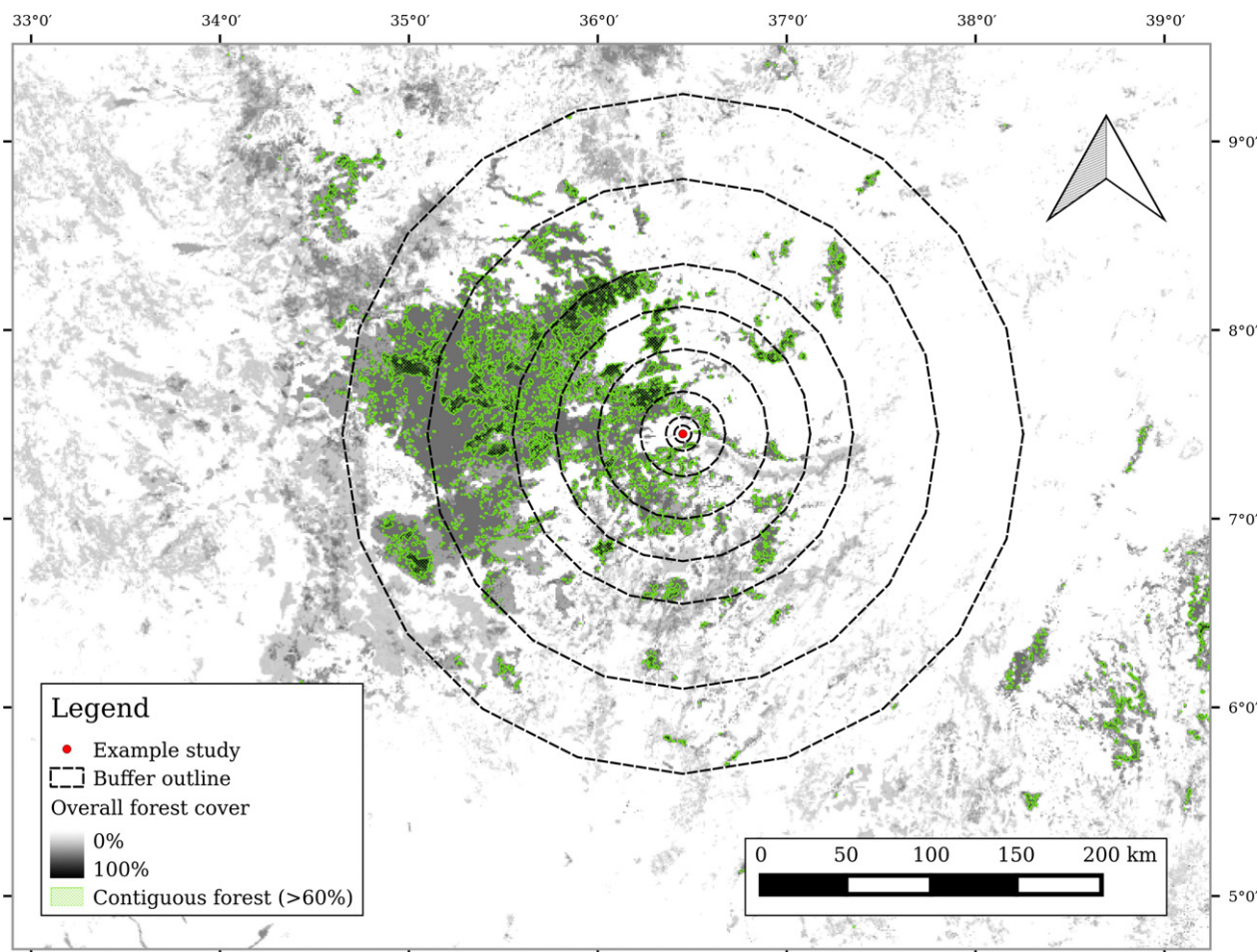


Fig. 1. Example of the eight buffer sizes (ranging from 5 to 200 km radius) in the study landscape of Aerts *et al.* (2008). Overall forest cover includes a gradient of forest ranging from 0 (white) to 100% (black) and differs in the amount of forest into each 1-km pixel (fine-scaled data). Contiguous forest cover includes each 1-km pixel with $\geq 60\%$ forest cover (green and hatched green).

five measures of vegetation structure vs. mean response ratio and response ratio variance vs. overall and contiguous forest cover. In each analysis, we compared nine models, eight containing the percentage of either overall or contiguous forest cover within each buffer size, plus a null model containing only the intercept and error as parameters. We log-transformed the percentage of overall and contiguous forest cover because it could be nonlinearly related with the response variables. We calculated for each model the Akaike Information Criterion corrected for small samples (AICc), the Δ_i as $AICc_i - \text{minimum AICc}$ and the Akaike weight (w_i), indicating the probability that the model i is the best model within the set (Burnham & Anderson 2002). Models with $\Delta_i < 2$ were considered equally plausible to the top-ranked model, that is the scale of effect can range across these scales (Jackson & Fahrig 2015). We used the generalized R^2 (for normal distribution) and adjusted R^2 (for gamma distribution) as a coefficient of determination to represent the goodness-of-fit of the model (Nagelkerke 1991). All analyses were carried out in R 2.12 (R Development Core Team 2011).

Results

From 269 selected studies (Table S2), 247 were suitable studies for further analysis (more than one response ratio for the same quantified variable), encompassing 196 study

landscapes and 4360 quantitative comparisons between reference and disturbed sites. More than 73% of these comparisons were between reference and restored sites. These data were collected in the field from 1981 to 2009. Six of the seven biogeographic realms proposed by Olson *et al.* (2001) were included in our analysis, but most studies (49.3%) were conducted in the Neotropics, encompassing 82 study landscapes. Data on biodiversity (83.2% of samples) were more common than vegetation structure.

The best buffer size varied for the following: (i) overall and contiguous forest cover, (ii) taxonomic groups and measures of vegetation structure and (iii) mean response ratio and response ratio variance (Tables 1 and 2). Only plant biodiversity was influenced by overall forest cover, while plants, mammals, invertebrates, cover, height and litter were influenced by contiguous forest cover (Tables 1 and 2). Multilevel buffers affected the same taxonomic group, but not the same measure of vegetation structure.

OVERALL FOREST COVER

In general, for all taxonomic groups and measures of vegetation structure, the null model was considered among

Table 1. Performance of models predicting either mean response ratio or response ratio variance as a function of percentage of overall forest cover derived from eight different buffer sizes of radius 5–200 km. Analyses were carried out separately for each taxonomic group and measure of vegetation structure. Buffer = km radius, Δ_i = AIC_c – minimum AICc and w_i = Akaike weight. R^2 = generalized for mean response ratio and adjusted for response ratio variance. R^2 was omitted when the null model was among the most plausible models ($\Delta_i < 2$). In parentheses, the number of study landscapes = sample size. In bold are the plausible models ($\Delta_i < 2$).

Mean response ratio															
(A) Plants (78)				(B) Mammals (27)			(C) Invertebrates (66)			(D) Birds (57)			(E) Herpetofauna (18)		
Buffer	Δ_i	w_i	R^2	Buffer	Δ_i	w_i	Buffer	Δ_i	w_i	Buffer	Δ_i	w_i	Buffer	Δ_i	w_i
Null	0.00	0.20		Null	0.00	0.25	100	0.00	0.22	Null	0.00	0.24	Null	0.00	0.27
50	0.96	0.12		75	1.27	0.13	150	0.80	0.15	75	1.49	0.11	25	1.69	0.12
25	0.98	0.12		100	1.50	0.12	75	0.83	0.14	50	1.57	0.11	50	1.69	0.12
75	1.17	0.11		50	1.75	0.10	200	0.92	0.14	25	1.78	0.10	5	2.02	0.10
200	1.34	0.10		25	2.06	0.09	Null	1.60	0.10	10	1.89	0.09	10	2.02	0.10
150	1.56	0.09		10	2.29	0.08	50	1.82	0.09	100	1.92	0.09	75	2.10	0.09
10	1.56	0.09		5	2.30	0.08	25	2.24	0.07	5	1.98	0.09	200	2.56	0.08
100	1.61	0.09		200	2.44	0.07	10	2.89	0.05	150	2.16	0.08	100	2.76	0.07
5	1.70	0.08		150	2.44	0.07	5	2.91	0.05	200	2.19	0.08	150	2.90	0.06
(F) Cover (35)				(G) Height (24)			(H) Density (34)			(I) Biomass (32)			(J) Litter (10)		
Null	0.00	0.26		Null	0.00	0.23	Null	0.00	0.15	Null	0.00	0.26	Null	0.00	0.43
200	1.46	0.13		10	1.43	0.11	100	0.10	0.14	150	1.80	0.11	25	3.50	0.08
150	1.66	0.12		25	1.46	0.11	150	0.14	0.14	200	1.80	0.11	10	3.50	0.08
100	2.13	0.09		50	1.49	0.11	200	0.41	0.12	100	1.86	0.10	5	3.51	0.07
25	2.37	0.08		5	1.60	0.11	75	0.78	0.10	5	1.97	0.10	150	3.58	0.07
50	2.38	0.08		75	1.63	0.10	50	0.90	0.09	10	2.20	0.09	200	3.60	0.07
10	2.39	0.08		100	2.00	0.09	25	0.98	0.09	75	2.25	0.08	100	3.72	0.07
75	2.40	0.08		150	2.43	0.07	5	1.08	0.09	50	2.37	0.08	50	3.73	0.07
5	2.40	0.08		200	2.59	0.06	10	1.13	0.08	25	2.38	0.08	75	3.82	0.06
Response ratio variance															
(K) Plants (78)				(L) Mammals (27)			(M) Invertebrates (66)			(N) Birds (57)			(O) Herpetofauna (18)		
5	0.00	0.30	0.08	Null	0.00	0.23	Null	0.00	0.26	10	0.00	0.15	Null	0.00	0.30
200	0.60	0.22	0.07	150	1.09	0.13	5	1.64	0.11	5	0.14	0.14	75	2.02	0.11
10	1.61	0.13	0.05	200	1.27	0.12	10	1.89	0.10	100	0.22	0.13	100	2.12	0.10
Null	2.26	0.10	–	100	1.57	0.10	200	2.07	0.09	150	0.37	0.12	5	2.28	0.10
150	2.57	0.08	0.03	5	1.62	0.10	100	2.09	0.09	25	0.65	0.11	50	2.44	0.09
25	3.33	0.06	0.02	10	1.65	0.10	25	2.10	0.09	50	0.82	0.10	150	2.68	0.08
50	3.97	0.04	0.01	25	2.08	0.08	150	2.13	0.09	75	0.85	0.10	10	2.76	0.08
100	4.24	0.04	0.00	50	2.43	0.07	75	2.17	0.09	200	1.08	0.09	25	2.85	0.07
75	4.35	0.03	0.00	75	2.49	0.07	50	2.17	0.09	Null	1.29	0.08	200	2.87	0.07
(P) Cover (34)				(Q) Height (24)			(R) Density (34)			(S) Biomass (31)			(W) Litter (10)		
Null	0.00	0.26		Null	0.00	0.17	Null	0.00	0.29	Null	0.00	0.22	Null	0.00	0.49
5	1.23	0.14		25	0.60	0.13	150	2.27	0.09	200	0.14	0.20	200	3.62	0.08
10	1.82	0.11		75	0.60	0.13	200	2.34	0.09	150	1.27	0.12	150	3.79	0.07
25	2.15	0.09		50	0.61	0.13	50	2.38	0.09	50	1.74	0.09	50	4.14	0.06
50	2.36	0.08		10	0.98	0.11	75	2.39	0.09	75	1.82	0.09	10	4.15	0.06
200	2.40	0.08		100	1.33	0.09	25	2.41	0.09	25	1.87	0.09	25	4.22	0.06
150	2.40	0.08		5	1.40	0.09	5	2.41	0.09	10	2.34	0.07	100	4.25	0.06
100	2.40	0.08		150	1.43	0.08	100	2.41	0.09	100	2.42	0.07	75	4.26	0.06
75	2.41	0.08		200	1.61	0.08	10	2.41	0.09	5	2.45	0.06	5	4.26	0.06

the most plausible models ($\Delta_i < 2$) to explain the mean response ratio (w_i always ≥ 0.10) (Table 1A–J) and response ratio variance (w_i always ≥ 0.08) (Table 1L–W). Only for plants, the top-ranked model to explain response ratio variance was the buffer size of 5 km radius

($w_i = 0.3$), with buffer sizes of 200 and 10 km radius considered equally plausible ($\Delta_i = 0.6$ and 1.61, $w_i = 0.22$ and 0.13, respectively) (Table 1K). The response ratio variance was negatively nonlinearly related with overall forest cover for these three plausible buffer sizes.

Table 2. Performance of models predicting either mean response ratio or response ratio variance as a function of percentage of contiguous forest cover (1-km pixels with >60% forest cover only). Analyses were carried out separately for each taxonomic group and measure of vegetation structure. Buffer = km radius, Δ_i = AICc_i – minimum AICc and w_i = Akaike weight. R^2 = generalized for mean response ratio and adjusted for response ratio variance. R^2 was omitted when the null model was among the most plausible models ($\Delta_i < 2$). In parentheses, the number of study landscapes = sample size. In bold are the plausible models ($\Delta_i < 2$).

Mean response ratio																			
(A) Plants (60)				(B) Mammals (22)				(C) Invertebrates (51)				(D) Birds (51)				(E) Herpetofauna (15)			
Buffer	Δ_i	w_i	R^2	Buffer	Δ_i	w_i	R^2	Buffer	Δ_i	w_i	R^2	Buffer	Δ_i	w_i	Buffer	Δ_i	w_i	R^2	
10	0.00	0.66	0.13	5	0.00	0.30	0.19	25	0.00	0.20		Null	0.00	0.25	Null	0.00	0.38		
25	2.82	0.16	0.09	10	1.06	0.18	0.15	50	0.58	0.15		50	1.64	0.11	150	3.09	0.08		
5	4.13	0.08	0.07	100	2.06	0.11	0.11	Null	0.90	0.13		5	1.83	0.10	10	3.09	0.08		
50	6.03	0.03	0.04	75	2.42	0.09	0.10	5	1.19	0.11		25	1.85	0.10	200	3.14	0.08		
Null	7.21	0.02	–	50	2.71	0.08	0.08	75	1.53	0.09		75	1.87	0.10	100	3.15	0.08		
75	7.29	0.02	0.02	150	2.75	0.08	0.08	10	1.66	0.09		100	1.99	0.09	50	3.17	0.08		
100	7.89	0.01	0.01	Null	3.01	0.07	–	100	1.90	0.08		150	2.11	0.09	25	3.17	0.08		
150	8.14	0.01	0.00	25	3.08	0.06	0.07	150	2.00	0.07		200	2.18	0.08	75	3.18	0.08		
200	8.33	0.01	0.00	200	3.75	0.05	0.04	200	2.07	0.07		10	2.19	0.08	5	3.18	0.08		
(F) Cover (26)				(G) Height (16)				(H) Density (28)				(I) Biomass (27)				(J) Litter (8)			
5	0.00	0.55	0.15	Null	0.00	0.35		Null	0.00	0.22		Null	0.00	0.30	100	0.00	0.44	0.56	
Null	2.93	0.13	–	5	2.29	0.11		200	1.17	0.12		10	2.29	0.09	Null	2.17	0.15	–	
10	4.10	0.07	0.01	10	2.85	0.08		100	1.22	0.12		200	2.37	0.09	25	2.75	0.11	0.38	
75	4.96	0.05	–0.02	25	2.95	0.08		5	1.22	0.12		75	2.43	0.09	50	3.27	0.09	0.34	
150	5.00	0.05	–0.02	200	3.07	0.08		150	1.29	0.11		100	2.47	0.09	10	4.07	0.06	0.27	
100	5.09	0.04	–0.03	75	3.07	0.08		75	1.54	0.10		50	2.49	0.09	75	4.13	0.06	0.26	
50	5.25	0.04	–0.03	100	3.07	0.08		50	2.11	0.08		25	2.51	0.09	150	4.40	0.05	0.23	
200	5.33	0.04	–0.03	150	3.07	0.08		10	2.35	0.07		5	2.53	0.08	200	5.24	0.03	0.15	
25	5.48	0.04	–0.04	50	3.08	0.08		25	2.41	0.07		150	2.54	0.08	5	5.72	0.03	0.1	
Response ratio variance																			
(K) Plants (60)				(L) Mammals (22)				(M) Invertebrates (51)				(N) Birds (51)				(O) Herpetofauna (15)			
200	0	0.6	0.15	100	0	0.27	0.34	5	0	0.33	0.17	Null	0	0.21	Null	0	0.2		
150	2.74	0.15	0.10	75	0.38	0.22	0.32	10	1.22	0.18	0.12	10	0.53	0.16	150	0.29	0.17		
100	4.37	0.07	0.06	150	0.51	0.21	0.32	Null	2.15	0.11	–	2	1.36	0.11	200	0.31	0.17		
Null	4.99	0.05	–	200	1.78	0.11	0.25	200	2.43	0.10	0.08	25	1.43	0.1	100	0.76	0.14		
75	5.57	0.04	0.04	50	1.79	0.11	0.25	150	3.01	0.07	0.05	5	1.48	0.1	75	1.55	0.09		
5	6.41	0.02	0.02	Null	3.54	0.05	–	100	3.44	0.06	0.04	150	1.62	0.09	50	1.94	0.08		
10	6.44	0.02	0.02	25	5.15	0.02	0.07	25	3.46	0.06	0.04	100	1.92	0.08	10	2.22	0.07		
50	6.67	0.02	0.01	10	6.13	0.01	0.01	75	3.69	0.05	0.03	75	2.08	0.07	25	2.83	0.05		
25	7.19	0.02	0.00	5	6.24	0.01	0.00	50	3.72	0.05	0.03	50	2.19	0.07	5	3.08	0.04		
(P) Cover (25)				(Q) Height (16)				(R) Density (28)				(S) Biomass (26)				(W) Litter (8)			
25	0	0.24		5	0	0.56	0.32	25	0	0.22		Null	0	0.24	Null	0	0.22		
Null	0.76	0.16		Null	2.52	0.16	–	Null	0.72	0.15		5	0.98	0.15	5	0.31	0.19		
200	1.61	0.11		10	4.12	0.07	0.1	100	1.44	0.11		10	1.07	0.14	25	0.39	0.18		
10	1.83	0.10		200	5.46	0.04	0.02	150	1.54	0.1		200	1.68	0.1	10	0.39	0.18		
50	1.99	0.09		25	5.55	0.04	0.01	50	1.55	0.1		150	2.06	0.09	50	2.19	0.07		
100	2.07	0.09		50	5.55	0.03	0.01	10	1.68	0.09		50	2.36	0.07	100	2.66	0.06		
75	2.1	0.08		75	5.6	0.03	0.01	200	1.97	0.08		25	2.47	0.07	75	3.46	0.04		
150	2.22	0.08		100	5.61	0.03	0.01	75	2.15	0.07		75	2.51	0.07	150	4.23	0.03		
5	2.92	0.06		150	5.67	0.03	0.00	5	2.36	0.07		100	2.55	0.07	200	4.74	0.02		

CONTIGUOUS FOREST COVER

For plants, mammals, cover and litter, at least one buffer size was considered plausible to explain the mean response

ratio (Table 2A–J). The only plausible model was the buffer size of 10 km radius for plants ($w_i = 0.13$), 5 km radius for cover ($w_i = 0.55$) and 100 km radius for litter

($w_i = 0.44$), the last having a small sample size ($n = 8$) (Table 2A, F and J, respectively). For mammals, the top-ranked model was the buffer size of 5 km radius ($w_i = 0.19$), with the buffer size of 10 km radius considered equally plausible ($\Delta_i = 1.06$, $w_i = 0.15$) (Table 2B). The null model was considered among the most plausible models for all other taxonomic groups and measures of vegetation structure (w_i always ≥ 0.13) (Table 2C– and G–I). The mean response ratio was negatively nonlinearly related with contiguous forest cover for plants (Fig. 2A), but positively nonlinearly related for mammals, cover and litter (Fig. 2C, G and K, respectively).

For plants, mammals, invertebrates and height, at least one buffer size was considered plausible to explain the response ratio variance (Table 2K–W). The only plausible model was the buffer size of 200 km radius for plants ($w_i = 0.15$) and 5 km radius for height ($w_i = 0.6$) (Table 2K and Q, respectively). For mammals, the top-ranked model was the buffer size of 100 km radius ($w_i = 0.34$), but other buffer sizes were also considered equally plausible (Table 2L). These ranged from 50 to 200 km radius (always $\Delta_i < 1.79$, $w_i \geq 0.25$). For invertebrates, the top-ranked model was the buffer size of 5 km radius ($w_i = 0.17$), with the buffer size of 10 km radius considered equally plausible ($\Delta_i = 1.22$, $w_i = 0.12$) (Table 2M). For birds, herpetofauna, cover, density, biomass and litter, the null model was considered among the most plausible models to explain the response ratio variance (w_i always

≥ 0.15) (Table 2N–P and R–W). The response ratio variance was always negatively nonlinearly related with contiguous forest cover for plants, mammals, invertebrates and height (Fig. 2B, D, F and J, respectively).

Discussion

Our global meta-analysis of ecological restoration of biodiversity and vegetation structure revealed the landscape size (scale of effect) at which the percentage of either overall or contiguous forest cover best explains restoration success (mean response ratio) and its predictability (response ratio variance). The results support our main hypotheses that the ‘best’ landscape size in terms of explaining restoration success and its predictability by forest cover was as follows: (i) stronger for contiguous than overall forest cover and (ii) more variable and stronger at larger scales for biodiversity than for vegetation structure. We revealed for the first time a clear pattern of increasing restoration success and decreasing uncertainty as the amount of contiguous forest cover increases. From an applied perspective, we emphasize that contiguous forest cover is integral to effective ecological restoration, with increasingly unpredictable restoration outcomes associated with low contiguous forest cover.

We found a stronger effect of contiguous than overall forest cover affecting restoration processes of both biodiversity and vegetation structure (Tables 1 and 2). This finding underscores the need to preserve connected forest

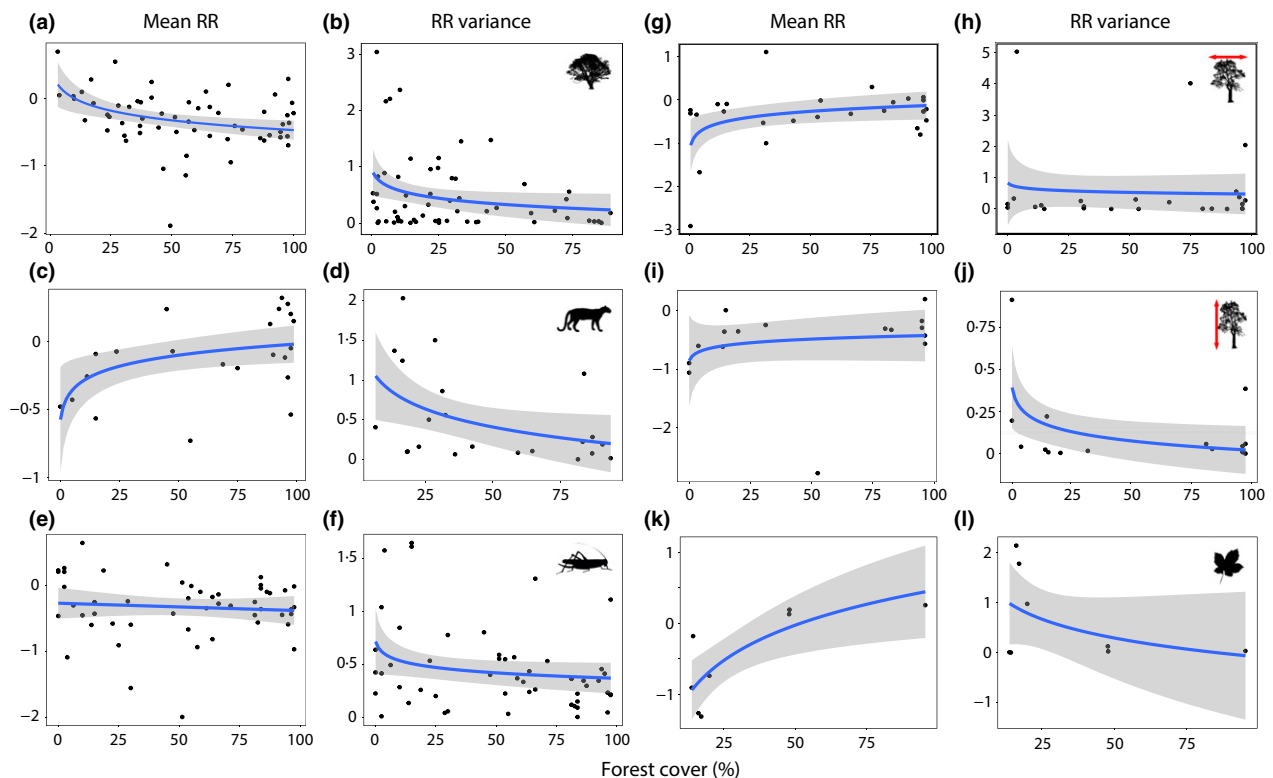


Fig. 2. Relationship between either mean response ratio (RR) or response ratio variance and percentage of contiguous forest cover for both biodiversity and vegetation structures that were affected by at least one buffer size (landscape size in km radius). (a, b) Plants (10), (c, d) mammals (5), (e, f) invertebrates (5), (g, h) cover (5), (i, j) height (5) and (k, l) litter (100). Points represent either mean or variance of all response ratios at each study landscape. Blue line = mean value and grey = 95% confidence intervals.

habitat as a *prerequisite* to the restoration of diverse ecosystems (e.g. Crouzeilles *et al.* 2015). Previous work has demonstrated how landscapes with low old-growth (source) forest cover exhibit impaired dispersal and colonization of plants and seed dispersers (Vellend 2003), and higher susceptibility to anthropogenic disturbance (Holl & Aide 2011; Markl *et al.* 2012). This could help to explain our results, although it cannot be confirmed as our definition of contiguous forest is not sufficient to differentiate source from sink habitat. In any case, an increase forest contiguity (i.e. connectivity) is also necessary in landscape restoration actions to maximize restoration success for both biodiversity and vegetation structure.

We revealed a clear pattern of increasing restoration success and decreasing uncertainty across the gradient of contiguous forest cover (Fig. 2). Previous work has shown immigration rates to be high in well-forested landscapes, facilitating population persistence/recovery and seed dispersal, even in small areas (e.g. Pardini *et al.* 2010; Leite *et al.* 2013; Crouzeilles *et al.* 2014). Contrarily, at lower forest cover, immigration rates are eroded by increased patch isolation and even large populations are subject to local extinction (Pardini *et al.* 2010; Holl & Aide 2011; Leite *et al.* 2013). While almost all of our results are consistent with this explanation, for plants we observed the opposite trend: restoration success (but not its predictability) decreased as forest cover increased (Fig. 2A). We attribute this to the mixing of early and late successional species and non-native species in highly deforested landscapes (Holl & Aide 2011), potentially increasing species richness and abundance (two metrics making up 77.8% of our biodiversity data set).

Identifying the scale at which landscape context affects biodiversity is a difficult task in empirical studies since a species may respond to influences at multiple scales (Bowen *et al.* 2007; Boscolo & Metzger 2009; Jackson & Fahrig 2015). We found more than one landscape size explaining either restoration success or its predictability for biodiversity. Mammals and plants responded strongly to restoration at smaller scales (5 and/or 10 km radii; Table 2A and B), but predictability showed an influence ranging up to a 200 km radius (Table 2K and L). For larger bodied organisms (e.g. Stevens *et al.* 2014) and high-range dispersing plant species (e.g. Kirmer *et al.* 2008; Kepfer-Rojas *et al.* 2014), rare long-dispersal events could reach many kilometres within time frames relevant for restoration. The overlapping scales of effect support a role for mammals as the main dispersal agent for zoochoric plants in regenerating areas (e.g. Wright 2003). For instance, it is recognized that slow recovery of animal communities can hinder the recovery of plant communities (Wunderle 1997).

A recent review of landscape restoration showed that the majority of studies demonstrate effects of landscape context on vegetation structure (Leite *et al.* 2013), but the mechanisms by which this occurs was not evaluated. Similarly, we found effects of contiguous forest cover on vegetation cover and height at the smallest scale (5 km). One obvious mechanism is an indirect influence of plant biodiversity, given

that the scales of effect overlapped (e.g. Tables 1A and 2F and Q). For litter, we found a large scale of effect (100 km radius, Table 2J), but our sample size was small, resulting in poorly fitted models. Our findings suggest that the optimal scale may not have been detected for both biodiversity and vegetation structure (Jackson & Fahrig 2015). The scale of effect that we detected is highly dependent on the coarse spatial resolution of the land cover data and on the detail of the biodiversity and vegetation structure data. Thus, restoration projects with higher resolution data should follow the similar methodological procedure to that performed here to assess the optimal spatial scale of effect for landscape context analyses.

CONCLUSIONS AND PRACTICAL IMPLICATIONS

Restoration initiatives are expanding globally. Overall, we show that ecological restoration is affected by the landscape context, particularly the amount of contiguous habitat up to 10 km around a disturbed site. Our results revealed an increasing uncertainty in restoration success when contiguous forest cover falls below about 50% (Fig. 2). Policymakers and restoration practitioners should account for this when setting targets and accounting for uncertainty. For example, halting and reversing deforestation early on will facilitate recovery and reduce the risk of irreversible biodiversity decline (e.g. Pardini *et al.* 2010). Ecological compensation policies ('biodiversity offsets') permit the loss of existing habitat in exchange for the restoration of habitat elsewhere. As forest cover declines, the requirements for compensation should be appropriately adjusted upwards to account for lower success and predictability (e.g. Moilanen *et al.* 2009).

Finally, it is worth highlighting that we have only investigated the influence of one factor (forest cover) on restoration outcomes. The specific local management context (e.g. restoration technique), characteristics of system under study (e.g. habitat type, climate), along with habitat configuration (e.g. patch size and isolation), are likely to play a significant role. Nonetheless, our meta-analysis provides globally relevant preliminary recommended landscape sizes for taxonomic groups and measures of vegetation structure, derived from data spanning many realms, habitat types, degradation states, restoration ages and habitat configurations. Our research thus offers a starting point for addressing policy issues and mapping out future research efforts on landscape restoration.

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Data accessibility

Mean response ratio, response ratio variance, forest cover data and R scripts are available from Dryad Digital Repository doi: 10.5061/dryad.v1r34 (Crouzeilles & Curran 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. The seven key reviews we used as a search criteria are described in detail.

Table S2. Reference list for the 269 studies we selected.