

SPECIAL FEATURE – STANDARD PAPER
META-ANALYSIS IN PLANT ECOLOGY**Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess–multiresponse dynamics****Inés Ibáñez*, Daniel S. W. Katz, Drew Peltier, Samantha M. Wolf and Benjamin T. Connor Barrie***School of Natural Resources and the Environment, University of Michigan, Ann Arbor, MI 48109, USA***Summary**

1. When human activities change the landscape, several processes affecting remnant vegetation take place simultaneously: there is less suitable habitat, populations become isolated and the environmental conditions of the fragments frequently shift. Such changes affect vegetation in different ways – populations become smaller, the genetic exchanges between populations decline and species interactions are altered. The combination of processes taking place during fragmentation and their subsequent consequences generate a large variety of responses, positive and negative, among plants and plant communities.

2. To assess the integrated effects of the processes taking place as a result of fragmentation (isolation, edge effects, fragment size and time since fragmentation) on organisms, we conducted a hierarchical meta-analysis of the studies reporting the effects of landscape fragmentation on plant species and plant communities. Our review included 259 peer-reviewed journal articles and 990 data entries.

3. We found the frequency of reports of positive and negative responses to fragmentation were comparable but largely variable. Negative effects of fragmentation due to isolation, edge effects and fragment size were significant; but only edge effects and fragment size had significant positive effects. When looking at specific types of responses to isolation, we found negative effects on density, fecundity, colonization, succession rates and species richness, while positive effects were found on fecundity, herbivory/predation and colonization. Positive responses to edge effects were significant for density, fecundity, survival, growth and richness, and significantly negative for density, survival, colonization and richness. Effects of patch size were mostly significant for both positive and negative responses.

4. We also assessed the effects of landscape fragmentation for different attributes of the studied system and found no differences among biomes, vegetation types, functional groups or life stages.

5. *Synthesis.* Results of this integrated assessment indicate that broad generalizations about the effects of fragmentation on remnant vegetation may not be possible due the large variety of processes and responses associated with fragmentation. Results also identified key knowledge gaps, and areas of research needed to improve assessment and future management of plant species and plant communities in fragmented landscapes (e.g. lag effects, the role of the matrix and the patch quality and integrated effects along life cycles).

Key-words: Bayesian analysis, diversity, effect size, habitat fragmentation, hierarchical models

Introduction

After habitat loss, fragmentation of the remnant vegetation has been considered one of the major threats to terrestrial ecosystems (e.g. Ehrlich & Ehrlich 1981; Hobbs & Yates 2003). Landscape fragmentation not only reduces the amount of area

available to plants and animals, but also alters the original flow of resources, the movement of organisms, the distribution of suitable habitat, and it often disrupts species interactions (for a review see Lindenmayer & Fisher 2006). Numerous studies have been conducted to document and quantify the effects of landscape fragmentation on plant species and plant communities (e.g. see meta-analyses on specific processes by Aguilar *et al.* 2006; Honnay & Jacquemyn

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2007; Angeloni, Ouborg & Leimu 2011; Damschen & Brudvig 2012; Vranckx *et al.* 2012). Still, there is not an overall agreement about what those effects, their magnitudes and their implications are. The lack of consensus mainly arises from the fact that landscape fragmentation affects organisms through multiple processes, for example isolation, less available area and shifts in environmental conditions, which may lead to less genetic exchange, smaller populations and altered species interactions (Fig. 1). Also, several aspects and life stages of the organisms can be simultaneously affected, for example their fecundity, growth or survival. This variety of processes and responses results in a wide range of outcomes (Magrach, Santamaria & Larrinaga 2012), from positive to negative and from highly significant to neutral. This diversity of potential outcomes thus reduces any assessment of the effects of fragmentation to an *ad hoc* exercise. To bring a more comprehensive understanding of the integrated effects, that is, the effects of multiple processes on multiple life stages, of landscape fragmentation on plant species and plant communities, we conducted a hierarchical meta-analysis of the studies reporting such effects. We investigated how the different processes that arise as a result of fragmentation (isolation, edge effects, fragment size and time since fragmentation) impact different aspects of the life cycle of plants and how attributes of the system or of the organism (biome, vegetation type, functional group or life stage) could each be differentially affected by landscape fragmentation. We use this information to identify knowledge gaps and research areas needed to overcome the difficulties inherent in the assessment of the effects of landscape fragmentation on plants.

Isolation of remnant populations is one of the major effects of landscape fragmentation (Fig. 1; e.g. Groom 2001; Brunet 2007). The impact of isolation can be complex and result in negative as well as positive outcomes simultaneously. Populations of a particular species can experience reduced gene flow depending on the distance between patches and their mode of pollination (Aguilar *et al.* 2006). Other trophic levels will also be impacted by fragmentation (e.g. herbivores, their predators or their parasitoids), which could result in a wide range of effects of fragmentation on plants (e.g. Elzinga *et al.* 2005). A decrease in plant performance within isolated populations may also be caused by increased herbivory pressure due to higher abundance of herbivores per unit area (Elzinga *et al.* 2005; Kolb 2008). Furthermore, reduced dispersal of propagules into isolated fragments may diminish the chances of colonization events, which may further exacerbate genetic isolation (Grashof-Bokdam 1997; Honnay *et al.* 2008). Alternatively, isolation may have a net positive effect for some species. Seed predation may decline in isolated patches (Farwig *et al.* 2009) or wind dispersed species may still colonize isolated patches and then be able to establish in the absence of more competitive animal dispersed species (Graae 2000; McEuen & Curran 2004).

In fragmented landscapes, the extent and abundance of any given plant population are predominantly determined by patch size (Kiviniemi 2008; Tomimatsu & Ohara 2010). Decreasing population size is a major consequence of landscape

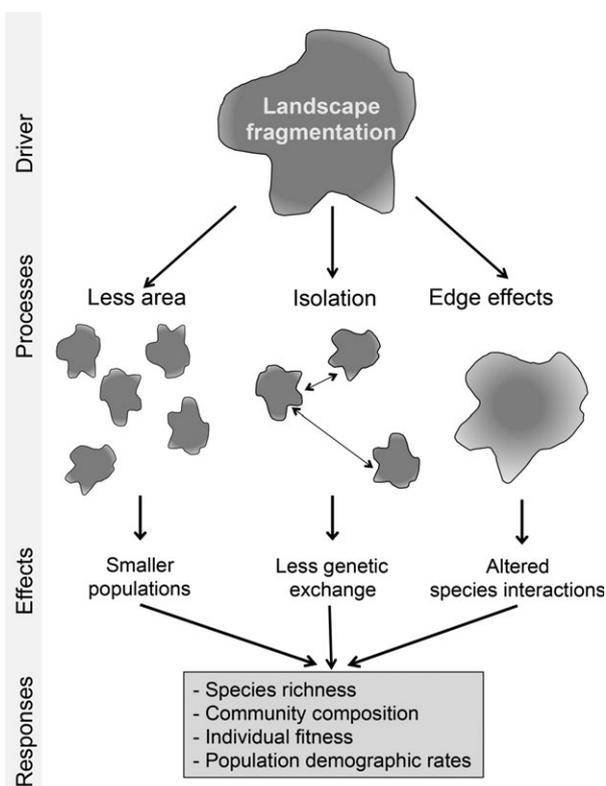


Fig. 1. Conceptual figure illustrating the processes and responses by which habitat fragmentation affects plant species and plant communities. The variety of processes and responses result in both positive and negative outcomes at several levels of the plant community.

fragmentation, which may lead to lower individual performance (Angeloni, Ouborg & Leimu 2011; Vranckx *et al.* 2012), diminished colonization capacity (Soons & Heil 2002; Seifert & Fischer 2010) and increased risk of local extinction (Joshi *et al.* 2006; Honnay & Jacquemyn 2007). The effect of fragment size on species diversity and extinction risk has been well studied and used to illustrate both the species–area relationship (larger areas host more species; Yaacobi, Ziv & Rosenzweig 2007; Stiles & Scheiner 2010) and the theory of island biogeography (number of species depends on the area and level of isolation; Cook *et al.* 2002; Collins, Holt & Foster 2009). Studies evaluating species diversity across fragment sizes overwhelmingly report a positive correlation between species diversity and patch size (Jha *et al.* 2005; Ferreras, Torres & Galetto 2008; Yamaura *et al.* 2008; Uriarte *et al.* 2010) although some studies have reported the opposite pattern (Adriaens, Honnay & Hermy 2006; Arroyo-Rodríguez & Toledo-Aceves 2009).

The increased edge habitat in fragmented landscapes also has diverse effects on the remnant vegetation (Esseen 1994). Plants in edge habitats experience increased temperatures, light levels and desiccation as well as wind exposure when compared to the forest interior (Chen, Franklin & Spies 1992; Laurance *et al.* 2000). Species interactions can also be altered at the edges of vegetation patches, for example, dispersal by animals (de Melo, Dirzo & Tabarelli 2006; Lindner 2009), herbivory pressure (Cadenasso & Pickett 2000; Valladares,

Salvo & Cagnolo 2006) or competition from other native or introduced species (Koper, Mozel & Henderson 2010; Tomimatsu *et al.* 2011) have all been reported to be modified at forest edges with respect to the interior habitat. These changes can also differentially affect several life stages of an individual, benefiting some stages while being detrimental to others (Bach, Kelly & Hazlett 2005; Cascante-Marin *et al.* 2009). Changes in species compositions and richness are also common in edge habitats with both increases and decreases having been reported (Kiviniemi & Eriksson 2002; Guirado, Pino & Roda 2006; Hamberg *et al.* 2008; Werner & Gradstein 2009). Idiosyncratic responses might also be the result of particular system or species attributes. For example, the edge effect greatly increases adult tree mortality in tropical forests (Laurance *et al.* 1998), while the opposite effect has been reported for temperate forests – where adult trees largely benefit from increased light availability at the edge (McDonald & Urban 2004; Bach, Kelly & Hazlett 2005).

To implement a comprehensive assessment of the effects of fragmentation on plant species and plant communities, we carried out a hierarchical meta-analysis of the published studies in this topic. The hierarchical meta-analysis allowed us to reflect on the complexity of these dynamics and assess the effects of each fragmentation process on the different responses reported (Helsler & Lai 2004; Sorte *et al.* 2013; Tuck *et al.* 2014), an approach similar to the Hierarchy of Hypothesis proposed for the analysis of biological invasions (Jeschke *et al.* 2012). In particular, we addressed these specific questions: (i) what type of responses, positive or negative, are more prevalent? And are these responses associated with particular processes? (ii) Are the effects of different fragmentation processes (connectivity/isolation, edge effects, fragment size and time since fragmentation) comparable? (iii) How do the different types of responses (biomass, density, extinction, fecundity, herbivory/predation, richness, survival, colonization, growth or succession rates) vary among each type of fragmentation process? (4) Do the effects of landscape fragmentation differ among biomes, vegetation types, functional groups or plant life stages? Answering these questions also allowed us to identify knowledge gaps and areas of research that should be addressed to improve our understanding of the integrated effects of landscape fragmentation on plants and plant communities.

Materials and methods

We conducted a systematic search of peer-reviewed journal articles published before 2013 that focused on the effects of landscape fragmentation on plants and plant communities. To conduct the search, we followed protocols established for the ecological sciences to ensure a systematic review, maximize transparency and repeatability and to minimize bias (Gates 2002; Pullin & Stewart 2006; Stewart 2010).

SEARCH METHODS AND DATA COLLECTION

In December 2012, we searched ISI Web of Knowledge by the topic line: (*landscape fragmentation OR habitat fragmentation*) AND

(*plant OR vegetation OR grassland OR shrubland OR wetland OR tree OR grass OR herb OR vine OR liana OR shrub*) AND (*effect OR affect OR impact OR consequences*). The search resulted in 5604 titles; we then used the 'refine' tool, set to 'ecology', which narrowed our search to 3511 publications. We searched through these abstracts and selected studies according to these criteria: (i) has to include vascular plants; (ii) has to refer to human-caused landscape fragmentation; and (iii) has to report a measure of fitness/dominance (e.g. population size, fecundity, growth and survival) or community species diversity. These criteria yielded a total of 335 articles, 259 of which we were able to extract data from (see Appendix S1 in Supporting Information) yielding a total of 990 data points.

From each of the publications, we collected data related to the study's location, time of data collection, the study's system and organisms researched. We also collected information about the fragmentation process studied, its effects and drivers and the sign of the response to fragmentation (positive or negative) regardless of statistical significance (Table 1). We grouped the data according to the fragmentation process reported, as due to: connectivity/isolation, fragment size, edge effect and time since fragmentation. We considered the 'control' responses to be those recorded for continuous vegetation, the largest fragment reported, forest interior habitat or undisturbed areas. 'Treatment' responses were only recorded for the end point if a gradient was reported (the farthest fragment, smallest fragment, edge habitat or longest time since fragmentation). We also grouped the studies by the type of response to fragmentation, reported as changes in: biomass, density, extinction, fecundity, establishment, herbivory/predation, richness, survival, colonization, growth and rate of succession (Table 1).

We extracted data from text, figures and tables, and recorded the data source to test for any potential bias. We extracted mean response and when available sample size and any measurement of the variability around the mean (standard deviation and standard error). If we extracted data from individual data points shown along a gradient in a figure, we recorded the values of the five points closest to each extreme and calculated their mean and standard deviation. If available, we also recorded the value of the fragmentation-related variable, for example distance to continuous vegetation, distance to edge, fragment size and number of years since fragmentation.

We calculated effect size (ES) of each observation as the ratio of the difference between the treatment and control responses to the average of the two types of responses: $ES = (\text{response}_{\text{treatment}} - \text{response}_{\text{control}}) / (\text{average of the responses})$. The range of responses varied between -2.77 and 2.19 . When data were available, we also used this equation to estimate the degree of fragmentation (DF), for example degree of isolation or of the differences in patch size, $DF = (\text{fragmentation}_{\text{treatment}} - \text{fragmentation}_{\text{control}}) / (\text{average of fragmentation})$. These estimations of ES and DF were highly correlated with the log-response ratio (e.g. third-order polynomial R^2 : 0.97 for ES) but allowed us to deal with zero values and avoid the issues raised by log transformations (Sweeting *et al.* 2004). It also helped to standardize the large variety of treatments and responses recorded in the data (Table 1).

Because positive (increase in individual fitness or community richness) and negative (decrease in individual fitness or community richness) responses are common, and this dichotomy is biologically relevant, a single mean was not the best way to describe ES, as it would have only informed on the significance of the treatment but not on the nature of the response. Thus, to better understand how the different processes associated with fragmentation may lead to both positive and negative responses of the vegetation, we divided the recorded responses into two groups: positive responses to fragmentation and negative responses to fragmentation (Sorte *et al.* 2013;

Table 1. Information gathered from the fragmentation studies considered in this meta-analysis

Type of information	Variables (categories considered)
Location	Continent, country Latitude, longitude Elevation
Time	Year of the study (first and last) Duration
System	Biome (alpine, arctic/boreal, desert/semi-arid, Mediterranean, savanna, subtropical, temperate, tropical) Type of vegetation (agricultural, forest, fen, grassland, shrubland, riparian) Degree of urbanization (rural, suburban, urban) Successional stage (early, mid-, late) Type of study (observational, experimental)
Organism	Functional group (epiphyte, forb, grass, liana, shrub, tree, plant community) Origin (native, introduced) Species and family Life stage [adult (includes studies of the entire community), flowering, fruiting, seedling, seedling, sapling] Pollination mode (animal, animal-birds/bats, animal-insect, animal-bird/insect, wind, auto) Dispersal vector (animal, animal-bird, animal-mammals, animal-bats, animal-insects, gravity, wind, mixed, auto) Special features [self pollination not possible, nitrogen fixing, ecotone habitat (treeline, lake shore)]
Fragmentation data	Type of fragmentation process (connectivity/isolation, edge effects, fragment size, time since fragmentation) Abiotic drivers (dispersal, pollination, disturbance, disturbance-light, disturbance-pollutants, moisture, temperature, soil, wind, mixed) Biotic drivers (dispersal, pollination, competition, herbivory, predation, pathogens, population size, inbreeding) Sign of response (positive, negative) Type of response (biomass, density, extinction, fecundity, establishment, herbivory/predation, species richness, survival, colonization/dispersal, growth, rate of succession) Response variable (mean, standard deviation/error, sample size) Type of treatment variable [fragment size, habitat (edge/interior), distance to forest] Treatment variable (mean, standard deviation/error, sample size)
Additional information	Source of data (figure, table, appendices)

Table 2; $ES > 0$ or $ES < 0$) and analysed them independently while still maintaining the variability reported around each measurement. The fact that the distribution of ES peaked at zero and that the reported variability associated with each ES was not biased towards any particular value (the range of standard deviations was similar among ES values) makes us confident that we were not biasing the results towards significance (see Appendix S2 for plots of the distribution of ES and its variability). We report on the significance of the

effect, that is, being different from zero or not, for both positive and negative responses once all sources of variability, within and among studies, have been accounted for. To facilitate comparisons between these two groups, we used absolute values for the negative responses.

DATA ANALYSIS

With the information gathered, we performed extensive data exploration, including regression analyses using the quantitative variables recorded (Osenberg, Samelle & Cooper 1997) and different types of random effects, for example publication, year. To address the research questions posed in the introduction, we then proceed to analyse ES as a function of the categorical variables recorded. In particular, we analysed ES as a function of the type of response nested within each category of fragmentation process. We then performed individual analysis of ES as a function of biome, type of vegetation, functional group and life stage. These were all variables for which we have large enough sample sizes to carry out the analyses. Here, we report the methods of the final analyses, based on models best fit [according to the Deviance Information Criteria (Spiegelhalter *et al.* 2000); for a list of some of the other analyses we tried see Appendix S3].

To reflect the multilevel structure of the analysis of ES as a function of response type nested within each fragmentation process, we used a hierarchical Bayesian framework for the analysis (Gelman & Hill 2007; Stevens & Taylor 2009; Tuck *et al.* 2014). A Bayesian approach was also useful to address the large number of observations, 173 of 990, which did not report a measure of variability (standard deviations or standard errors) associated with the response. The Bayesian framework allowed us to consider those missing values as latent variables that were also estimated as part of the model (Clark 2007; see below). For each group, positive and negative responses to fragmentation, the observed ES for observation i , $ES_{\text{obs } i}$, was estimated from a normal likelihood:

$$ES_{\text{obs } i} \sim \text{Normal}(ES_{mi}, \sigma^2)$$

$$ES_{mi} = \mu_{\text{fragmentation process}(i), \text{type of response}(i)} + v_i \text{ and } \sigma^2 \sim \text{Gamma}(0.01, 0.01)$$

The mean ES was represented by the parameter, μ , which was estimated hierarchically at three different levels:

- 1 For each type of response nested within each fragmentation process

$$\mu_{\text{fragmentation process}(i), \text{type of response}(i)} \sim \text{Normal}(\mu_{\text{mean fragmentation process}(i)}, \sigma_{\text{fragmentation process}(i)}^2)$$

- 2 For each fragmentation process

$$\mu_{\text{mean fragmentation process}} \sim \text{Normal}(M, \sigma_{\mu_{\text{mean}}}^2)$$

- 3 Overall response

$$M \sim \text{Normal}(0, 10000)$$

All standard deviations were estimated as: $\sigma_{\text{fragmentation process}}, \sigma_{\mu_{\text{mean}}} \sim \text{Uniform}(0, 100)$. The variability reported around each observed effect size ($\sigma_{ES \text{ obs}(i)}$); estimated after running 10 000 simulations calculating ES from the mean and standard deviation values reported, was included as $v_i \sim \text{Normal}(0, \sigma_{ES \text{ obs}(i)}^2)$, to improve

Table 2. Proposed mechanisms/processes explaining the sign of the response, positive or negative, to fragmentation (number of studies reporting that response). The specific citation numbers [see Supporting Information for full articles' references] are listed in superscript

Type of responses	Sign of response	Negative
Biomass	Positive	
Density	Positive	
Extinction	Positive	
Fecundity	Positive	
Establishment	Positive	
Herbivory/predation	Positive	
Species richness	Positive	
Survival	Positive	
Colonization/dispersal	Positive	
Growth	Positive	
Rate of succession	Positive	
	Negative	
Biomass	Negative	Reduced site suitability (18) ^{15,47,71,76,105,117,135,150,154,175,194,198,201,204,207,218,237,238}
Density	Negative	Reduced propagule availability, pollen limitation, inbreeding depression, Allee effects (39) ^{1,5,7,14,17,19,20,27,28,32,34,37,38,39,40,43,67,78,80,84,90,93,96,100,103,140,152,150,159,189,194,214,224,229,230,242,243,244,255}
Extinction	Negative	Lack of sufficient colonization to maintain the population (2) ^{128,160}
Fecundity	Negative	Pollen limited, decrease in cross-pollination (63) ^{3,4,6,15,20,23,25,28,32,36,47,61,66,70,79,80,81,82,83,85,51,88,90,93,99,102,110,111,117,119,130,134,136,137,149,155,158,163,171,174,178,181,185,187,193,195,199,205,210,226,229,231,232,236,237,238,239,240,245,246,251,258,259}
Establishment	Negative	Decreased site suitability (17) ^{4,15,27,36,47,106,147,158,182,188,194,204,211,212,232,237,256}
Herbivory/predation	Negative	Increased herbivore/predator density, increased exposure to herbivores/predators (14) ^{4,33,42,49,161,172,184,194,199,200,222,234,252,259}
Species richness	Negative	Decreased site suitability, decreased colonization (50) ^{8,9,13,18,21,26,30,31,34,35,44,48,56,57,64,65,76,86,87,91,97,98,108,113,116,118,122,123,125,144,146,148,161,162,164,167,173,174,190,191,194,196,197,207,217,242,243,248,253,254}
Survival	Negative	Decreased site suitability, increase competition from edge species (35) ^{4,16,27,36,37,41,53,59,63,69,74,75,89,90,92,95,117,134,138,139,157,158,159,165,175,179,182,186,219,241,247,249,250,256,257}
Colonization/dispersal	Negative	Decreased dispersal (14) ^{10,39,46,50,83,95,99,106,114,120,129,131,133,170}
Growth	Negative	Decreased site suitability (15) ^{16,17,19,24,36,37,40,46,58,73,90,96,117,137,168}
Rate of succession	Negative	Decreased propagule availability (4) ^{45,142,143,153}

convergence v_i was limited to range between -2.5 and 2.5 , the range of the bulk of our ES values. For the data points for which estimates of variability were not reported, we estimated their variance as part of the model, $1/\sigma_{ES(i)}^2 \sim \text{Gamma}(0.01, 0.01)$. Thus, parameters μ , μ_{mean} , M , $\sigma_{\text{fragmentation process}}$ and $\sigma_{\mu, \text{mean}}$ represent the means, and the variability around the means, of the reported responses, while parameters $\sigma_{ES \text{ obs}}^2$ and σ^2 represent the variability within and among responses, respectively.

We then performed similar independent analyses of ES as a function of the system biome, type of vegetation, plant functional group and life stage:

$$ES_{\text{obs } i} \sim \text{Normal}(ES_{mi}, \sigma^2)$$

$$ES_{mi} = \mu_{\text{biome}(i)} \text{ or type of vegetation}(i) \text{ or functional group}(i) \\ \text{ or life stage}(i) + v_i,$$

We estimated the parameters σ^2 and v_i following the same steps described above. All μ parameters were estimated from non-informative prior distributions, $\mu_s \sim \text{Normal}(0, 10\,000)$.

We ran the analyses in OPENBUGS (Thomas *et al.* 2006). After a burn-in period of 50 000 simulations, we ran an additional 50 000 iterations thinning every 100 to estimate posterior mean, standard deviation and 95% credible interval values of parameters μ , μ_{mean} or M and of all the variances. Parameter values for which 95% CI did not include zero were considered significantly different from zero. To better assess the significance of the ES, we estimated predicted ES, which included not only the variability around the parameters, μ , μ_{mean} or M , but also the variability around the responses, σ^2 .

We also analysed ES following a traditional meta-analysis that weighted the reported variances associated with each ES; this analysis only included observations for which standard error or standard deviations were reported ($n = 817$; see Appendix S4). We multiplied each individual ES by the inverse of its variance to give observations with lower variance more weight in the calculation of group mean ES (Harrison 2011); to estimate the means and the bias-corrected 95% credible interval around the mean, we carried out a bootstrap in R (R Development Core Team 2011; Appendix S4).

Results

We found both positive and negative effects of fragmentation among most of the categories recorded in our data (402 positive responses vs. 588 negative ones). A majority of the reported effects, 549, were related to fragment or population size, followed by the effects of connectivity/isolation, 218, and edge habitat, 202. The effects of time since fragmentation were only recorded in 21 entries (six publications). We found no patterns in ES when regressed neither against any of the continuous variables recorded, for example elevation, longitude, latitude or duration, nor to the DF. The inclusion of different random effects (publication, year, continent, country, degree of urbanization, successional stage, type of study, species origin) that would have accounted for publication outliers (due to study system, sample size, number of entries, etc.) neither improved the fit of the models we tried (Appendix S3) nor revealed any significant patterns. Funnel plots of ES regressed against reported variability, that is, ES standard deviation, show similar ranges across ES values, and histograms of ES do not show a publication bias to larger, usually significant, ES values (Appendix S2).

The overall responses, parameters M , were not statistically significant (Table 3). Among the responses to fragmentation processes only the parameters for negative responses to connectivity/isolation and for negative and positive responses to edge effects and fragment size were significant (Table 3). Among the parameters related to the type of response, nested within each fragmentation process (parameters μ), most of the significant values, positive and negative, were responses to fragment size (Table 3). One of the advantages of the hierarchical approach was that parameters and predictions could still be estimated for groups for which we had very few observations. We obtained those estimates through their prior distributions, letting the data from other groups and the relationships between groups inform them (Gelman *et al.* 2000). Predicted values of ES, which also considered the variability among and within responses, show the same patterns and levels of significance as those reported for the model mean parameters (Figs 2 and 3). The magnitude of the responses did not differ among fragmentation processes or types of responses (95% predicted intervals overlap).

Results from the independent analyses of ES as a function of several attributes of the system of study show a large number of parameters, μ , to be statistically different from zero, especially among the different life stages (Table 4). However, when the variability associated with ES was weighed into the predictions, the number of significant results dropped substantially (Fig. 4). Among biomes, the largest ES predictions corresponded to positive responses in subtropical areas (based on five entries from three publications), this was also the only statistically significant prediction. When looking at the effects of fragmentation along plant functional groups, epiphytes had the largest responses to fragmentation, both positive and negative, and these were significant. Finally, among life stages, the only statistically significant prediction was for positive responses of saplings.

The variance weighted analysis of ES, using the subset of observations that reported variability of the response (817 out of 990), show a similar pattern of significance to the hierarchical meta-analysis (Appendix S4). Of the 86 estimates of mean ES that the two analyses have in common, 19 of them differed between the two analyses; the estimates of ES for the variance weighted analysis were significant in these comparisons and non-significant for the hierarchical meta-analysis, making the results of the latter analysis rather conservative.

Discussion

For the last few decades, numerous studies, including meta-analyses, have reported particular effects of landscape fragmentation on plant species and plant communities; in this study, we expanded those analyses by carrying out a hierarchical meta-analysis to assess not only the overall effects of landscape fragmentation on plants but also its effects according to the type of fragmentation process and the type of response (Table 1 and Fig. 1). We found that both positive and negative responses to fragmentation are common, but neither dominates. Negative effects of fragmentation due to

Table 3. Results of the hierarchical/multilevel analysis performed on our measure of effect size ([treatment response–control response]/average response). We report parameter posterior means and SDs, 95% credible intervals are included in parenthesis. Bold values indicate the parameter is statistically significant (when 95% CI does not include zero)

Parameter	Sign of response	
	Positive	Negative
Overall response (M)	0.47 ± 0.63 (–0.73, 1.83)	0.56 ± 0.66 (–0.73, 1.95)
Overall variance (σ^2)	0.2 ± 0.02 (0.16, 0.25)	0.28 ± 0.02 (0.23, 0.33)
By type of fragmentation process (μ .mean)		
Connectivity/isolation	0.31 ± 0.22 (–0.11, 0.83)	0.46 ± 0.16 (0.14, 0.79)
Edge effects	0.52 ± 0.25 (0.004, 1.08)	0.49 ± 0.22 (0.04, 0.91)
Fragment size	0.59 ± 0.12 (0.32, 0.85)	0.75 ± 0.13 (0.47, 1.01)
Time since fragmentation	0.32 ± 0.69 (–1.1, 1.73)	0.55 ± 0.87 (–1.16, 2.42)
Variance (σ^2_{μ .mean)	1.48 ± 0.89 (0.1, 3.05)	1.48 ± 0.89 (0.12, 3.07)
By type of response nested within each type of fragmentation category (μ)		
Connectivity/isolation		
Biomass	0.17 ± 0.23 (–0.32, 0.61)	0.28 ± 0.19 (–0.1, 0.65)
Density	0.41 ± 0.48 (–0.42, 1.6)	0.65 ± 0.27 (0.16, 1.25)
Extinction	0.3 ± 0.69 (–0.95, 1.81)	0.45 ± 0.51 (–0.54, 1.59)
Fecundity	0.28 ± 0.13 (0.007, 0.54)	0.38 ± 0.14 (0.09, 0.67)
Establishment	0.24 ± 0.34 (–0.43, 0.93)	0.41 ± 0.29 (–0.16, 0.97)
Herbivory/predation	0.39 ± 0.15 (0.1, 0.72)	0.4 ± 0.25 (–0.11, 0.92)
Species richness	0.14 ± 0.23 (–0.31, 0.61)	0.67 ± 0.12 (0.44, 0.92)
Survival	0.19 ± 0.21 (–0.24, 0.63)	0.27 ± 0.14 (–0.04, 0.57)
Colonization/dispersal	0.59 ± 0.28 (0.1, 1.29)	0.73 ± 0.21 (0.35, 1.18)
Growth	0.16 ± 0.35 (–0.57, 0.82)	0.51 ± 2.33 (–4.28, 5.24)
Rate of succession	0.032 ± 0.66 (–0.96, 1.76)	0.58 ± 0.29 (0.04, 1.24)
Variance ($\sigma^2_{\text{connectivity/isolation}}$)	0.39 ± 0.67 (0.01, 1.99)	0.23 ± 0.28 (0.02, 0.97)
Edge effects		
Biomass	0.25 ± 0.14 (–0.02, 0.58)	0.23 ± 0.3 (–0.33, 0.82)
Density	1.08 ± 0.17 (0.74, 1.43)	0.49 ± 0.16 (0.16, 0.82)
Extinction	0.48 ± 0.79 (–1.3, 1.93)	0.52 ± 0.69 (–0.82, 1.92)
Fecundity	0.72 ± 0.21 (0.31, 1.17)	0.27 ± 0.32 (–0.4, 0.87)
Establishment	0.55 ± 0.77 (–0.89, 2.28)	0.63 ± 0.33 (–0.007, 1.33)
Herbivory/predation	0.28 ± 0.21 (–0.11, 0.7)	0.35 ± 0.28 (–0.21, 0.91)
Species richness	0.48 ± 0.11 (0.26, 0.69)	0.42 ± 0.19 (0.06, 0.8)
Survival	0.51 ± 0.15 (0.2, 0.78)	0.9 ± 0.18 (0.55, 1.28)
Colonization/dispersal	0.55 ± 0.64 (–0.67, 1.9)	0.63 ± 0.18 (0.29, 1)
Growth	0.57 ± 0.25 (0.09, 1.09)	0.29 ± 0.22 (–0.13, 0.71)
Rate of succession	0.24 ± 0.15 (–0.06, 0.54)	0.45 ± 0.67 (–1.04, 1.83)
Variance ($\sigma^2_{\text{edge effects}}$)	0.53 ± 0.72 (0.06, 2.32)	0.4 ± 0.57 (0.03, 2.08)
Fragment size		
Biomass	0.66 ± 0.12 (0.41, 0.89)	1.05 ± 0.08 (0.88, 1.22)
Density	0.8 ± 0.14 (0.52, 1.1)	0.8 ± 0.12 (0.55, 1.05)
Extinction	0.40 ± 0.24 (–0.12, 0.87)	0.67 ± 0.31 (0.04, 1.24)
Fecundity	0.43 ± 0.09 (0.24, 0.62)	0.53 ± 0.07 (0.39, 0.67)
Establishment	0.68 ± 0.2 (0.28, 1.12)	0.94 ± 0.16 (0.62, 1.28)
Herbivory/predation	0.6 ± 0.17 (0.25, 0.95)	1.04 ± 0.16 (0.71, 1.37)
Species richness	0.35 ± 0.12 (0.11, 0.57)	0.47 ± 0.09 (0.28, 0.66)
Survival	0.8 ± 0.15 (0.51, 1.12)	0.79 ± 0.12 (0.55, 1.04)
Colonization/dispersal	0.49 ± 0.17 (0.13, 0.81)	0.84 ± 0.21 (0.43, 1.28)
Growth	0.75 ± 0.24 (0.28, 1.25)	0.65 ± 0.24 (0.17, 1.54)
Rate of succession	0.56 ± 0.29 (–0.07, 1.15)	0.56 ± 0.29 (–0.06, 1.1)
Variance ($\sigma^2_{\text{fragment size}}$)	0.15 ± 0.23 (0.02, 0.54)	0.18 ± 0.18 (0.03, 0.7)
Time since fragmentation		
Biomass	0.28 ± 2.03 (–3.86, 4.66)	0.63 ± 2.32 (–4.1, 5.47)
Density	0.35 ± 2.02 (–3.86, 4.88)	0.51 ± 2.31 (–4.25, 5.22)
Extinction	0.31 ± 2.07 (–3.99, 5.03)	0.48 ± 2.47 (–4.62, 5.72)
Fecundity	0.32 ± 0.43 (–0.57, 1.19)	0.29 ± 0.17 (–0.04, 0.63)
Establishment	0.38 ± 2.07 (–4.03, 4.58)	0.52 ± 2.35 (–4.2, 5.75)
Herbivory/predation	0.08 ± 0.35 (–0.61, 0.77)	0.57 ± 2.39 (–4.2, 5.8)
Species richness	0.29 ± 0.26 (–0.26, 0.78)	0.42 ± 0.51 (–0.6, 1.34)
Survival	0.29 ± 1.99 (–4.01, 4.45)	0.52 ± 2.33 (–4.14, 5.42)

(continued)

Table 3. (continued)

Parameter	Sign of response	
	Positive	Negative
Colonization/dispersal	0.21 ± 2.11 (−4.45, 4.64)	0.63 ± 2.42 (−4.53, 5.6)
Growth	0.27 ± 1.91 (−3.5, 4.2)	0.51 ± 2.33 (−4.78, 5.24)
Rate of succession	0.14 ± 0.47 (−0.78, 1.12)	0.69 ± 0.56 (−0.36, 1.83)
Variance ($\sigma_{\text{time since fragmentation}}^2$)	3.77 ± 2.85 (0.19, 9.59)	4.89 ± 2.88 (0.33, 9.78)

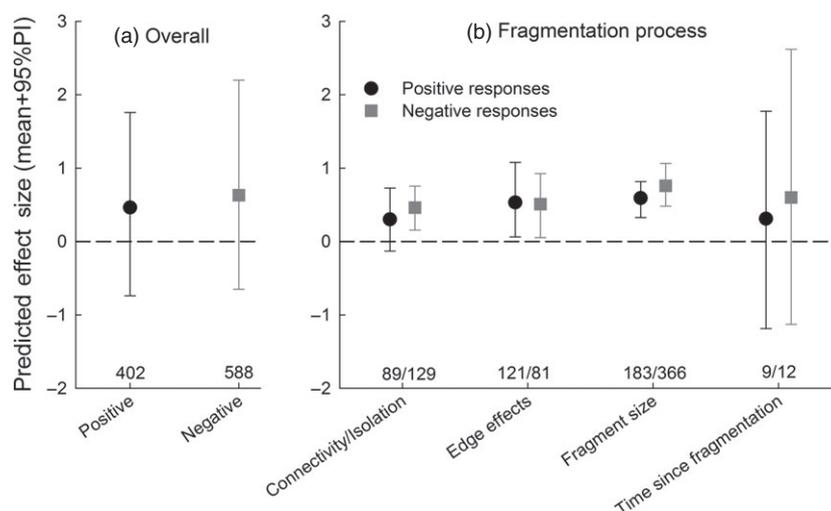


Fig. 2. Predicted effect size (ES) for the hierarchical model, (a) overall responses, positive and negative; and (b) predicted ES for each type of fragmentation category. Numbers at the bottom of the graph indicate the number of observations included in that category (positive/negative). Statistically significant results (the 95% predicted interval does not overlap zero) are marked with an asterisk.

isolation, edge effects and fragment size were significant; yet, we only found significant positive effects due to edge effects and fragment size. We also evaluated the effects of fragmentation among types of responses nested within each fragmentation process; sign, magnitude and significance of the results varied across fragmentation processes and between positive and negative responses. In our assessment of the effects of landscape fragmentation as a function of different attributes of the studied system, we found out that subtropical biomes significantly benefited from fragmentation (although this is based on only three publications), epiphytes were the most affected functional group, and saplings were the most affected life stage. In addition, these results have allowed us to identify knowledge gaps and areas of research that need to be pursued to better assess the effects of landscape fragmentation on plant communities and plant species.

Overall, our results show a lack of a unidirectional response, an important finding in itself, and they also show that the responses of plants vary by species, process and context, which means that studies focused on one process or response will not be sufficient to understand the complexities of which life stages and species will be impacted by fragmentation. These outcomes indicate that broad generalizations of the effects of landscape fragmentation on plants based on one

particular process or response will miss many of the subtleties associated with the multiple processes and the responses taking place. Only an integrated approach that incorporates the different processes and responses can provide a comprehensive assessment of the effects of fragmentation on plants and plant communities. Because an integrated approach incorporates many of the key ecological processes that are usually absent in more specialized assessments a comprehensive study of the different processes and responses occurring during fragmentation can help us to address many of the differences found across studies. For the same reason, an integrated approach will likely be more informative in scenario analyses that test the potential consequences, and associated uncertainties, of landscape fragmentation.

EFFECTS OF CONNECTIVITY/ISOLATION

In our analysis of the effect of connectivity/isolation on plants, only negative responses as a group were statistically significant (Fig. 2). But, when we studied more specific responses, the outcome of our analysis showed both positive and negative responses to isolation. In most reported studies, isolated vegetation patches experience either limited genetic flow as pollen exchange (e.g. Steffan-Dewenter & Tscharntke 1999;

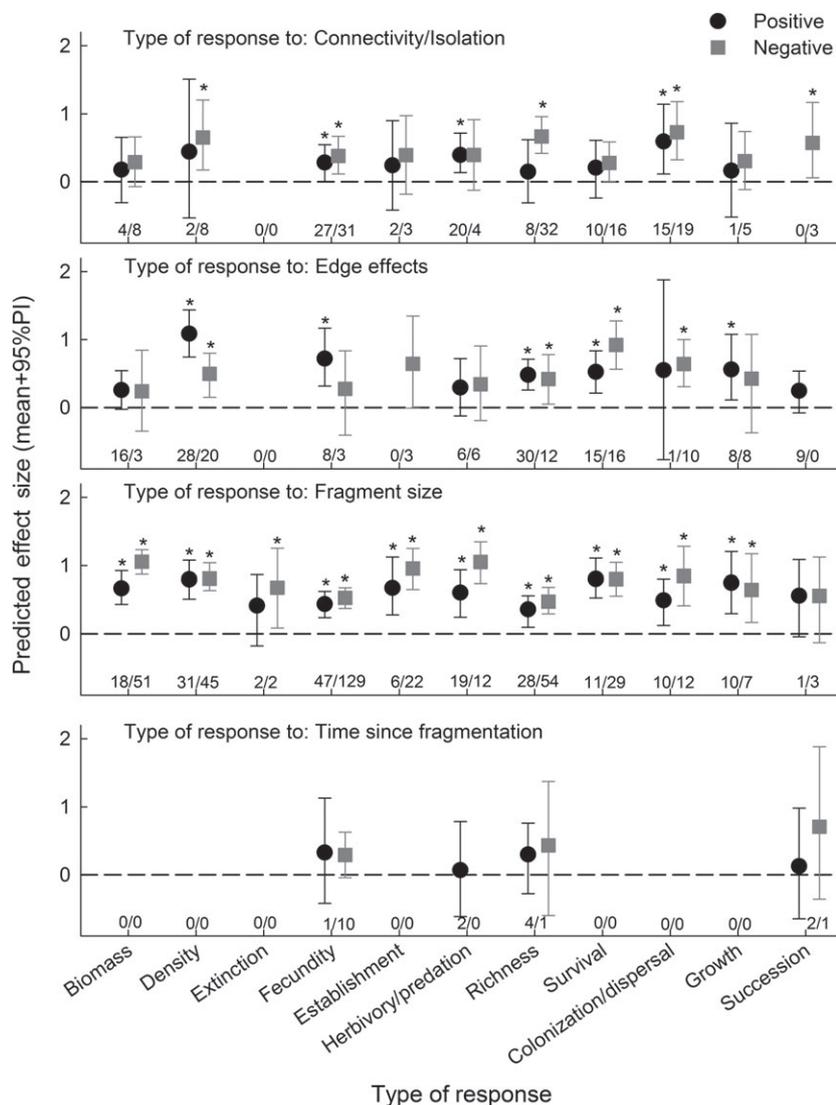


Fig. 3. Predicted effect size for the hierarchical model for each combination of fragmentation and response type. Numbers at the bottom of the graph indicate number of observations included in that category (positive/negative). Statistically significant results (the 95% predicted interval does not overlap zero) are marked with an asterisk.

Seltmann *et al.* 2009) or limited seed dispersal (e.g. Kiviniemi 2008; Seifert & Fischer 2010), leading to inbreeding depression or founder effects (e.g. Groom 2001; Seltmann *et al.* 2009). The effects of isolation seem to be particularly damaging for self-incompatible species that depend on outcrossing pollination for reproduction (Aguilar *et al.* 2006; Lopes & Buzato 2007), and for species dispersed by animals that may not occupy or visit isolated patches (McEuen & Curran 2004). There were instances of isolation benefiting plant species by increasing fecundity [Cascante-Marin *et al.* 2009; although the increase in flowers may not translate to an increase in seeds (Taki, Kevan & Yamaura 2008)], decreasing herbivory/predation (Farwig *et al.* 2009) and by increasing colonization, mainly of wind dispersed species [Graae 2000; although these may also be negatively affected by isolation (Soons *et al.* 2005)]. Negative responses to isolation seem to be more widespread, and again, these effects were explained by a variety of factors that implied both changes in individual performance due to inbreeding depression (Groom 2001; Wagenius *et al.* 2010) and reduced dispersal (Grashof-Bokdam 1997; Dams-

chen & Brudvig 2012). However, it should be noted that different plant species interact with conspecifics at a variety of spatial scales; the same distance between patches may lead to isolation for one species but not for others. This, and varying permeability of the matrices (Herrera & García 2009; Jamoneau *et al.* 2011), could also explain why we found such a wide range of effects for isolation. The effects of isolation on plants vary among species and within a species among life stages, but in general, they seem to be mostly detrimental, and when isolation benefits particular plants, it does it by reducing competition for resources, pollinators or dispersal agents.

EFFECTS OF FRAGMENT SIZE

In this analysis, we report a large number of both positive and negative significant responses of the plant community to patch size (Fig. 3). At the community level, according to the species-area relationship (Rosenzweig 1995), decreasing available area results in a decrease in the number of species. Also, lack of sufficient colonization and the decline in habitat suitability may

Table 4. Results of the individual analyses for Biome, Vegetation type, Functional group and Life stage, performed on our measure of effect size ([treatment response–control response]/average response). We report parameters posterior means and SD (95% credible intervals). Bold values indicate the parameter is statistically significant (when 95% CI does not include zero)

Analysis	Sign of response	
	Positive	Negative
Biome		
Alpine	0.16 ± 0.13 (–0.8, 0.44)	0.22 ± 0.16 (–0.1, 0.53)
Arctic/boreal	–	0.44 ± 0.53 (–0.7, 1.4)
Mediterranean	0.38 ± 0.17 (0.04, 0.7)	0.77 ± 0.14 (0.48, 1.05)
Desert/semi-arid	0.14 ± 0.12 (–0.08, 0.38)	0.23 ± 0.1 (0.04, 0.46)
Savanna	0.36 ± 0.33 (–0.28, 1.04)	0.42 ± 0.23 (–0.006, 0.91)
Subtropical	1.01 ± 0.27 (0.49, 1.52)	0.65 ± 0.18 (0.29, 1.01)
Temperate	0.44 ± 0.04 (0.35, 0.53)	0.58 ± 0.04 (0.5, 0.68)
Tropical	0.71 ± 0.06 (0.59, 0.84)	0.87 ± 0.05 (0.75, 0.98)
Variance (σ^2)	0.19 ± 0.02 (0.16, 0.25)	0.3 ± 0.02 (0.25, 0.36)
Vegetation type		
Agricultural	0.17 ± 0.09 (–0.007, 0.35)	0.5 ± 1.26 (–1.79, 2.82)
Forest	0.52 ± 0.04 (0.44, 0.61)	0.7 ± 0.03 (0.63, 0.78)
Fen	0.39 ± 0.17 (0.05, 0.72)	0.27 ± 0.17 (–0.05, 0.61)
Grassland	0.26 ± 0.08 (0.09, 0.43)	0.4 ± 0.07 (0.25, 0.55)
Shrubland	0.54 ± 0.21 (0.12, 0.95)	0.69 ± 0.16 (–0.33, 2.09)
Riparian	0.57 ± 0.38 (–0.17, 1.34)	0.81 ± 0.63 (–0.33, 2.09)
Variance (σ^2)	0.23 ± 0.02 (0.18, 0.28)	0.31 ± 0.02 (0.27, 0.37)
Functional group		
Epiphyte	1.24 ± 0.16 (0.91, 1.55)	1.38 ± 0.09 (1.2, 1.56)
Forb	0.32 ± 0.06 (0.19, 0.45)	0.41 ± 0.05 (0.29, 0.52)
Grass	0.33 ± 0.18 (–0.003, 0.68)	0.26 ± 0.11 (0.05, 0.49)
Liana	–	0.86 ± 0.51 (–0.1, 1.92)
Shrub	0.34 ± 0.16 (0.01, 0.65)	0.44 ± 0.1 (0.23, 0.64)
Tree	0.67 ± 0.06 (0.53, 0.8)	0.79 ± 0.05 (0.68, 0.9)
Plant community	0.38 ± 0.05 (0.28, 0.49)	0.53 ± 0.06 (0.41, 0.64)
Variance (σ^2)	0.18 ± 0.02 (0.14, 0.23)	0.23 ± 0.02 (0.19, 0.28)
Life stage		
Adult	0.42 ± 0.04 (0.33, 0.51)	0.62 ± 0.04 (0.53, 0.7)
Flowering	0.34 ± 0.12 (0.09, 0.6)	0.4 ± 0.15 (0.09, 0.72)
Fruiting	0.58 ± 0.18 (0.26, 0.95)	0.62 ± 0.14 (0.34, 0.9)
Seeding	0.51 ± 0.07 (0.37, 0.66)	0.5 ± 0.07 (0.36, 0.65)
Seedling	0.69 ± 0.13 (0.44, 0.95)	1.04 ± 0.09 (0.87, 1.23)
Sapling	1.12 ± 0.19 (0.75, 1.5)	0.65 ± 0.2 (0.25, 1.04)
Variance (σ^2)	0.21 ± 0.02 (0.17, 0.26)	0.3 ± 0.02 (0.26, 0.36)

further contribute to the decline in the number of species, as again is predicted by the theory of island biogeography (MacArthur & Wilson 1967). Other processes that could result in a negative effect of decreasing patch size on species richness include inbreeding, genetic drift and genetic Allee effects. These all lead to a decrease in genetic variability, which may prevent a particular species from recovering from stochastic events, for example drought, fire, late frost and potentially result in local extinction. This helps to explain why we found a large number of significant negative responses to fragment size.

However, we also found significant positive effects of decreasing fragment size on plant communities. This could be because fragmentation may promote the recruitment of new species, which may be rare in intact landscapes (e.g. introduced species). Key species interactions such as pollination, seed dispersal, predation, herbivory and competition can also vary according to fragment size (Groppe *et al.* 2001; Simonetti *et al.* 2007; Ferreras, Torres & Galetto 2008), and in some instance promote establishment or increase

performance of some species in smaller patches. Although we found both positive and negative effects, the loss or gain of species does not seem to be an *ad hoc* process. Rare and less common species and large seeded species dispersed by vertebrates are usually the most vulnerable to extinction in small fragments (Godefroid & Koedam 2003; Yates & Ladd 2005; Hofmeister *et al.* 2013). It is also worth noting that some studies also indicated that the decline in biodiversity may not be due to reduced area alone but also to other factors such as disturbance dynamics (Ross, Fox & Fox 2002), historical processes (Baessler, Klotz & Durka 2010) or land uses around the fragment (Guirado, Pino & Roda 2006).

EFFECTS OF INCREASED EDGE HABITAT

The importance of edge versus interior habitat to plant populations and communities is reflected in the large number of significant results we found among both positive and negative responses (Fig. 3). Edge habitats differ from those in the

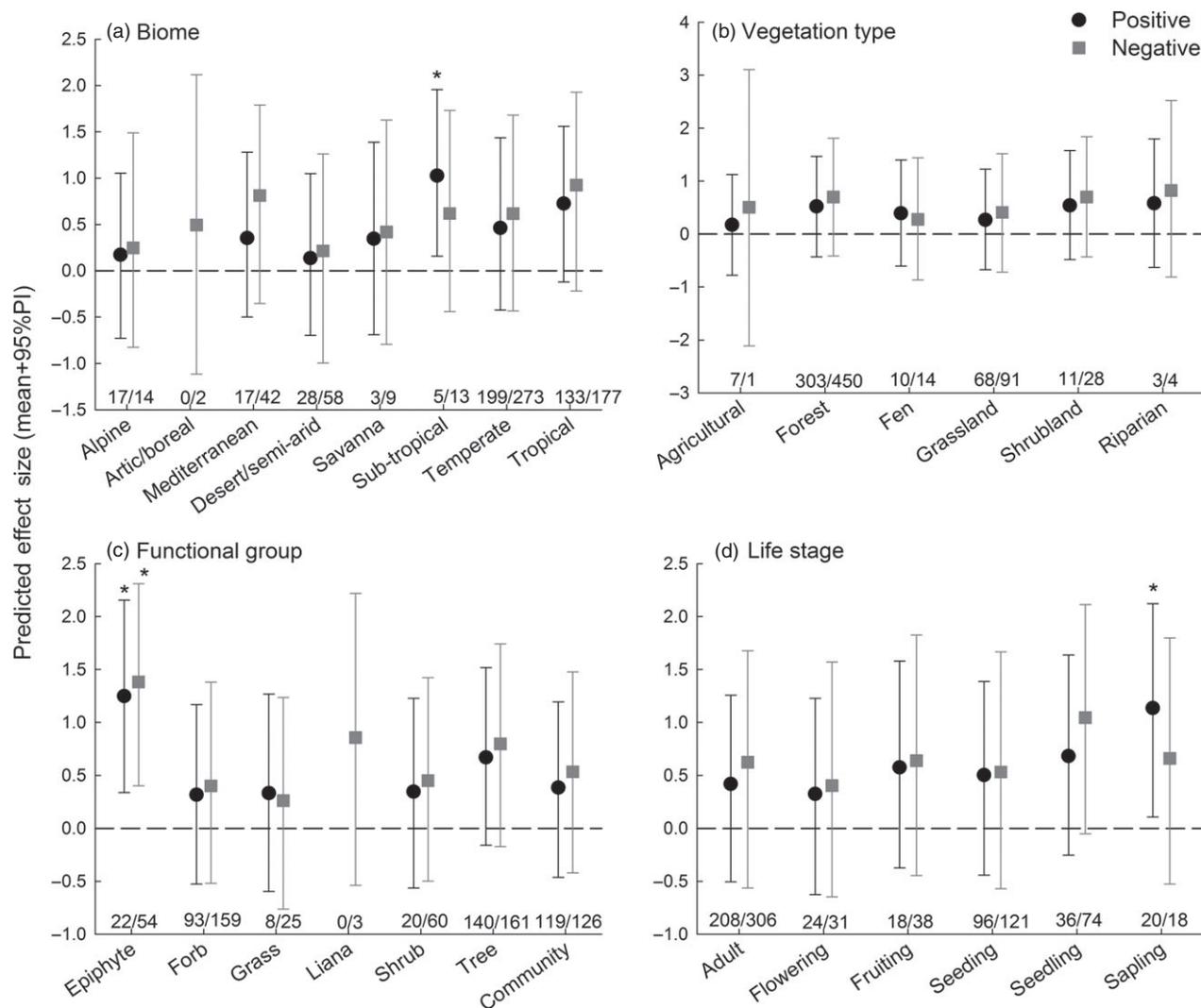


Fig. 4. Predicted effect size for the individual models for (a) Biomes, (b) Vegetation type, (c) Functional group and (d) Life stage. Numbers at the bottom of the graph indicate the number of observations included in that category (positive/negative). Statistically significant results (the 95% predicted interval does not overlap zero) are marked with an asterisk.

patch interior in that the physical environment is altered (Saunders, Hobbs & Arnold 1991; Esseen 1994) and as a consequence species interactions may also be disrupted (Galletti, Alves-Costa & Cazetta 2003; Donoso, Grez & Simonetti 2004). Light, wind exposure and desiccation increase at the edge, shifting competitive interactions among plant species and largely promoting pioneer and fast-growing species (Ferreira & Laurance 1997; D'Angelo *et al.* 2004). The reported gains associated with edges for the community, population or individuals were explained by several factors such as: increased resources (McDonald & Urban 2004; Schedlbauer, Finegan & Kavanagh 2007), increased recruitment of additional species (Santos *et al.* 2008; Tabarelli *et al.* 2010) or increased dispersal (Kollmann & Schneider 1999; de Melo, Dirzo & Tabarelli 2006). We also observed this type of response in the analysis of biomes (Fig. 4). The significant positive ES of the subtropical biome is explained by higher habitat suitability causing an increase in survival or density of

juveniles (Neal, Hardner & Gross 2010; Souza *et al.* 2012) or increased dispersal at the edges (Melo *et al.* 2010).

Negative responses to edge habitat were less common. Seed predation may increase in this habitat as the structure of the vegetation in forest edges changes providing protection for seed predators (Meiners & LoGiudice 2003). Also, the suitability of edge habitats may be reduced for the recruitment stages, for example germinating seeds and seedlings (Jules 1998; Benitez-Malvido & Martinez-Ramos 2003); and for late-successional species that are out-competed by fast-growing species that thrive under the high light levels characteristic of forest edges (Laurance *et al.* 2006; Santos *et al.* 2008).

KNOWLEDGE GAPS AND NEEDED AREAS OF RESEARCH

As the effect of habitat fragmentation on particular communities may take decades to fully manifest, lag effects are critical

to achieve a comprehensive understanding of the effects of fragmentation (Bennett & Saunders 2010). Our review has revealed there is little work reporting on the time-lag effects of fragmentation on remnant communities (six publications). Effects of time since fragmentation incorporate, even if they do not identify, the complex dynamics that take place in fragmented landscapes over time. Long-lived species may persist as adults but may not be able to recruit enough individuals to maintain their populations, and the consequences of reduced genetic exchange that lead to inbreeding depression may only be expressed after several decades of isolation. Thus, lag effects is an area of research that will need further consideration if we aim to fully understand the effects of landscape fragmentation on plant species and plant communities. The use of historical surveys and herbarium records could greatly aid with the assessment of time-lag effects (Vellend *et al.* 2013).

Other important variables determining how fragmentation affects the vegetation are the role of the matrix, that is, the modified area around fragments, and the effect of the quality of the remnant patch. Different land uses around the remnant patches determine how individual organisms, populations and communities respond to the altered environment (Ricketts 2001; McGarigal & Cushman 2002; Montero-Castano & Vila 2012). The quality of the patch has also proven important when determining the resilience of the plant community to the changes imposed by landscape fragmentation (Mortelliti, Amori & Boitani 2010; Didham, Kapos & Ewers 2012). Few studies have addressed these issues (e.g. Cook *et al.* 2002; Haynes & Crist 2009; de Souza *et al.* 2010), and again more work in this area will be critical to assess how the different processes that take place during fragmentation affect the remnant vegetation (Saunders, Hobbs & Arnold 1991; McGarigal & Cushman 2002).

Although it is commonly asserted that fragmentation of the landscape has a negative effect on plant species and plant communities (e.g. Aguilar *et al.* 2006; Honnay & Jacquemyn 2007; Angeloni, Ouborg & Leimu 2011; Vranckx *et al.* 2012), we found a large number of reported positive effects of fragmentation on plants. We also found wide variability in the response to fragmentation. This large range of responses is probably due to the numerous and interacting processes that take place during fragmentation: the area available to plant communities decreases, the remnant populations become isolated from each other and environmental shifts take place. Such processes create complex dynamics that affect plant species in many different aspects of their life span. Therefore, to truly understand, quantify and manage the effects of landscape fragmentation on plants, we need a more holistic approach to better encompass the complexity of these dynamics.

As generalizations among biomes, vegetation types, functional types or life stages do not seem to enhance our understanding of the effects of fragmentation on plant species and plant communities, we advocate for evaluating the effects of fragmentation across the life span of particular organisms, including demographic rates, their meta-population dynamics and their interactions with other species in the community. In

particular, we suggest a larger focus on demographic studies of particular species, as demographic rates represent the product of all these processes and integrate several responses (O'Connor *et al.* 2012). Thus, a combined study of the demographic responses to fragmentation will be very useful to make projections of future dynamics under scenarios of fragmentation and to identify limitations of single studies. These comprehensive demographic studies will also be fundamental for understanding the full scope of landscape fragmentation on plants, and in particular, they will allow identification of the winners and losers under particular scenarios of fragmentation, facilitating the assessment and management of the remnant vegetation.

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Received 23 September 2013; accepted 11 February 2014
Handling Editor: Christopher Lortie

Supporting Information

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

Appendix S1. List of reviewed articles.

Appendix S2. Distribution of effect sizes.

Appendix S3. Models tested.

Appendix S4. Variance weighted analysis.