Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis

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ABSTRACT

Ecosystem engineering is increasingly recognized as a relevant ecological driver of diversity and community composition. Although engineering impacts on the biota can vary from negative to positive, and from trivial to enormous, patterns and causes of variation in the magnitude of engineering effects across ecosystems and engineer types remain largely unknown. To elucidate the above patterns, we conducted a meta-analysis of 122 studies which explored effects of animal ecosystem engineers on species richness of other organisms in the community. The analysis revealed that the overall effect of ecosystem engineers on diversity is positive and corresponds to a 25% increase in species richness, indicating that ecosystem engineering is a facilitative process globally. Engineering effects were stronger in the tropics than at higher latitudes, likely because new or modified habitats provided by engineers in the tropics may help minimize competition and predation pressures on resident species. Within aquatic environments, engineering impacts were stronger in marine ecosystems (rocky shores) than in streams. In terrestrial ecosystems, engineers displayed stronger positive effects in arid environments (e.g. deserts). Ecosystem engineers that create new habitats or microhabitats had stronger effects than those that modify habitats or cause bioturbation. Invertebrate engineers and those with lower engineering persistence (<1 year) affected species richness more than vertebrate engineers which persisted for >1 year. Invertebrate species richness was particularly responsive to engineering impacts. This study is the first attempt to build an integrative framework of engineering effects on species diversity; it highlights the importance of considering latitude, habitat, engineering functional group, taxon and persistence of their effects in future theoretical and empirical studies.

Key words: tropical *versus* temperate, facilitation, meta-analysis, ecosystem engineers, functional group, richness, diversity, indirect interactions, 'stress-gradient hypothesis', metafor.

CONTENTS

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I. INTRODUCTION

(1) The ubiquity and role of ecosystem engineers

Naturalists and ecologists have long been aware that plants and animals modify the physical and chemical processes occurring in ecosystems (Buchman, Cuddington & Lambrinos, 2007; Hastings *et al.*, 2007). Twenty years ago, Jones, Lawton & Shachak (1994) formalized these non-trophic processes as 'ecosystem engineering'; as defined, ecosystem engineers are organisms that directly or indirectly control the availability of resources for other organisms by causing physical state changes in biotic or abiotic materials (Jones, Lawton & Shachak, 1997). Despite controversies about the appropriate use of the term 'ecosystem engineering' (Reichman & Seabloom, 2002; Wilby, 2002; Jones & Gutiérrez, 2007), it is currently a well-recognized type of ecological interactions (Byers *et al.*, 2006; Crain & Bertness, 2006; Jones *et al.*, 2006, 2010; Hastings *et al.*, 2007; Berke, 2010; Burchsted *et al.*, 2010) that integrates several ecological disciplines (Kéfi *et al.*, 2012; Odling-Smee *et al.*, 2013).

Ecosystem engineers can create new habitats or modify ecosystem features (e.g. bioturbation; Meysman, Middelburg & Heip, 2006). Habitat creation by beavers (i.e. dams) and mussel beds are classical examples of ecosystem engineering; the former being defined as allogenic (i.e. change the environment by transforming living or non-living material), and the latter as autogenic engineers (i.e. change the environment *via* their own structure; Jones *et al.*, 1994). The effects of engineers can be variable in space and time; some forms of engineering (e.g. leaf rolling) may last for a relatively short time (up to a year; Vieira & Romero, 2013) and impact species locally whereas others may persist for decades or even over geological time (Erwin, 2008) and affect species at a regional or global scale (Wright, Flecker & Jones, 2003; Erwin, 2008). Moreover, their effects on the biota can vary from negative to positive (e.g. Flecker, 1996; Wright & Jones, 2004). Essentially all organisms may act to some extent as ecosystem engineers at least in certain phases of their life, highlighting the ubiquity of ecosystem engineering (Hastings *et al.*, 2007). However, species effects on physicochemical and geological processes, as well as the biota, may vary from trivial to enormous (Jones *et al.*, 1994; Jones & Gutiérrez, 2007).

Numerous empirical studies on ecosystem engineering have accumulated in the ecological literature; they report effects caused by various engineer taxa across many different terrestrial and aquatic ecosystems (reviewed in Wright & Jones, 2004, 2006; Jones & Gutiérrez, 2007; Jones *et al.*, 2010). However, 20 years since the concept of ecosystem engineering was formalized, only a few quantitative reviews have explored specific ecological applications (Wright & Jones, 2004) or effects of specific taxa of engineers (Ward & Ricciardi, 2007; Arredondo-Núñez, Badano & Bustamante, 2009; Root-Bernstein & Ebensperger, 2013) precluding the examination of general patterns and comparisons across engineer types.

(2) Motivation for meta-analysis

The concept of ecosystem engineering allows one to classify engineer effects within a logical set of interactions rather than a collection of unrelated case studies, thus allowing integrative and comparative studies (Jones & Gutiérrez, 2007; Berke, 2010). The ability to predict in which ecosystems and environments, and what type of engineering and engineer taxa play the most critical roles is of considerable value for conservation and management (see Jones *et al.*, 1997; Wright & Jones, 2006). In an attempt to seek patterns in ecosystem engineering effects on species diversity globally, we conducted a meta-analysis of 122 studies containing 263 estimates of effects of different engineer types and taxa on species richness of other organisms across diverse ecosystems. We focus on species richness because it is an important attribute of community structure and composition, it is of great importance to conservation and is the response variable most commonly examined in studies assessing the impact of ecosystem engineers. We focus on the effects of animal ecosystem engineers only, since the mechanisms inherent to animal activities (mostly physical) can be very different to the mechanisms of engineering by plants (e.g. nurse plants, physical and physicochemical; Berke, 2010).

(3) Predictions and questions

We made several predictions about the strength of engineering effects in different conditions. First, we predicted that the magnitude of engineering effects will be stronger at lower latitudes (i.e. tropics) than at higher latitudes (temperate

and upwards), because density-dependent interactions (predation, parasitism, competition) are expected to be stronger in the tropics (Schemske *et al.*, 2009); thus, it is likely that new habitats/shelters provided by engineers could minimize competition and predation of resident species in tropical communities. Extreme conditions have been suggested to strengthen the importance of ecosystem engineers (Jones *et al.*, 1997). Thus, we expected that harsh conditions in many terrestrial ecosystems might make engineering processes more important than in aquatic ecosystems. Following the same logic, we predicted that engineering effects within the same ecosystem will intensify under dry conditions (Vieira & Romero, 2013).

Functional characteristics of engineers may also affect species diversity (Berke, 2010). Some ecosystem engineers create new habitats whereas others modify existing habitats or cause bioturbation (Meysman *et al.*, 2006). We predicted that engineers that create new habitats for local species to colonize (ponds created by beavers and porcupines, coral and mussel reefs, leaf-rolls by caterpillars) will have stronger positive effects than those that simply modify the existing habitats (through digging, grazing, and browsing) (Jones *et al.*, 1997). Some ecosystem engineers are large (many vertebrates) while others are relatively small, but build large structures (beaver dams, coral reefs, termite mounds) that have ecosystem-level effects and may persist for years or centuries (Jones *et al.*, 1997). Therefore, we predicted that engineering by large animals and those producing structures of longer persistence may have stronger impacts on the biota.

The main questions addressed in our meta-analysis were: (*i*) what is the overall net magnitude of the effect of ecosystem engineers on species diversity? (*ii*) Is this magnitude comparable to other ecological processes affecting species diversity? (*iii*) Do the strength and direction of engineering effects vary across regions and ecosystems? (*iv*) Which types and taxa of engineers cause larger effects?

II. METHODS

(1) Search strategy and database

We extensively searched the literature reporting effects of ecosystem engineers on species richness using the expanded database (timespan: 'all years') from *Web of Science* until June 2013. Although the term 'ecosystem engineer' was coined in 1994 (Jones *et al.*, 1994), the habitat-modulating mechanism was reported in ecological literature much earlier. Thus, we used more general key words in order to include as many pre-1994 studies as possible. The combinations of key words used were 'ecosystem engineer* AND richness', 'ecosystem engineer* AND diversity', 'habitat modification AND richness AND diversity', 'habitat modification AND community structure AND disturbance', 'bioengineer* AND diversity', 'landscape modulat* AND richness', 'bioturbation AND ecosystem engineer* AND diversity', 'bioturbation AND ecosystem engineer* AND richness'.

We also conducted haphazard searching in *Google Scholar* using some of the key words listed above. In addition, we examined references cited in the papers found. Finally, we surveyed studies included in previous related meta-analyses (Wright & Jones, 2004; Ward & Ricciardi, 2007; Root-Bernstein & Ebensperger, 2013), and general literature reviews on ecosystem engineering (Jones *et al.*, 1994, 1997; Folgarait, 1998; Alkon, 1999; Farji-Brener & Illes, 2000; Fukui, 2001; Crooks, 2002; Ellis, 2005; Rosell *et al.*, 2005; Byers *et al.*, 2006; Crain & Bertness, 2006; Moore, 2006; Wright & Jones, 2006; Cuddington *et al.*, 2007; Delibes-Mateos *et al.*, 2007; Hastings *et al.*, 2007; Jones & Gutiérrez, 2007; Ohgushi, 2008; Anderson *et al.*, 2009; Mosepele *et al.*, 2009; Bartel, Haddad & Wright, 2010; Burchsted *et al.*, 2010; Eisenhauer, 2010; Sueiro, Bortolus & Schwindt, 2011). It is likely therefore that we retrieved nearly all relevant papers published on the topic.

(2) Inclusion criteria, data handling, non-independence and data extraction

The literature sources found are listed as supporting online information in Appendix S1. In order to be included in a meta-analysis, the study had to satisfy the following inclusion criteria: (*i*) a study had to address our main study question, i.e the effects of ecosystem engineering on species richness. (*ii*) Only mechanisms strictly and explicitly involving ecosystem engineering (i.e. physical state changes in biotic or abiotic materials, Jones *et al.*, 1994, 1997), and not other confounding effects caused by engineering activities that may lead to changes in species richness (e.g. herbivory, predation, competition), were considered. (*iii*) The study provided a comparison of species richness in the presence of ecosystem engineering and under conditions where the engineering was absent or the engineer density was reduced. We included experimental studies that manipulated occurrence or intensity of engineering as well as observational studies conducted in sites where engineering or engineers were naturally present or absent, or present at different densities. We excluded comparisons among engineers (e.g. mussel *versus* oyster) without an explicit control. (*iv*) Plot size was held constant between control and experimental (engineering) treatments to avoid confounding variation (e.g. Gotelli & Colwell, 2001). (*v*) Studies comparing the control and experimental groups were carried out simultaneously. (*vi*) Studies reported mean species richness of focal species in the presence and the absence of engineers as well as corresponding sample sizes and measure of variation (e.g. S.D., S.E., C.I.) from control and experimental treatments.

A common issue in meta-analysis is the non-independence of study outcomes, i.e. a single study may report several outcomes. In our meta-analysis, many studies reported several estimates (>10) of the effect of ecosystem engineers on species richness. Non-independence of the data can lead to underestimation of the standard error of the mean effect and thus inflate significance levels for statistical tests (Type I error; Mengersen, Jennions & Schmid, 2013). However, selecting only one outcome for

each study is far too conservative and sacrifices information (Rothstein *et al.*, 2013). We minimized non-independence of multiple estimates in our database as follows: (*i*) independent experiments reported in the same paper that were conducted in distinct geographic regions, or in different years or seasons, were treated as independent comparisons; (*ii*) for time series measures, only data from the last estimate were included, to decrease the likelihood of evaluating transient dynamics; (*iii*) when effects of engineering were compared for different engineer densities or engineering intensities, we only included data from sites with minimum and maximum engineering intensities or engineer densities.

Multiple moderators (explanatory variables in meta-analysis) also may be not independent from each other. We verified the associations among them by consucting contingency table showing frequency distributions for each pair of moderators and using the *G*-test of independence (Zar, 1996). When significant associations emerged, we evaluated effects of moderators hierarchically (Hedges & Olkin, 1985; Gurevitch *et al.*, 1992), comparing effects of one moderator at each level of the other moderator (Koricheva, 2002; Romero & Koricheva, 2011).

Means, standard deviations and sample sizes of control and experimental treatments were obtained from texts, tables or graphs. When results were presented in graphs, data were digitized using ImageJ 1.47t (http://rsb.info.nih.gov/ij) and Web Plot Digitizer v.2.5 software (http://www.arohatgi.info/WebPlotDigitizer).

(3) Sources of variation

For each study, we recorded several characteristics that were used as moderators in the meta-analysis (see online Appendix S1). These moderators were organized hierarchically (see online Appendix S2). First, depending on the location of the study, it was classified as either tropical ($<23°$N or S) or higher latitude ($>23°$N or S). Within each region, we classified environments as either 'aquatic' or 'terrestrial'. Within aquatic environments, we distinguish between the following ecosystem types: 'marine', 'estuary', 'lake', 'marsh' or 'stream'. Within terrestrial environments, ecosystems were classified as 'forest', 'grassland', 'savanna', 'desert', 'wetland', 'tundra' or 'artificial'. Grasslands included steppes, prairies, and meadows. Savannas included Brazilian cerrados and African savannas. Depending on total annual precipitation, each terrestrial ecosystem was classified as arid (<200 mm), moderate ($201–999$ mm) or wet (≥1000 mm). Precipitation data were obtained directly from the papers, from the websites of field stations where the study was conducted or from other published studies performed at the same site.

Within each region, environment and ecosystem, we classified types of ecosystem engineering in two different ways (Berke, 2010). First, we classified engineers as either 'habitat forming', 'habitat modifying' or 'bioturbators' according to the prevalence of their effects. The habitat formers are those that directly or indirectly create new environments for other organisms (e.g. coral reefs, tubes from polychaetes, dams or small ponds constructed by beavers and peccaries, barnacles, mussels, clams and oysters, plant shelters constructed by caterpillars or beetles etc.). Habitat-modifying engineers included grazers and browsers (elephants, bison, elk, reindeer, moose, deer, cattle) which change vegetation structure, oysters (which change physicochemical components of the environment) etc. Bioturbation refers to the biological reworking of soils and sediments (Meysman *et al.*, 2006) and thus can be considered as a special mechanism of habitat modification. Examples of bioturbators included in the meta-analysis were small- to medium-sized digging mammals (e.g. pocket gophers, porcupines, kangaroo rats, prairie dogs), soil-nesting birds, ants and termites, and bivalves, worms and crustaceans that dig in soft sediment. Second, we have classified engineers as either 'autogenic' or 'allogenic' (Jones *et al.*, 1997). We have also classified the engineers as 'invertebrates' or 'vertebrates', and recorded whether they were exotic or native to the location studied. Finally, we classified the temporal persistence of the engineering activities into two large classes: <1 year (e.g. peccaries, browsers and grazers, crabs, leaf- and stem-shelters built by caterpillars, beetles and galling arthropods etc.), and >1 year (e.g. beaver dams, termite and ant nests, bivalve beds, bioturbation by small mammals etc.), based on information provided by the authors of primary studies; these were then used as a proxy for other similar systems for which no information was provided. Finally, we recorded the taxon of the organisms affected by the engineering (e.g. mammals, birds, herptiles, fish, invertebrates, microbes, fungi, plants, algae). A complete list of the moderators and subgroups is presented in Appendix S1.

(4) Meta-analysis

The magnitude of the engineering effect on species richness was evaluated by converting the data from primary studies to log response ratio (ln$R$) (Hedges, Gurevitch & Curtis, 1999), ln$R = Xe/Xc$, where Xe and Xc are mean species richness in the presence (or higher density) and absence (or reduced density) of engineers, respectively. Positive or negative effects indicate that engineers increase or decrease species richness, respectively. We back-transformed ln$R$ to obtain % difference between control and treatment [(exp ln$R - 1) \times 100\%$] for ease of interpretation. It is recommended that ln$R$ is used as a metric of effect size when $\sqrt{N_E}X_E/SD_E$ and $\sqrt{N_C}X_C/SD_C > 3$ (Hedges *et al.*, 1999), where N, X and SD mean respectively sample size, mean and standard deviation of experimental (E) and control treatments (C). Our data met this requirement, since 91% of the values of $\sqrt{N_C}X_C/SD_C$ and 93% of the values of $\sqrt{N_E}X_E/SD_E$ were >3. To ensure that the results are unbiased due to the choice of the effect-size metrics, and to compare the magnitude of effects of engineering with those of other common interactions (e.g. trophic cascades) reported in other meta-analyses, we also conducted meta-analysis using Hedges' d (standardized mean difference; Hedges & Olkin, 1985).

All statistical analyses were conducted using metafor package (Viechtbauer, 2010) implemented in R environment

(R Development Core Team, 2011). Prior to the analyses we inspected visually the normality of the residuals using normal quantile–quantile (Q–Q) plots. We also evaluated outliers through diagnostic plots (e.g. Cook's distance). Then, we estimated overall effect using random-effects models, and examined the effects of moderators using mixed-effects models which assume that there is random variation among studies within a group, and fixed variation among groups (Gurevitch & Hedges, 2001); for this, we used a restricted maximum likelihood (REML) estimator. Effect sizes were weighted by the inverse of study variance. Total heterogeneity (Qt) was obtained through Wald-type tests and I^2 statistic was used to estimate percentage heterogeneity due to between-study variation. Comparisons between subgroups were conducted using Cochran's Q-test (Qm; Hedges & Olkin, 1985) with model fitting through 'mods' argument to ignore the intercept and rma() function (Viechtbauer, 2010). Subgroups with less than three cases were excluded from categorical analyses. Effect sizes of subgroups within moderators were considered statistically significant if their 95% confidence intervals did not overlap with 0.

(5) Publication bias

We tested for potential publication bias in our database using several methods. First, we calculated weighted fail-safe numbers (Rosenberg, 2005) using the Fail-Safe Number Calculator (www.rosenberglab.net/software.php#failsafe). This estimates the number of non-significant, unpublished studies that would have to be included in the meta-analysis to change the results from significant to non-significant. A *t*-test based on a normal distribution is provided to test if the mean effect size differs from the null model (Rosenberg, 2005). In addition, we produced funnel plots of ln$R$ effect size against standard error (see Viechtbauer, 2010) and calculated rank correlations (z) between ln$R$ effect size and standard error to verify whether funnel plots are asymmetrical, i.e. if small and/or non-significant findings remain unpublished (see Viechtbauer, 2010). We also ran the trim and fill method, a non-parametric data augmentation technique used to estimate the number of studies missing from a meta-analysis due to the suppression of the most extreme results on one side of the funnel plot (see Viechtbauer, 2010). Funnel plots, rank correlations and trim and fill methods were run using the metafor package (Viechtbauer, 2010) implemented in the R environment (R Development Core Team, 2011).

III. RESULTS

(1) Database and overall effects

The final database included 122 studies published between 1974 and 2013 and containing 263 estimates of effects of animal ecosystem engineers belonging to many different taxa and functional groups and occurring in diverse regions,

biomes, and ecosystems worldwide (see online Appendices S1 and S2). Engineering effects were more commonly studied in regions of higher latitudes (80% of estimates) than in the tropics, and in terrestrial environments (69%) than in aquatic habitats. Within aquatic environments, studies in marine (74%) and stream ecosystems (13%) predominated. Within terrestrial environments, the engineering effects in forests (39%), grasslands (37%), savannas (12%), and deserts (9%) were most commonly studied. Studies were equally split between those studying effects of invertebrate and vertebrate engineers, but the majority of studies examined effects of animal engineers on species richness of invertebrates (44%) and plants (41%).

Overall, engineering had a positive and significant effect on species richness (ln$R = 0.22$, 95% C.I. 0.14–0.31, $N = 263$), corresponding to 25.3% increase in species richness in the presence of engineering. Hedges' *d* metrics provided similar results ($d = 0.56$, 95% C.I. 0.34–0.79, $N = 263$). Total heterogeneity in the overall model was very high ($Qt = 14730.6$, d.f. $= 259$, $P < 0.0001$), and almost all of the observed variance was due to differences among studies ($I^2 = 99.1\%$), thus further exploratory analyses of the moderators was warranted.

(2) Engineering effects at different latitudes and environments (aquatic *versus* terrestrial)

Engineering effects significantly differed between higher and lower latitudes ($Qm = 18.8$, d.f. $= 1$, $P < 0.001$). The magnitude of the effect was higher in the tropics (Fig. 1A), where engineering increased species richness by 83.4% whereas at higher latitudes engineering resulted in only a 15% increase in species richness. Because the magnitude of engineering effects differed between regions, we performed further analyses for lower and higher latitudes separately. At higher latitudes ($>23°$), the effects of engineers varied between aquatic and terrestrial environments ($Qm = 4.8$, d.f. $= 1$, $P = 0.028$); in the aquatic environment engineers increased species richness by 29.7% whereas in terrestrial ecosystems the effect did not differ from 0 (Fig. 1A). By contrast, in the tropics, the effects of engineers did not differ between aquatic and terrestrial environments ($Qm = 0.9$, d.f. $= 1$, $P = 0.33$), and effects in both environments were positive and significantly different from 0 (Fig. 1A). There was no significant interaction between effects of region and environment ($z = 1.81$, $P = 0.071$).

(3) Engineer effects in different ecosystems

Within aquatic environments, engineering effects in marine ecosystems were similar in tropics and at higher latitudes ($Qm = 0.65$, d.f. $= 1$, $P = 0.42$); no data were available on effects of engineers in tropical streams. Therefore, we conducted a comparison of marine ecosystems and streams across all latitudes. Engineering had opposite effects on species richness in marine ecosystems and streams ($Qm = 11.6$, d.f. $= 1$, $P < 0.001$) with 53% increase in species richness in marine
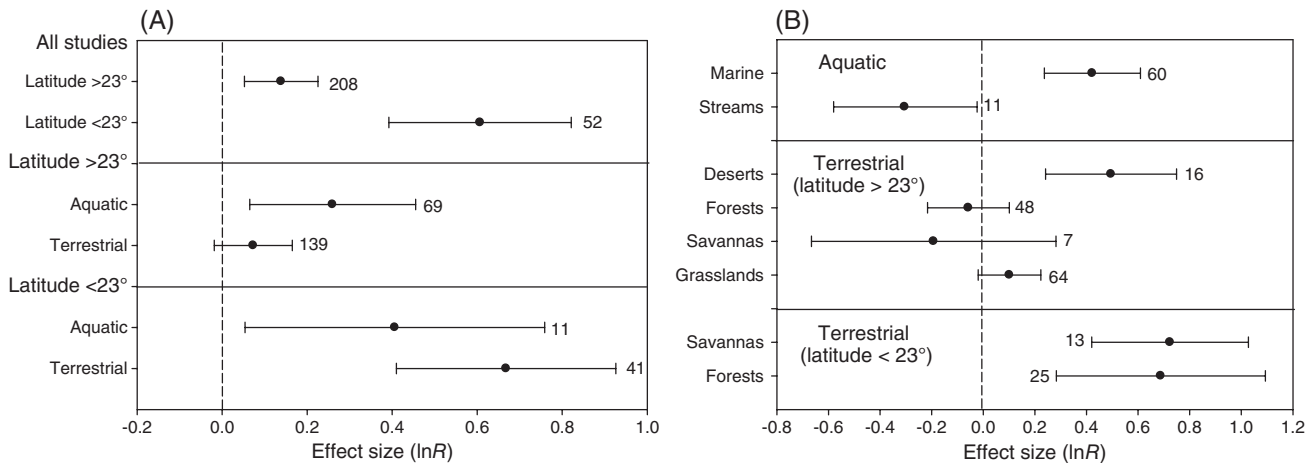
Fig. 1. Effects of ecosystem engineers on species richness in (A) aquatic *versus* terrestrial environments from lower (tropical; $<23°$) and higher ($>23°$) latitudes, and in (B) different types of ecosystems within aquatic and terrestrial environments. Error bars represent 95% confidence intervals. Numbers next to error bars indicate number of studies in each category. Effects are considered significantly different from 0 if 95% confidence intervals do not cross 0 (dashed line).

ecosystems and 26.2% decrease in species richness in streams (Fig. 1B). In tropical terrestrial environments, the effects of engineers did not differ between forests and savannas ($Qm = 0.16$, d.f. $= 1$, $P = 0.68$), and engineering increased species richness in both ecosystems by 99–106%. By contrast, at higher latitudes, the strength of engineering effects differed among the ecosystems ($Qm = 13.2$, d.f. $= 3$, $P = 0.004$): no significant effects of engineering were observed in forests, savannas and grasslands, but engineers increased species richness in deserts by 64% (Fig. 1B). Degree of aridity was not independent of ecosystem type (e.g. forests were only moderate or wet, and deserts were only arid; see online Appendix S2). Therefore, assessment of aridity effects was only possible within grasslands from higher latitudes (see online Appendix S2), and effects of engineers on species richness were independent of amount of annual precipitation ($Qm = 2.2$, d.f. $= 2$, $P = 0.32$; wet: $\ln R = 0.10$, C.I. $= -0.13$–0.33, $N = 12$; moderate: $\ln R = 0.03$, CI $= -0.14$–0.20, $N = 33$; arid: $\ln R = 0.19$, CI $= -0.02$–0.43, $N = 19$).

(4) Effects of different types of ecosystem engineers

No difference among effects of habitat forming, habitat modification and bioturbation was found in aquatic (marine) ecosystems (pooled latitude data; $Qm = 0.22$, d.f. $= 2$, $P = 0.89$, Fig. 2A) and terrestrial environments from higher latitudes ($Qm = 3.3$, d.f. $= 2$, $P = 0.19$, Fig. 2A). By contrast, in tropical terrestrial ecosystems the type of engineering mattered ($Qm = 43.8$, d.f. $= 1$, $P < 0.001$): habitat-forming engineers increased species richness by 300% whereas bioturbators had no significant effect on species richness (Fig. 2A). Data on forests, grasslands, savannas (for higher latitudes) and on forests and savannas (from the tropics) were pooled together for these analyses, since they did not differ from each other (see above results).

Classification of engineering into autogenic *versus* allogenic was not independent of the above classification ($G = 94.6$,

d.f. $= 2$, $P < 0.0001$), i.e. most autogenic engineers were habitat-formers (see online Appendix S2). Therefore, comparisons of effects of autogenic *versus* allogenic engineers could not be conducted.

Within aquatic ecosystems from higher latitudes, engineer taxon (vertebrates *versus* invertebrates) affected the strength of engineer effects ($Qm = 18.17$, d.f. $= 1$, $P < 0.0001$). Effects of vertebrates did not differ from 0 whereas invertebrate engineers increased species richness by 41.3% (Fig. 2B). Similar results were also observed for terrestrial ecosystems from higher latitudes (Fig. 2B, $Qm = 8.9$, d.f. $= 1$, $P = 0.003$). By contrast, both invertebrate and vertebrate engineers increased species richness in the tropics by 91–116% (Fig. 2B, $Qm = 0.14$, d.f. $= 1$, $P = 0.71$).

(5) Effects of engineering persistence and engineer origin (native versus exotic)

At higher latitudes, temporal persistence of engineers was not a good predictor of their effects on species richness in aquatic (Fig. 2C, $Qm = 0.03$, d.f. $= 1$, $P = 0.86$) and terrestrial environments (Fig. 2C, $Qm = 0.22$, d.f. $= 1$, $P = 0.64$). By contrast, in the tropics engineering activities lasting <1 year increased richness by 201%, but more long-term engineering had no significant effects (Fig. 2C, $Qm = 12.6$, d.f. $= 1$, $P < 0.001$). Because of low sample sizes, we only ran analyses on the effects of native *versus* exotic engineers for invertebrates in aquatic environments and for vertebrates in terrestrial environments from higher latitudes. In both comparisons, there was no significant difference between effects of native and exotic engineers ($Qm \geq 3.4$, d.f. $= 1$, $P \geq 0.063$), and overall only native invertebrates increased species richness (Invertebrates: native – $\ln R = 0.47$, 95% CI $= 0.32$–0.64, $N = 37$, exotic – $\ln R = 0.05$, 95% CI $= -0.42$–0.53, $N = 22$; Vertebrates: native – $\ln R = 0.02$, 95% CI $= -0.09$–0.12,
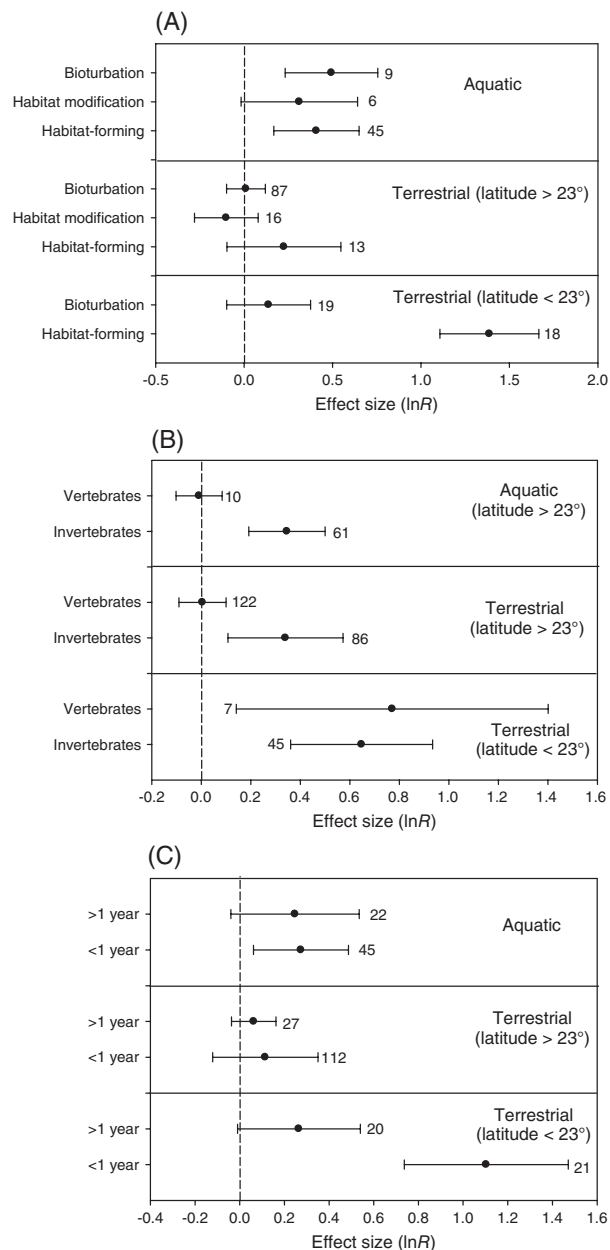
Fig. 2. Effects of ecosystem engineer (A) functional groups, (B) taxon (vertebrates *versus* invertebrates), and (C) persistence on species richness in aquatic and terrestrial ecosystems. Error bars represent 95% confidence intervals. Numbers next to error bars indicate number of studies in each category. Effects are considered significantly different from 0 if 95% confidence intervals do not cross 0 (dashed line).

$\mathcal{N} = 100$, exotic: $\ln R = -0.10$, 95% CI = $-0.31 - 0.11$, $\mathcal{N} = 12$).

(6) The organisms affected by engineering

The effects of engineers varied depending on the taxon of the organisms affected within both aquatic and terrestrial environments from higher latitudes (Aquatic:
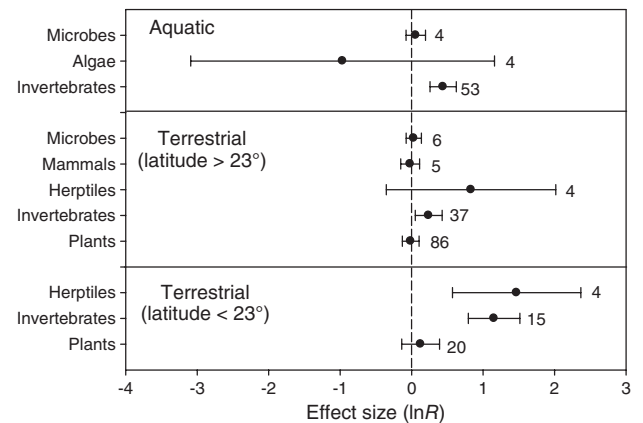

Fig. 3. Effects of ecosystem engineers on species richness of different taxa. Error bars represent 95% confidence intervals. Numbers next to error bars indicate number of studies in each category. Effects are considered significantly different from 0 if 95% confidence intervals do not cross 0 (dashed line).

$Q_m = 9.36$, d.f. $= 2$, $P = 0.010$; Terrestrial: $Q_m = 10.8$, d.f. $= 2$, $P = 0.030$), and terrestrial environments from the tropics ($Q_m = 45.1$, d.f. $= 2$, $P < 0.001$). Within aquatic environments, engineers only increased species richness of invertebrates (55.5%). Within terrestrial environments, again engineers increased invertebrate species richness at higher latitudes (27%) and in the tropics (217%), but also increased herptile richness (334%) in the tropics (Fig. 3).

(7) Publication bias

A regression test for funnel plot asymmetry was not significant for overall comparisons (Fig. 4A, $z = 1.02$, $P = 0.31$), and for data on higher latitudes (Fig. 4B, $z = -1.08$, $P = 0.28$), but the funnel plot was slightly asymmetrical in the tropics (Fig. 4C, $z = 2.32$, $P = 0.020$), suggesting that studies with small and/or non-significant findings might be less likely to be published, and therefore are less likely to be included in the meta-analysis. However, the weighted fail-safe numbers (t−N+) for the overall effects of ecosystem engineers on species richness, as well as their effects in higher (>23°) and lower latitudes (<23°) showed, respectively, that 1867830, 1067777 and 157296 non-significant studies would have to be added to the analysis to change the statistical significance of the observed effects. This suggests that our results are very robust to possible publication bias. Moreover, the trim and fill method estimated that the number of missing studies on the left side of funnel plots from overall comparisons (Fig. 4A) and the tropics (Fig. 4C) was 0. The estimated number of missing studies on the right side of funnel plots from higher latitudes (Fig. 4B) was 40, and magnitude of the effect size increased after the trim and fill correction (before correction: $\ln R = 0.14$, 95% C.I. $0.05 - 0.22$; after trim and fill correction: $\ln R = 0.33$, 95% C.I. $0.24 - 0.43$), suggesting that, if anything, we underestimated the magnitude of the effect of ecosystem engineers at higher latitudes.
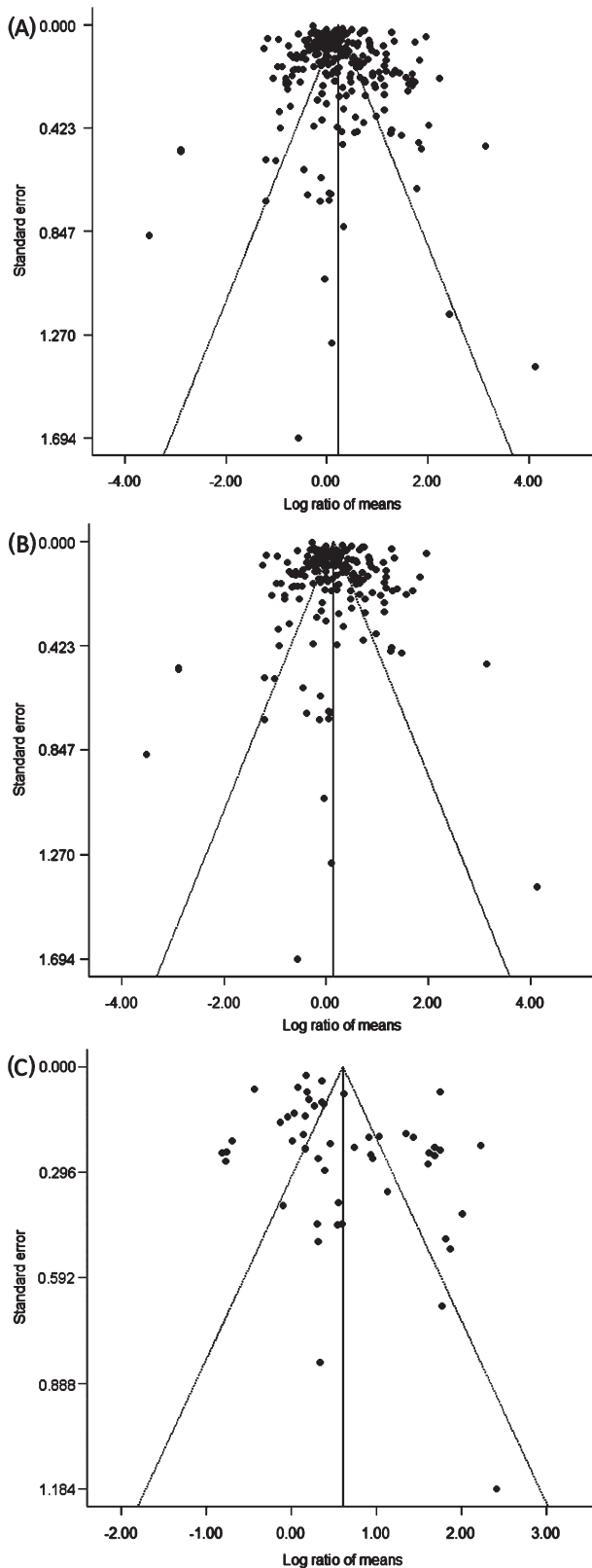
Fig. 4. Funnel plot of (A) the overall effect size (lnR), (B, C) for the effects of ecosystem engineers on species diversity in (B) higher latitudes (>23°), and (C) lower latitudes (<23°).

IV. DISCUSSION

Our meta-analysis showed that the overall net effect of animal ecosystem engineers on species diversity is positive (25% increase in species richness; $\ln R = 0.22$, $d = 0.56$). This is similar to the magnitude of effect of plant ecosystem engineers (i.e. nurse plants; Arredondo-Núñez *et al.*, 2009). These findings allow us to interpret ecosystem engineering globally as a facilitative process, thus corroborating previous narrative reviews (Jones *et al.*, 1997). This result is interesting *per se*, but can also add new ecological knowledge in a broader sense if integrated and compared to the magnitude of other well-known ecological processes (Wilby, 2002; Wright & Jones, 2006; Kéfi *et al.*, 2012). It is worth noting that the magnitude of ecosystem engineering effects is comparable to that of trophic cascades (Schmitz, Hambäck & Beckerman, 2000: $\ln R = 0.22$; Halaj & Wise, 2001: $d = 0.84$; Shurin *et al.*, 2002: $\ln R = 0.10$; Romero & Koricheva, 2011: $\ln R = 0.27$). It is also interesting to compare biodiversity effects of non-human ecosystem engineers with the reported effects of anthropogenic activities on species richness, as arguably humans are the most important ecosystem engineers in many ecosystems. In contrast to non-human ecosystem engineers, human activities appear to have largely negative effects on biodiversity. For instance, forest management has been reported globally to decrease species richness by 6.8% with responses of different taxonomic groups varying from −30 to +13% (Paillet *et al.*, 2010). Similarly, conventional farming results in 30% reduction in species richness as compared to organic farming (Bengtsson, Ahnström & Weibull, 2005). Therefore, our findings add to a growing consensus that ecosystem engineering is an ecologically important interaction (Hastings *et al.*, 2007; Berke, 2010; Jones *et al.*, 2010; Kéfi *et al.*, 2012; Odling-Smee *et al.*, 2013) that has a significant role in structuring biological communities. Moreover, given its positive effect on biodiversity, ecosystem engineering emerges as an important mechanism which might potentially counteract negative effects of human activities on species richness.

Although the positive effects of engineering on species diversity have been detected for different latitudes, as predicted, these effects were stronger in the tropics (latitudes <23°). It is known that there are more species in the tropics than at higher latitudes (reviewed in Hillebrand, 2004). Moreover, the outcomes of many biotic interactions (e.g. mutualisms, herbivory, parasitism, competition, predation and trophic cascades, plant and animal defences) are density dependent and tend to be more prevalent or stronger in the tropics than in temperate biomes (Dyer & Coley, 2002; Schemske *et al.*, 2009). Therefore, it is reasonable to predict that new or modified habitats provided by engineers in the tropics may help minimize competition and predation pressures; these new habitats may be immediately populated by more individuals and species which cannot be supported by existing habitats. Our review adds ecosystem engineering as another biotic interaction of higher relevance in the tropics. Yet, to date, 80% of studies on ecosystem engineering

were carried out at higher latitudes; there is a need for more research on impacts of ecosystem engineers in the tropics.

According to Niche Construction Theory (NCT), through modification of their own niches, ecosystem engineers may also change the niches of other species (e.g. enhance their realized niche; Bruno, Stachowicz & Bertness, 2003). When these interactions among engineers and other organisms are effectively coupled, they can lead to coevolution (Odling-Smee *et al.*, 2013; Matthews *et al.*, 2014, but see Scott-Phillips *et al.*, 2014). In turn, new species favoured by engineering may introduce novel resources and interactions and, hence, expand even more the number of niche dimensions available within tropical communities (Schemske *et al.*, 2009). Taking into account that biotic interactions may increase rate of adaptation, speciation and coevolution, and that these processes are more important at lower latitudes (Schemske *et al.*, 2009), we expect higher relevance of NCT in the tropics. Future empirical studies should focus on tropical biotic interactions involving engineers, and theoretical studies should include latitude (and processes involved) as an important predictor of the magnitude of engineering effects.

Our prediction that more extreme conditions experienced by organisms in terrestrial environments could strengthen engineering effects as compared to aquatic ecosystems was not fully supported. Instead, at higher latitudes engineers had positive effects in aquatic environments, but no effect on land. Marine ecosystems were the only aquatic environment in which positive effects of engineering emerged. The mechanisms that could explain this phenomenon are threefold. First, most experiments in marine ecosystems were carried out in rocky shores, where wave disturbance is an important selective agent. Second, rocky shores are among the most stressful environments, in which organisms are frequently exposed to desiccation. Finally, it is known that marine benthic zones are among the environments with strong predation pressures and trophic cascades (Menge & Sutherland, 1987; Shurin *et al.*, 2002). The main benthic engineers in the intertidal zone, the encrusting organisms (i.e. bivalves, coral, polychaetes, ascidians, barnacles), seem to provide suitable refuges for large numbers of invertebrates against wave disturbance, desiccation and predation. In fact, within aquatic environments, engineers only increased species richness of invertebrates. By contrast, in streams, where the most common engineers were beavers, the engineering decreased species richness of plants, invertebrates and fishes. Most of the studies included in our analysis assessed effects of ecosystem engineering at small spatial scales, but it is known that engineers like beavers may increase species diversity at regional scales, by creating highly heterogeneous landscapes (e.g. Wright *et al.*, 2003). In the tropics, by contrast, engineers increased species diversity, and this phenomenon could also be explained by the fact that engineering habitats may be populated by more individuals and species which cannot be supported by existing habitats, as discussed above.

Among the terrestrial ecosystems from higher latitudes analysed here (forests, grasslands, savannas, deserts), deserts were the only one in which engineers played a significant positive role. This pattern seems to be analogous to shift from negative to positive interactions with increase in environmental stress predicted by the 'stress-gradient hypothesis' for plants (e.g. Maestre *et al.*, 2009), except that there were no negative effects of engineers (competition, exclusions) under wetter conditions (e.g. forests). Taking into account that deserts are among the least productive ecosystems, and that organisms (plants) from arid ecosystems respond strongly to resource supply (Ehleringer, Cerling & Flanagan, 2001), engineering activity resulting in patches with higher productivity than unmodified patches can increase local species richness (Wright & Jones, 2004). In fact, the main engineers in deserts were bioturbators (porcupines, kangaroo rats, gophers and ants), and the main organisms who benefited from these activities were plants. In these xeric environments bioturbating engineers seem to benefit plants by providing them with nutrients and organic matter from deeper soils and with suitable places (e.g. pits, mounds) for seed germination and seedling recruitment (e.g. Wilby, Shachak & Boeken, 2001 and references therein). There was no evidence that engineers provide stronger effects in arid sites within temperate grasslands, possibly because these sites are not as harsh as deserts.

As predicted, habitat-forming engineers had stronger positive effects on species richness than habitat modifiers and bioturbators, but this was true only in the tropics. While habitat-modification and bioturbation cause disturbances of soils and vegetation, thus disrupting components of the habitats or microhabitats to which local species are adapted, habitat-formers create new suitable habitats for species to colonize and reproduce (Jones *et al.*, 1997; Berke, 2010). It is likely that many species would not be able to live in certain environments if this type of engineering was absent. The main habitat-forming engineers in the tropics were peccaries that build ponds used by frogs, termite nests that provide shelters to birds, and beetles, caterpillars and nematodes that build leaf shelters used by a large variety of invertebrate species. These engineers likely increased species richness in the tropics for reasons discussed earlier (more species and stronger competition and predation in the tropics). Most of these habitat-creating engineering effects in the tropics were of short persistence. Ephemeral habitats created by such engineers may be of extreme relevance to many species with short life cycles (e.g. insects, frogs) and for those that only use engineered habitats as shelter for a short period (e.g. arthropods inside rolled leaves). In fact, within terrestrial environments the organisms most benefited by engineering were herptiles and invertebrates (arthropods). Overall, these results shed light on the relevance of different functional groups of engineers and persistence of their effects on species diversity, and add knowledge that may guide future decision-making on the protection, management and restoration of natural ecosystems.

Contrary to our expectations, invertebrate engineers had stronger effects on species richness at higher latitudes than vertebrate engineers, and both invertebrate and vertebrate engineers were similarly important in the tropics. This can be explained by the fact that the most commonly studied vertebrate engineers were beavers, which tend to decrease species richness, whereas the most commonly studied invertebrate engineers were encrusting invertebrates (bivalves, barnacles) which increase species richness, as discussed earlier.

In all environments, regions and ecosystems the invertebrates were the organisms that most benefited from the effects of engineering. Invertebrates comprise ∼99% of the animals on Earth and provide food for a variety of predators and parasites. Moreover, terrestrial invertebrates and those living in transitional habitats (e.g. rocky shores) are prone to desiccation. Engineered habitats can provide shelter against predation and desiccation for invertebrate species. In addition, engineers may increase fractal dimension of the habitats, i.e. the surface or volume per unit of area (e.g. leaf-rolling, interstices from mussel beds, burrows and digs). Given that higher fractal dimensions benefit smaller organisms (Morse *et al.*, 1985) and that many invertebrate species are small, fractal theory may explain the facilitative mechanism of engineers' effects on invertebrates.

V. CONCLUSIONS

(1) Understanding the ecological factors that explain where, when and what engineer functional groups will trigger stronger effects is important for predicting the function of ecosystem engineers in nature. Our meta-analysis is the first to review the effects of different types of animal ecosystem engineers across various ecosystems and adds new knowledge on ecosystem engineering theory that we believe may help future ecological studies of theoretical and applied nature.

(2) By evaluating the relative importance of ecosystem engineers on species diversity across many ecosystems, we found that the overall effect of engineering is positive, and its magnitude is comparable to other well-known ecological processes such as trophic cascades. Thus, in a broad sense engineering is an ecological process that amplifies species diversity by providing shelters, supporting structures, new or modified habitats to other organisms. This makes ecosystem engineering a relevant facilitative process within virtually all environments.

(3) This facilitative effect was stronger in the tropics, likely because new or modified habitats provided by engineers in this region may help minimize competition and predation pressures on resident species. Positive effects of engineering were stronger in (*i*) aquatic ecosystems under constant disturbance and predation pressure (rocky shores), and (*ii*) in arid ecosystems (deserts).

(4) Engineers that create new habitats or microhabitats had stronger effects on species richness than engineers that modify habitats or cause bioturbation. Overall, the magnitudes of the effects were stronger for low-persistence engineering and invertebrate engineers, suggesting that impacts of these types of engineers were the most important, at least at the scale studied.

(5) This study highlights the importance of considering the latitude and aridity of the study site as well as the functional type, size and persistence of ecosystem engineers in future ecological models predicting engineering impact.

VI. ACKNOWLEDGEMENTS

VII. REFERENCES

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Studies used in the analysis with sources of variation.

Appendix S2. Scheme representing the hierarchical organization of the moderators tested, with number of studies in each category in parentheses.